Introduction

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Sailing for 5 or 6 days from Cape Town to Marion Island the research ship *R.S.A.* crosses one of the most tempestuous parts of the ocean, battling through high seas of the Roaring Forties and at night, in thick mist, proceeding slowly to avoid a possible encounter with a stray iceberg. During a rare calm voyage it is interesting to note the changes in the surrounding ocean. After crossing the Subtropical Convergence suddenly, overnight, the "Portuguese man-o'-war" and the "flying fishes" of the subtropical waters have disappeared, the temperature has dropped by as much as 10° and the immense Antarctic Ocean with its cold bluish water stretches to the horizon. After this journey it seems a miracle to see, on a quiet day, the small forlorn islands appear over the horizon. These small specks of land, lost in this endless mass of water, can look hospitable and friendly when the bleak sunlight shines on the gentle slopes covered with all shades of brown, green and bronze, while the red-tinted volcanic cones and the snow-covered higher peaks stand out clearly against the sky. The inquisitive porpoising penguins which concentrate around the ship seem to give it a hearty welcome. But, unpredictable as the weather is in these regions, this scene of calm can be changed abruptly into a turmoil of wind and water while enormous waves will crash against the steep shores, dissolving into clouds of spray. Under these conditions the ship has for safety reasons to leave without delay and ride out the storm, away from the treacherous shores, to return perhaps on a perfect sunny day surrounded by uncountable flocks of white seabirds.

Such is the setting of the islands with which this book deals. To scientists they are of immense value as their geological and oceanographic position is unique and their isolation makes them ideal laboratories for biologists interested in ecology, biogeography and evolution at work.

The present report on the Expedition gives a detailed description of the results obtained by the various specialists. The aim of this introductory chapter is to present a general and integrated picture of the different aspects which are covered in the following chapters. It is not intended to repeat what has been competently said in the following pages, but to provide a reader who is less familiar with research in the Antarctic region with a general synthesis of the main subjects. This presentation is based on the personal views of the author and the conclusions which are proposed here are entirely his own responsibility. In addition to giving a short description of the results of the South African Expedition suggestions for future research are also made.

The first and most important aim of the Expedition was to assess the physical and biological character of the islands. Although some data had been provided by former visiting scientists, the islands Marion and Prince Edward, and especially the latter, were, until 1965, practically unknown to the scientific world. This task of the Expedition was accomplished by the members of the small team and the many colleagues who assisted in working up the results. The first aim for the biologists was to make a taxonomic reconnaissance, but it was, at the same time, possible to conduct ecological, behaviour and palynological studies which shed considerable light on the island ecosystems. In this way an important gap in our knowledge of the sub-antarctic region has been filled in close co-operation with colleagues from other SCAR-countries. It is to be hoped that the results of the South African Expedition will stimulate further research on these interesting islands and may lead to the establishment on Marion Island of a modern research station which will enable scientists from various countries to contribute to our knowledge of these virgin islands. Well-equipped scientific bases have been in existence for several years on the following islands: Signy Island in

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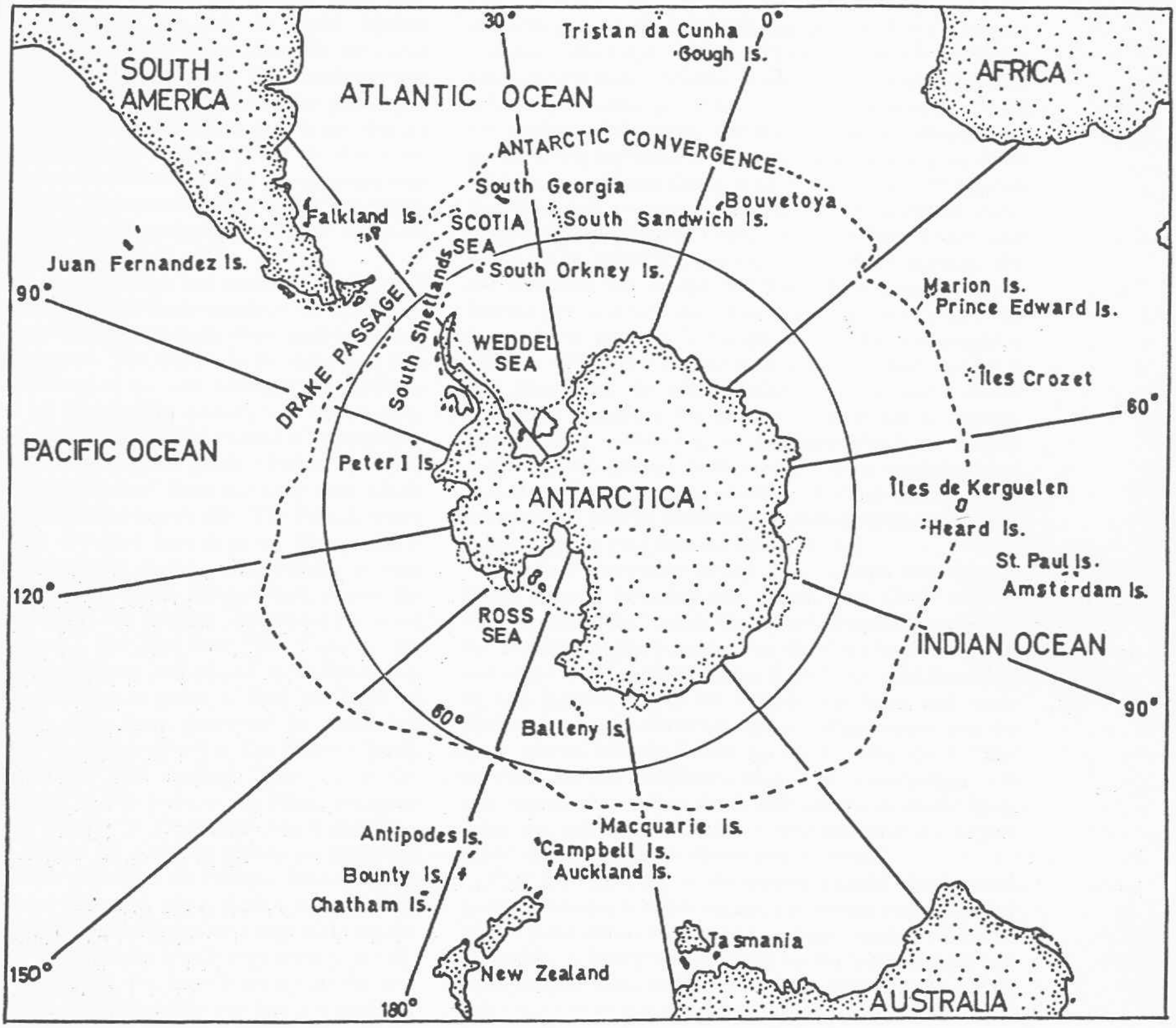


Figure 1. The Antarctic and Subantarctic Region.

the Antarctic region, maintained by the British Antarctic Survey; on the Crozet and Kerguelen Archipelagos erected by the "Comité National Français pour les Recherches Antarctiques (C.N.F.R.A.); on Campbell Island belonging to New Zealand and on Macquarie Island sponsored by the Australian Antarctic Division (A.N.A.R.E.) (Figure 1).

THE DISCOVERY AND EXPLORATION OF THE ISLANDS

The geographers of the Classical World and the Middle Ages strongly believed in the existence of a Terra Australis, an Antichthone, and this imaginary land appeared on many world maps, even on those of the 16th and 17th century. This continent was supposed to keep the earth in equilibrium and was the aim of many explorers after the Portuguese discovered the most important sea routes of the southern hemisphere. One of these illustrious explorers who enlarged the world known to mankind, was Pedro Fernandez de Queiros but he sought in vain for this enormous continent which should be the southern equivalent of the Indies. His fantastic descriptions of the unseen land stimulated progress of geographical discoveries (A. Rainaud, 1893). In particular the Norman, Binut Paulmyer de Gonneville, a contemporary of Magellan and Vasco da Gama, roused the interest of France in the Southern Continent, despite the failure of the sailors to find this fabulous land. Scientists like Buffon and Maupertuis urged the French to take an active part in the exploration of the southern end of the world and famous French sailors like Bouvet de Lozier, Bougainville, Surville, de Kerguelen and Marion-Dufresne braved the dangerous southern seas in their small ships and discovered many of the circumantarctic islands while in search for the mysterious continent.

Marion-Dufresne sailed on 28 December 1771 from the Cape of Good Hope with two flutes, the *Mascarin* with 22 cannons and a crew of 140 and the *Marquis de Castries* which had 16 cannons and 100 men on board. Marion himself was commander of the *Mascarin*, while the other ship was in the charge of Du Clesmeur. The armament was licensed by the King, but the expenses were paid by a group of private persons including Marion. It is not strange that Marion had his ships so well armed for the discovery of the southern continent since Queiros, whose name was mentioned previously, was accompanied by six Franciscan monks to christianize the native population of those unknown lands (Rainaud, 1893).

On 10 January 1772 the ships had reached the cold and misty region of 44° S where large numbers of birds presumed the nearness of land and three days later the island Marion was discovered. The explorers thought that this land was a promontory of the vast southern continent as the NW, W and SE limits of the island could not be seen. Marion therefore named this island "Terre d'Espérance", while the smaller island further north (Prince Edward) was named "Ile de la Caverne" from the large cave which exists in the steep cliff on the eastern side. The French, when attempting to land, damaged their ships so, disappointed, they left those inhospitable regions after looking in vain for a safe approach to the island. Marion then named the inaccessible islands "Iles des Froides" and sailed eastward where he discovered a few days later "Iles Crozet". He was able to disembark here and hoped to continue his voyage in a SE direction in order to find the Land of Gonneville. As his ships were dismasted he could not continue his course and had to divert to Van Diemen Land, from where he sailed to New Zealand, "that part of the austral lands", where he and many of his ships' company were killed by the Maoris. In the journal which describes this unfortunate voyage the southern islands are supposed to be small debris left over from the volcanic disintegration of a large continent (Rainaud, 1893, p. 427, note 6). The discoveries of Marion were published on a map of the southern hemisphere by Vaugondy in March 1773 (ibid, p. 427/8).

It seems very likely that the first discovery of the two small islands Marion and Prince Edward was not made by French sailors but by skipper Barent Barentsz. Ham of the galleon *Maerseveen*. He probably sighted the islands already in 1663, 109 years before Marion-Dufresne sailed the Southern Ocean. The *Maerseveen* of the Dutch East India Company left the Cape of Good Hope under the command of Ham on 14 February 1663 on its way to Java. It experienced very quiet weather, which is unusual in these latitudes, and the first mate Michiel Gerritsz. Boos mentions in his log-book that the islands were sighted on 4 March 1663. The position is given as about 40° 51′ L for Dina and 41° 13′ L for Maerseveen. The longitude of the islands is "by guess" given as 43″ 40′ E (for the description see the Photos 3 and 4). (Leupe, 1868). Skipper Ham reached the island Amsterdam on 29 March and Strait Sunde on 30 April 1663. The islands Maerseveen and Dina (often called Denia) appear on many maps of the 18th century, but could since their discovery by Ham not be found again. The rumour that the islands were covered with woods spread at the end of the 17th century, although these details are not mentioned in the short report on the discovery. As a result of this the galleon *Wezel* was sent out from the Cape of Good Hope on the advice of the Governor Willem Adriaen van der Stel in 1699 to investigate whether the trees growing on the islands could be used for much needed timber. The *Wezel* sailed near the position given in the log-book of the discoverers from 9–15 April 1699, but could not find a trace of the islands. It appears that Ham was a very experienced sailor who visited India, China, Japan, Malaya, Ceylon and the East Indies and made many valuable observations on these regions. We can therefore not accept that his discovery of Dina and Maerseveen was fictitious. The only conclusion which can be made is that his observations on the geographical position of the two islands were inaccurate and that he in fact discovered the islands Marion and Prince Edward which are situated a few degrees more to the southwest. The incorrect position given for these islands on the old maps was not unusual in those days and is reminiscent of the case of Bouvetøya, the existence of which was uncertain for 159 years after its discovery. Marion-Dufresne had made more accurate geographical observations.

The next discoverer to see these islands was Captain Cook. During February and March 1775 Cook tried in vain to locate the islands Denia and Maerseveen seen by the Hollanders. On his return to the Cape he met Crozet, one of the officers of the Marion Expedition, who described to him the discoveries the French expedition had made (Rainaud, p. 428). However, not knowing that it was the same islands already found by the French, Cook "discovered" the Prince Edward Islands on 12 December 1776 and named them after the fourth son of Britain's king. Later on, realising his error, Cook renamed the largest island after the French discoverer Marion.

After the discovery of the several isolated islands in the Southern Ocean, whalers, sealers, buccaneers and merchants visited these bleak, boisterous and foggy regions in search of wealth. A heavy toll was paid by the whales, seals and birds and on some of these southern islands not a single seal was to be seen at the end of the first quarter of the 19th century. Captain Fanning reported that in 1802 sealers were living on both Marion and Prince Edward Islands (Marsh, 1948). Big blubbertanks and huts have been seen on their beaches. Remains of huts have also been found on the north coast of Marion Island and on the east coast of Prince Edward. The survivors of many ships such as the *Richard Dart*, *The Maria*, the *Solglimt*, and the *Seabird* which foundered on the treacherous cliffs in the foggy weather and gales, lived a miserable existence in some of these huts (Marsh, 1948). During our Expedition a heavy anchor was found just south of the Cave on the east side of Prince Edward Island. Later visitors to the islands may have been German marines who lived here for short periods during the two world wars. Cartridges of German manufacture were found by members of the Expedition and are also shown on a photograph in Marsh's book (1948).

The inaccessible islands have for a long time prevented scientists from studying their treasures. Famous expeditions like those of Sir James Clark Ross in 1840 with his ships the *Erebus* and the *Terror* did not succeed in landing on the islands because of bad weather conditions. On board one of these ships was the eminent botanist Sir Joseph D. Hooker, the author of "Flora Antarctica", who missed the opportunity of studying the islands' natural history. The well-known Challenger Expedition was able to visit Marion Island for only a few hours on 26 December 1873 and collected very interesting material (Hemsley, 1885b) (Huntley, chapter 8). It has sometimes been stated (Marsh, 1948, p. 39) that Charles Darwin was amongst the "Challenger" party which visited Marion Island. This, however, is a serious error as Darwin in his later years suffered from poor health and did not then make any long and fatiguing journeys comparable with the voyage of the Beagle. For further information on scientific activities on the islands, such as the landing of the French "Bougainville Expedition" on Marion Island on 23 January 1939, the reader is referred to the chapters on geology, ornithology, entomology and botany in this volume and to the article by Verwoerd (1966).

The activities of the sealers who slaughtered most of the elephant seals on the islands must have come to an end early in this century. The firm Irvin and Johnson made a last attempt in 1930 to resume the sealing industry, but their ship *Kildalkey* had to return without any success mainly because of the bad weather. (Marsh, 1948). It seems as if by this time the fur seals had practically disappeared from these shores.

After World War II a new era commenced for the two islands as the South African Government on the initiative of Field-Marshal Smuts, annexed them for strategic reasons. On boxing day December 1947 Lt Cdr J. Fairbairn, captain of H.M.S.A.S. *Transvaal*, landed with a company of marines at Transvaal Cove, raised the Union Flag, and read a deed of sovereignty. The same ceremony was repeated on Prince Edward Island in front of the Cave on 4 January 1948. The islands have since then been declared nature reserves by the South African Government and their plant and animal life has been completely protected. The geographic position of Marion Island is of special importance for South African weather forecasts and immediately after the annexation a weather station was established on the north-eastern side of the island at Transvaal Cove. A continuous record of surface synoptic observations is available from 20 March 1948 and since May 1949 radiosonde ascents have been organised.

The name of A. B. Crawford is intimately connected with the early stages of the small settlement on the island as he was the leader of a group of Tristan islanders who erected the first buildings and also was the first to take charge of the meteorological station. Since those days the research ship *R.S.A.* has regularly plied the stormy Southern Ocean under the command of the experienced Captain K. T. McNish, yearly bringing a new team of young energetic meteorologists and technicians to the lonely island and taking home the men who had stayed there for nearly 13 months. Several of the members of these teams l been active in collecting biological specimens for scier investigations. Special mention must be made of R. Rand who conducted the first study on the seals and b of Marion Island.

ORIGIN OF THE ISLANDS

Volcanic islands have in the recent past provided convin evidence in favour of the theory of continental drift. In connection the islands Marion and Prince Edward situated in an extremely interesting position. Accordin Heezen and Tharp's physiographic diagram of the In Ocean the islands are only a few hundred kilometres a from the crest of the Mid-Indian Ridge (see Verwo chapter 3). The ocean ridges are supposed to be the re of the upwelling of the slow convection which takes p in the mantle of the earth. The material which is brou to the surface of the ocean floor by this creep turns a from the ridges and spreads in zones parallel to th These mid-ocean ridges are centres of earthquakes volcanic activity. This has been demonstrated particul for the Mid-Atlantic ridge. In its northern part just sc of Iceland some new islands emerged between 1963 1967, but of these only Surtsey survived the onslaugh the ocean. Much farther south the volcano of Tristan Cunha, situated very near the same mid-ocean ridge, beca active again in 1961. Islands such as Tristan da Cur which are closely associated with the mid-ocean ridge in general of a young age while others such as the Kergue and Heard, situated at greater distance, as a consequenc the spreading of the ocean floor, are much older.

The age of these volcanic islands can be determined by potassium-argon method which is based on the decay potassium-40 to argon-40. Young samples have accur lated little argon-40. Twenty samples from Tristan show that the island was only 1 million years old (Miller, 19 565–569). The position of Marion and Prince Edw therefore also suggested a young age. The age determi tions of lava samples made by McDougall (chapter 5) remarkable in that they are among the youngest K, dates ever reported. The magna apparently lost all radiogenic argon before it crystallized, so that the amo of argon-40 contained in the lava originated through de after crystallization. The older lavas, which are ea recognised in the field because of their grey colour, h an age of 276,000 $\pm$ 30,000 years to 100,000 years. C sample of grey lava apparently had a much younger age only 48,000 $\pm$ 25,000 years.

A second volcanic phase, which can be recognised by black lava flows, has an age of about 15,000 years. T parasitic cones which occur in Tristan are about 10,0 years old (Baker et al., 1964, p. 481) and can be compa in age with the second volcanic phase of Marion Isla which left nearly 130 conical volcanoes behind as typi landmarks. The colour of many of these cones is brick r brown or yellow, probably depending on the influence steam which was blown out (Verwoerd, chapter 3).

The determinations made by Snape and Retief of the direction of magnetization of ten samples of lava from the islands (chapter 4) show that this direction does not differ significantly from the normal magnetic field. These data are well in accordance with the K/Ar age determinations of the rock samples and prove that the samples fit into the recent Brunhes Normal Epoch of palaeomagnetism.

The development of a volcanic island in mid-ocean is a gigantic process which can be visualised by following the description by Thorarinsson (1967) of the recent birth of the island Surtsey. Earthquakes herald the event, after which boiling lava, pouring out of the vents from the earth's crust into the sea, causes enormous explosions, the columns of which can reach the tropopause. Once the island has grown above sea level the mobile lava extrudes without explosions and flows down the slopes, gradually building up a shield volcano of the Hawaiian type. Geochemical analyses (Kable, Erlank, Cherry, chapter 6) indicate that the islands Marion and Prince Edward are probably not remnants of one single volcano but are two coalescing shield volcanoes.

When a volcanic island first emerges the new land surface is devoid of any form of life. The extremely interesting process of migration to the islands Marion and Prince Edward began thousands of years ago and the biota still give the impression of being impoverished and in a state of disharmony. The first life on the islands not only had to face the dangers of prolonged volcanic activity but to these risks can be added the hazards of extensive glaciations. Geological and botanical research have shown that the islands must, at least once, have been partly covered by glaciers during their relatively short history. Unequivocal evidence for extensive glaciation can be inferred from striated platforms which are found on the old grey lava as low as 140 m a.s.l. (Verwoerd, chapter 3). The smooth topography of the older grey lava surface also indicates glaciation of a long duration. As the younger black lava does not show any sign of glacial action this glaciation must have been less than 100,000 and more than 15,000 years old and was therefore practically synchronous with the cold Wisconsin-Würm glaciation of the northern hemisphere. Judging by the oldest dates of the grey lava the islands must also have experienced an equivalent of the penultimate or Riss glaciation.

A comparison of fossil pollen and glacial evidence from many sites in the southern hemisphere has revealed that the last Pleistocene glaciation was world wide (van Zinderen Bakker, Sr., 1969). The latter part of it has also been assessed by fossil pollen studies on Marion Island. Here the oldest pollen spectra analysed show that between ca. 16,000 and ca. 14,000 years ago the temperature on the island must have been 2 to 3°C lower than at present. This lower temperature was enough, taking the heavy precipitation into account, to increase the accumulation of snow on the higher peaks and to push the glaciers down the gentle slopes. It is not unreasonable to infer that the oceanic influence of the southern hemisphere dampened the effect of the glaciation. Another factor which must be considered here is the Antarctic glaciation which lowers the temperature of the southern hemisphere so much that the thermic equator is situated 5° to 7° latitude north of the geographic one.

From a botanical point of view it is interesting to note that practically all the flowering plants and ferns known in the present day flora of Marion Island were present about 16,000 years ago. This means that certain oases must have been ice free and that the glaciation of this island was not complete.

The glaciation was followed by tectonic movements which ended with a second volcanic phase during late glacial times. On the black lava flows which were then formed many swamps developed. The radiocarbon age of some of these swamps provides minimum ages of 3,180 ± 120 and 4,020 ± 65 years for this volcanism.

Important geological phenomena resulting from weathering and frost action on both the islands are awaiting further research. Especially in the elevated parts small polygons are found in fine debris. Most ridges are covered with coarse angular slabby fragments of grey lava which have been formed by frost wedging. On the slope of the Van Zinderen Bakker Peak on Prince Edward Island I encountered a field of parallel stone lines, 270 m long, which probably belong to the category of "small sorted stripes" described by Washburn (1969) from N.E. Greenland. These narrow stone stripes could be the result of rillwork caused by meltwater from snow. The features will have to be studied in detail to assess whether they are still active.

Geological research has not so far revealed that typical moraines occur on the islands. It has been pointed out by Bellair (1965) in a study of similar conditions on the Kerguelen Archipelago that the moraines may be found under sea level as the general lowering of that level was more or less 100 m during the maximum of the last glaciation.

THE CLIMATOLOGICAL AND OCEANOGRAPHIC SETTING (Chapter 1)

The islands are situated in the belt of the Brave West Winds which do not blow as steadily as the name would suggest. During 150 days per year the windspeed accelerates to moderate or full gale force with maximum gusts of 130 to 200 km per hour so that seamen speak with good reason of the Roaring Forties and the Whistling Fifties. The steadiness of this circumpolar wind is constantly interrupted by cyclones which pass the islands in a south-east direction. In the middle latitudes over the Atlantic Ocean west of Africa, subtropical humid air masses penetrate the cold Antarctic air front to the south. A low pressure centre is thus formed as a wedge in the cold air. The forward or warm front of the wedge produces much rain when it passes over the islands while it can be dry for a while before the cold rear front brings rain or snow. Anticyclones on the other hand, which mostly move eastward north of the islands, are accompanied by dry spells, just as in the case of winds which come from a southerly direction. This wind system and especially its force are of great importance for the understanding of the ecology of the islands and for the dispersal of floral and faunal elements over the Southern Ocean.

The high pressure systems situated over the oceans at about 30° S on both sides of Africa show slight seasonal displacements in a meridional direction so that it is only in winter that the cold fronts of the cyclones touch the south-western part of the African coast. It is not unreasonable to suppose that similar shifts, of slightly greater amplitude, in the position of these highs could have occurred during the glacial and interglacial periods of the Pleistocene with the consequence that the influence of the West Wind system could penetrate some degrees further into the interior of Southern Africa. A general lowering in temperature which accompanied the ice ages could generate such shifts.

The regular cyclones which pass near the islands are the cause of much cloudiness, a high relative humidity and a precipitation of about 260 cm per annum. Rain falls on the average on 25 days every month. Not more than 50% of the solar radiation reaches the soil surface and in consequence bright sunshine is very rare on the islands (Schulze, chapter 1).

The oceanic environment keeps the temperature fairly constant on the small islands with only minor diurnal variations. It is of interest that these islands which are situated at the same latitude as Budapest, Zürich, Quebec and Seattle in the northern hemisphere differ so much in temperature and have an average monthly temperature in summer of only about 7.3° and in winter of about 3.3°C. The influence of the nearby Antarctic ice cap explains this apparent anomaly. This generally low temperature together with the extreme force of the wind and the low incidence of photosynthetic energy explains the absence of trees from these islands, which have, quite appropriately, been called "wind deserts". The facts that snow can fall in any month of the year and that frost occurs regularly, not only high up on the mountains but also at low altitude, are responsible for the tundra-like vegetation and the periglacial phenomena which are widespread. It is of interest, in this connection, to note that the grass-minimum temperature is 1.5–2.0° lower than the temperature measured in a Stevenson screen (Schulze: chapter 1). The 0°C isotherm comes down to an altitude of 600 m in late winter and it will be important to study the altitudinal distribution of present and former frost action in detail as this can give important indications on the lowering of temperature in former times. Such results could then be compared with the fossil pollen evidence and other proof of former glaciation (chapters 3 and 9).

Biologists are very apt to compare the climate of the subantarctic islands with that of the alpine regions of the world and sometimes even refer to the tundras on the high tropical mountains. Such comparisons of superficially similar habitats are of very limited value to ecologists as the climatic conditions, at least for plant growth, are entirely different on the highest parts of the mountains at low latitudes as compared with the circumpolar regions. The diurnal climate of high tropical mountains, where practically no seasons occur, cannot be compared with the seasonal climate of the alpine belt of the Alps with its great diurnal fluctuations. On the subantarctic islands we are concerned with an oceanic climate with a dampened seasonal effect, a radiation pattern which differs fundamentally from that of the alpine belt, and with minor diurnal changes. Another extremely important difference from the lower latitudes is the day length which varies on Marion Island from 8.6 hours in winter to 15.8 hours in summer.

The climatology of the islands Marion and Prince Edward is closely related to their oceanographic setting in the middle of the three water masses which surround Antarctica. The cold Antarctic Upper Water, which is nearest to the Antarctic Continent, reaches as far north as 2° latitude south of Marion. The subantarctic Surface Water which surrounds the islands stretches as far as 5° north of them where it is replaced by Subtropical Water. Daily measurements of temperature of the surface sea water around Marion Island have shown that the average summer temperature is 6.1°, while the average winter temperature is 4.0°C (Schulze, chapter 1). Crossing the southern boundary of the Subantarctic Surface Water the surface temperature of the water drops 2°C (Orren, 1966). The position of this boundary is very important for the understanding of the ecology and especially of the palaeoecology of the islands. A northward shift of only a few degrees of the Polar Front will change the conditions on the islands entirely, and will have the same effect as would a small overall drop of the world temperature. Northward displacements of limited extent of the Polar Front have been inferred by Hays (1965) for the last 0.4 to 0.5 million years from microfossil studies of ocean bottom sediments. At present displacements of the Polar Front of 80 kilometres either way are not uncommon and extreme changes in the latitudinal position may even reach 160 kilometres.

In summer the air temperature on the island is higher than that of the ocean water, but in winter the opposite is found, so that during periods of a northward displacement of the Polar Front the air temperature will in winter have decreased by more than 2°C. Besides this the minimum temperatures at soil surface are 1.5 to 2.0°C lower than indicated by the minimum thermometer in the Stevenson screen, with the consequence that the average winter temperature at soil level will, during glacial periods, have been near zero. In summer the average temperature will, however, have been about the same as is at present experienced during winter. Changes of this amplitude in temperature will have brought the snow-line (which lies at present in summer between 610 and 850 metres (Schulze, chapter 1; Verwoerd, chapter 3)) to a much lower level and will have lowered the position of the 0°C isotherm so much that right through the year the mountain tops would be well above the freezing level (figure 11, chapter 1). Such conditions would cause a considerable accumulation of snow on the mountains and consequently enhance the growth of glaciers. As the west side of the island is much more exposed to the rain-bringing winds, the east side may have been less covered by ice, with the consequence that the flora could survive there in ice-free oases (chapter 7).

THE ORIGIN OF THE ISLAND BIOTA

As mentioned the birth of a volcanic island is a massive geological event which gives opportunities for the study of fundamental biological processes such as dispersal, invasion and establishment of plant- and animal-life on a virgin surface. Once the lava flows have solidified and the ash fields have cooled propagules of all kinds may arrive by various means. This interesting process has, since the great eruption of Krakatau in 1883, attracted the attention of many scientists on the rare occasions on which nature has presented these opportunities. Much attention was given to the dispersal of plant and animal life across the oceans by the scientists of the Challenger Expedition (Hemsley, 1885a and c). Research on such problems is at present being conducted by an international team on the new island Surtsey, south of Iceland. Fridriksson (1968) found here that six months after the first eruption started in 1963 various strains of bacteria, a few moulds, one fly (*Diamesa zeryni*) and living plant fragments had already drifted on to the shore of the new island. In 1968, one year after the last eruption, Behre and Schwabe (1968) could isolate 8 species of Cyanophytes, 74 Diatoms and 23 species of other algae from little moist areas on Surtsey where 3 species of mosses had already formed small cushions. Similar investigations on the first invasion of living organisms under polar conditions had also recently been made on Deception Island of the South Shetland Islands (at about 63° S), where Cameron and Benoit (1969) found algae, fungi and bacteria present within 12–13 months after the volcanic blast of December 4th, 1967.

Information of this type is very valuable for the explanation of the origin of the biota of Marion and Prince Edward Islands. The possibility of former land connections of these islands with source areas can be dismissed as no geological evidence can support the existence of such land bridges. In consequence only long distance dispersal by ocean currents, wind, or birds can explain the migration of propagules to the islands.

No quantitative experimental work was done on this aspect during the Expedition, but a few observations demonstrate the practical feasibility of this transport over long distances.

After our arrival on Marion Island a turtle dove was caught by my son E. M. van Zinderen Bakker Jr. in January 1966. This dove which certainly did not belong to the South African species was kept alive in the greenhouse on the island in order to take it home in April for determination. A member of the relief party which arrived then, evidently had a great love of animals and released the bird without asking permission to do so. This well-intended act must certainly have resulted in the early death of the dove which was probably a specimen of *Streptopelia picturata picturata* Temminck from Madagascar (van Zinderen Bakker, Jr., chapter 9). Other important records are the Cattle Egret (*Ardeola ibis ibis* L) reported by Crawford in 1952, and the Yellow-billed Egret (*Egretta intermedia* Wagler) seen by La Grange in 1963. A young European Swallow (*Hirundo rustica* L.) was caught and brought back in 1967 by van Zinderen Bakker, Jr. The number of these stragglers seen on Marion Island in such a short time shows that birds under certain conditions are able to negotiate the distant travel to the islands, which they can probably reach from South Africa in a matter of a few days when aided by winds of gale force.

Besides these rare immigrants which are unable to settle in the environment which differs so much from their normal habitat, many birds which belong to the regular avifauna of the islands move regularly over great distances. The bird banding programme organised on the Antarctic Continent and some of the southern islands has shown e.g. that the two species of Giant Petrel which both occur on Marion Island, spread over the Southern Ocean in a circumpolar fashion when they are young (van Zinderen Bakker, Jr., chapter 9). A Giant Petrel banded on Macquarie Island in 1950 was shot on South Georgia four months later, which proves that it travelled 8,000 km (Taylor, 1954). A Skua (*Stercorarius skua*) banded on Marion Island during the Expedition was reported on Fernando Po. ca. 6,000 km away. Similarly the Wandering Albatross (*Diomedea exulans*), *Procellaria aequinoctialis*, *Pachyptila* spp., *Pterodroma mollis*, *Fregetta tropica* and other species move far away from the islands as has been observed by van Zinderen Bakker, Jr., during the return voyage of the Expedition in April 1966 (chapter 14).

That a certain exchange of the bird population of the islands can occur is clearly shown by the two records of Royal Penguins (*Eudyptes chrysolophus schlegeli*) on Marion Island in 1960 and 1965. These birds must have come from Macquarie Island which is the only known breeding site of the species (Alexander, 1955). The Royal Penguin is not generally considered to be of full species rank and is at least closely related to the Macaroni Penguin. The 20 specimens which were recorded in 1960 can, however, not have been locally developed genetic aberrants but must have been migrants.

These movements of the great bird populations of the islands will have a considerable influence not only on the gene pool of these populations but also on the distribution of all kinds of propagules, especially seeds and eggs of invertebrates, such as earth worms, spiders and plankton organisms. During the Expedition Giant Petrels and Wandering Albatross were often seen with many clusters of the hooked seeds of Acaena attached to their feathers.

Taylor (1954) describes an important way in which birds such as albatrosses may transport seeds attached to their beaks and feet. "These birds in common with most sea birds, regurgitate an oily fluid when building nests and as a means of defence against intruders. This fluid on drying had encased the seeds noted. In such a condition seeds could be carried almost indefinitely in flight and could withstand immersion in sea water if the bird alighted to rest, yet on landing the seeds could be easily rubbed off". A similar example is described by Godley (1967) for the seeds of *Hebe elliptica* attached to Macronectes.

That birds can also transport snails such as *Notodiscus hookeri* Reeve, which occurs on Marion Island is discussed by Dell (1964) and Solem (1968). It is possible that this snail produces sticky mucus which causes it to stick to the feathers of birds.

The possibility that eggs of zooplankton which are desiccation-resistant can be transported by birds or wind is mentioned by Smith and Sayers in their study of the Entomostraca collected by the expedition (chapter 29).

The available evidence, although it is limited, clearly indicates the important role played by birds in transporting propagules to the subantarctic islands.

Wind may be a factor of similar importance especially for the distribution of spores of lower plants, insects and also birds (as shown above). Gressitt and Yoshimoto (1963) gave interesting details on this means of dispersal of animals in the Pacific. A programme of trapping insects at sea in the tropical Pacific, carried out by the Bishop Museum of Hawaii, resulted in 1,054 insects being trapped from 25 cubic kilometres of air. A study of the records showed that a strong correlation exists between the groups of insects trapped and the taxa which inhabit isolated oceanic islands. These results are of importance in accounting the explanation for airborne migration to Marion and Prince Edward Islands, although the discrepancy discussed by Gressitt and Yoshimoto for the Curculionidae may call for some other explanation. These beetles, which are very common on the islands (Kuschel, chapter 27) have not been found in the air samples of these two scientists. Freeman (1945) has, however, shown that Curculionidae are well represented in aerial plankton trapped over England.

Lawrence (chapter 21) in his study on the spiders collected by the expedition discusses the aerial dispersal of spiders. *Erigone vagans* Audouin is the only species found on the islands which "practises the ballooning habit in the distribution of the emergent young and of the adults as well". Gressitt and Yoshimoto (1963) report that young Araneida form 3.3% of the animals trapped in air over the ocean (35 of 1,054 animals).

Quantitative data on the dispersal of spores to Marion Island are not available but, during February 1965, slides were exposed in a Hirst Spore Trap near Marion House in order to obtain some records. Large numbers of spores of liverworts which grow in the neighbourhood were collected on the sticky slides. The trapping programme had, unfortunately, to be discontinued after the apparatus was severely damaged during a storm. The distribution pattern of the Hepaticae collected on the islands Marion and Prince Edward (Grolle, chapter 11) strongly emphasises the importance of long distance dispersal of these lower plants by wind and perhaps also by birds. The basic pattern of distribution of these liverworts in the Antarctic and subantarctic regions may be ancient but the occurrence of such genera as Acroboltus, Andrewsianthus, Blepharidophyllum, Herzogobryum and Hygrolembidium, some of which are very primitive, can only be explained by wind dispersal. The same applies to the distribution of the rich moss flora.

The possibility of such long range influence could be demonstrated by the pollen analytical research carried out on Prince Edward and Marion Island (Schalke, van Zinderen Bakker, Sr., chapter 7). In a snow sample collected between Delta Kop and Jan Smuts at 990 m a.s.l. one Nothofagus and a Podocarpus pollen grain were found. This pollen must have been transported from South America, a distance of 7,500 km. Four other snow samples collected at high altitudes did not contain pollen. Several grains of Podocarpus and three of Nothofagus were found at various depths in cores from both islands as was a doubtful grain of Ephedra. It is therefore possible for spores of mosses and liverworts to travel the same distance. The question of the viability and the sex of such spores is, however, an important factor for the establishment of such migrants on outlying islands.

Besides transport by birds and wind another alternative for biota to reach the islands is with the circumpolar current or West Wind Drift but no data are available for living propagules which could have been transported to these oceanic islands in this way. The buoyancy and viability of seeds of island plants has not been investigated, but the morphological structure of the seed points more to transport by birds and perhaps by wind. In this connection the speed of the ocean currents is of importance for the transport of terrestrial organisms and of species of the littoral biotas by drift. The speed of the West Wind Drift is probably of the order of 0.4 to 0.8 knots (chapter 1).

The possibility that stray insects, spiders or other invertebrates or seeds can reach the islands with driftwood can not be ruled out. Nothofagus logs have been reported to have drifted from South America to the west coast of Macquarie Island, a distance of 16,000 km (Barber, et.al., 1959). Many driftwood samples were collected by Verwoerd, van Zinderen Bakker, Jr., and Huntley at Mixed Pickle Cove on the west coast of Marion and on the northeastern coast of Prince Edward below Albatross Valley. These crooked branches and trunks could not have been timber lost by a ship but must have drifted from their natural source of origin.

Through the kind intermediation of Professor G. L. F. Hartwig of Stellenbosch the anatomy of these samples has been studied by the Division of Forest Products, C.S.I.R.O., Melbourne, Australia. Dr J. D. Boyd identified the samples as being wood of *Nothofagus pumilio* from the Andes Mountains in Southern Chile and Patagonia. Driftwood of the same species has been received by the C.S.I.R.O. from shores as widely scattered as N.W. Australia, Macquarie Island, Tasmania, South Georgia and even Tristan da Cunha.

As well as other driftwood many bamboo stems have been found on the north coast on Prince Edward and near Kaalkoppie on the west coast of Marion (30 March 1966), which points to transport by the Agulhas Current from tropical regions or to commercial traffic, which is, however, very rare in these latitudes. Darwin (1875) had already pointed to the possibility that seeds might be transported by driftwood.

The information so far available strongly indicates that the biota reached and still reach the islands Marion and Prince Edward mainly through dispersal by wind and birds. The migration of flora and fauna of the littoral round the islands depends on the ocean currents, and on the presence or absence of pelagic phases in the life histories of marine invertebrates. According to Thorson (1950) up to 50% of the species of these invertebrates are either viviparous or brood their eggs in the polar seas. This must result in a much lower ability to migrate and will therefore favour endemism, especially amongst echinoderms, molluscs and polychaetes.

THE DIVERSITY OF THE BIOTA

The dispersal of propagules and migration to the uncolonised volcanic islands is only the beginning of a long process which eventually results in the establishment of the insular ecosystems. The biological work of our expedition team and the colleagues who assisted us was primarily directed to taxonomic problems of biogeography and was dominated by the historic viewpoint. For future work the islands offer extremely interesting possibilities for the study of immigration, colonization and extinction rates which should be assessed in quantitative terms (MacArthur & Wilson, 1967). Newly established colonies will have to be studied in detail in order to obtain accurate information on the colonizing success and the ability of new arrivals to occupy existing open niches. Such population studies will also be extremely important for our understanding of the speciation process. The interesting problem of the flightlessness which is so well illustrated in the Lepidoptera, Curculionidae and Diptera on the islands should receive more attention. Biogeographic facets of this nature are closely connected with the degree of endemism which occurs on the islands.

These phenomena cannot be separated from the historic background as the number of species which inhabit an island is determined by the geological history of the relevant island, together with its size and the diversity of its habitats.

Although the geological history of the islands Marion and Prince Edward is now fairly well known it is still difficult to understand their biogeography. It seems anomalous that these islands, situated between the important source areas of the southern end of South America and the Crozet and Kerguelen Archipelagoes, should have biota which are more impoverished than those on these last mentioned islands. The West Wind system and the ocean current should favour these islands more than those situated farther to the east and this also applies in regard to immigrants originating on the African continent. Several taxonomists have cautiously expressed their disappointment with the collections assembled by the Expedition. The explanation for the general lack in endemic forms and for the comparatively small diversity of the biota should perhaps be sought in the historical aspect as has been done by Holdgate (1960). I would in this connection suggest the following explanation. The Kerguelen and Crozet Archipelagoes are of a much greater age than Marion and Prince Edward Island. When Marion and Prince Edward Island originated the biota of those archipelagoes already possessed a very varied flora and fauna. Holdgate (1965) suggests a similar reason for the low level of strict endemism on Tristan da Cunha, the youngest island of the archipelago of the same name. Besides this the Crozet and Kerguelen Islands did not experience glacial phases of the same magnitude as did Marion Island, so that autochtonous ancient forms could survive the climatic hazards while far more time was available for speciation. The devastating effect of volcanic activity in the Crozet and Kerguelen island groups will have been counter-balanced by the nearness of the islands in these archipelagoes. If the biota of one of the islands suffered great losses through volcanic eruptions it could be re-colonised by migrants from nearby sources. The stepping-stone effect would in such cases be of great value for the survival of the biota.

Marion and Prince Edward are on the other hand young islands which have not had the time to acquire diversified biota. The lowering in sea and air temperature during the glaciations which affected the islands could also have had a strong influence on the richness of the terrestrial and marine biota. This may have caused depauperization of the flora and fauna through extinction, while the present low endemicity can be the result of repopulation in recent times. (McDowall, 1968.) Kuschel in his discussion on the Curculionidae collected on Marion and Prince Edward Island (chapter 27) mentions in this connection that it is sometimes possible for endemic species to withstand adverse conditions. The four endemic Curculionidae were probably able to survive the glaciations on the islands because of their wide range of food plants, and because their larvae live in the soil.

Special studies on speciation were not undertaken during the Expedition although, in this connection, some ornithological observations are very interesting. The two sympatric species of the Giant Petrel are effectively separated by such barriers as the choice of the nest site, the nesting habit and also the time of egg laying (van Zinderen Bakker, Jr., chapter 9). Similarly the Soft Plumage Petrel and the Kerguelen Petrel may be separated by ecological barriers.

Marion and Prince Edward Island will also have received diaspora from western and northern directions, but they depended much more on the invasion of propagules from the ancient Crozet and Kerguelen Archipelagoes with which they consequently have strong taxonomic affinities inside the Kerguelen Province. This explanation would mean migration against the direction of the present prevailing westerly winds (Holdgate, 1960). Determinations of the age of the Crozets islands and experimental work on dispersal of biota may in future throw more light on this subject.

In general the subantarctic islands show strong biogeographical connections with the temperate and cold temperate zones of South America and the Tasmanian-Southern Australia–New Zealand regions. The connections with South Africa are of minor importance which points to dispersal by wind and birds along the West Wind drift at higher latitudes south of the Cape of Good Hope.

BIOGEOGRAPHY

In our discussion on the islands Marion and Prince Edward we will follow the classification proposed by Wace and amended by Green (1964) according to which these islands belong to the Subantarctic Zone. The northern boundary of this zone of terrestrial vegetation is formed by the southern limit of trees and woody shrubs, while the southern boundary is formed by the southern limit of closed phanerogamic communities (Wace, 1965).

The Subantarctic Zone also comprises the following islands: Iles Crozet, Iles de Kerguelen, Heard Island, Macquarie Island and South Georgia. In biogeographical discussions it is very appropriate to use the three provinces proposed by C. Skottsberg, viz.:

(1) Magellanian Province (Patagonia, Andian Patagonia, Tierra del Fuego, Falkland Islands and South Georgia).
(2) Kerguelen Province (Prince Edward, Marion, Crozet and Kerguelen Archipelagoes, Heard Island).
(3) New Zealand Province (New Zealand and the surrounding southern islands).

Our knowledge of the distribution of phanerogams, birds and mammals in these regions is fairly comprehensive. The cryptogams, invertebrates and the intertidal biota have, however, not been studied intensively except for certain limited areas. It is therefore not yet possible to give a detailed account of the biogeographic position of the islands Marion and Prince Edward. A number of species on these islands are cosmopolitan, but the majority have a limited distribution in southern regions and these can give some indication of the affinities which exist between the various biota.

The phanerogams recorded from Marion and Prince Edward Islands strongly indicate the close relationship which exists within the Kerguelen Province. In the survey given by Huntley (chapter 8) in table 5.1 it appears that the Coefficient of Similarity (according to Sorenson's formula) of the vascular flora of the Crozet Islands with the flora of Marion as high as 78, while this figure for Kerguelen–Marion is 71.

The islands of the Kerguelen Province also have a very characteristic feature in common, namely the *Poa cookii* tussock grassland. Some species such as *Pringlea antiscorbutica* R.Br. and *Colobanthus kerguelensis* Hook.f., are endemic on all the islands of this Province, so that this group of islands shows much coherence from the botanical point of view.

Many records for the Hepaticae show that the circum-subantarctic element is very strongly represented among cryptogams and that long distance dispersal must be an important factor in their distribution. A large number of primitive genera of the Jungermanniales are supposed to be of Gondwana origin (Schuster, 1969) as they are found on the land masses and islands which formed part of this super-continent. The recent records of some species are not so readily explained.

The genus Andrewsianthus of which two new species have been described in this volume for Marion Island has a wide oceanic distribution, predominantly in the southern hemisphere with centres of evolution in New Zealand and Malaysia. The map published by Schuster (1969, no. 11) suggests that the genus consists of widely scattered species which may not be well known and some of which are certainly of comparatively recent origin (such as the species described for Marion Island). Schuster tentatively explains this entire pattern as being ancient and comparable with the age of the range of the Winteraceae.

The genus Herzogobryum (Jungermanniales) is one of the most primitive of the Gymnomitriaceae. This genus is circum-subantarctic and the three species now found on Marion Island stress the possibility of long distance dispersal in more recent times.

The primitive genus Blepharidophyllum is another example of circum-subantarctic distribution. The species *B. densifolium* is not only recorded from the older islands such as Kerguelen and Gough but its occurrence on Marion shows that it must be able to cross wide expanses of water. *Acrobolbus ochrophyllus* has a similar distribution pattern and has even been recorded from the southern end of the African continent (Schuster, 1969, map 8). This species has now been found on the "young" volcanic island Marion.

The species *Hygrolembidium ventrosum* seems, on the other hand, to be an endemic form of the Kerguelen Province as it was first known only from the Kerguelen Archipelago and has now also been recorded on Marion Island. Much caution has still to be exercised in the explanation of this distribution pattern as the flora and fauna of several islands is still very incompletely collected.

In his description of the relationship of the avifauna of Marion Island Winterbottom (chapter 13) in comparing the southern islands uses the Coefficient of Community. This coefficient reaches the highest values for Marion-Crozet (57%) and Marion-Kerguelen (50%), while it is below 39% for all the other islands in relation to Marion. The relationship of the avifaunas worked out in a dendrogram based on "nearest neighbour" also shows a close affinity within the Kerguelen Province, which is again biogeographically strongly linked with South Georgia. The oldest island group of the Kerguelen seems to be the heart of the subantarctic avifauna.

Strong taxonomic contacts within the Kerguelen Province and also with the Antarctic Continent can be inferred from the distribution of the planktonic Entomostraca of Marion and Prince Edward Islands (Smith & Sayers, chapter 29). Smith and Sayers, who studies this material, found that of the 9 species recorded on the two islands 6 occur on the Crozet Islands, 8 on the Kerguelen Islands, 5 on New Amsterdam, 5 on Antarctica, 4 in Australasia and only 2 species on each of the following: Falkland Island, South Georgia and Heard Island. The affinity with the South American mainland does not seem to be very strong as only one of the species (*Pleuroxus aduncus wittsteini* Studer) occurs there. The eggs of Entomostraca can apparently be transported by wind and birds.

The subantarctic land snail *Notodiscus hookeri* Reeve has an interesting distribution pattern as it is recorded from the islands of the Kerguelen Province and from New Amsterdam. This distribution is explained by Dell (1964) and Holdgate (1960) in connection with the former glaciations of the southern islands.

More proof of the taxonomic unity of the Kerguelen Province has arisen from the study of the spiders and insects which have been collected on the islands Marion and Prince Edward. The spiders *Myro kerguelenensis* and *M. paucispinosus* have, according to Lawrence, so far been recorded only from the islands of the Kerguelen Province and New Amsterdam (chapter 21). Dreux and Séguy in their studies of the insects strongly support the biogeographic unity of the Kerguelen Province (chapters 24 and 25) while a limited degree of endemism on the subspecies level was observed on Marion and Prince Edward Island. Kuschel characterises the subfamily Ectemnorhininae of the Curculionidae as being incredibly plastic in morphology, anatomy and habits (chapter 27). From this group of beetles four species which are endemic to Marion and Prince Edward Island have been described by Kuschel. It is well possible that the Curculionidae are prone to rapid evolution in small isolated populations (Holdgate, 1960).

The offshore fauna recorded so far also provides good evidence for the interrelationship within the Kerguelen Province and for distant affinities with the Magellanic fauna. Four Asteroids studied by Irene Bernasconi (chapter 18) and three species of Holothuroidea identified by Pawson (chapter 19) may have a wide range in the subantarctic and have also sometimes been recorded in the coastal waters of Tristan, South Africa and Antarctica, while some species are cosmopolitan.

The intertidal zone has, however, also provided some new species, viz. one Ophiuroid (Bernasconi, chapter 18) two Isopodes (Cléret, chapter 31) and two species of Hydroids studied by Dr Millard (chapter 35). The Hydroid fauna shows relationships with the Antarctic and Subantarctic Waters, but none with South Africa.

It is not yet possible to draw biogeographic conclusions from the interesting analyses of the Rhizopod faunas made by Grospietsch (chapter 37). More species have, at present, been recorded from Marion Island than from any of the other southern islands, and even one new species and five new subspecies have been described. A comparison of the different faunas will have to be postponed until much more work has been done on the other islands.

THE ISLANDS' ECOSYSTEMS

Small oceanic islands are valuable open air laboratories for the study of animal and plant communities, their interrelationship and their dependence on the physical and chemical environment. The number of species on the subantarctic islands is limited and it is therefore possible to follow in detail which niches they occupy and how they react to such factors as supply of certain nutrients, microclimatological parameters such as temperature, sunshine and wind, to soil characteristics, altitude, competition, the intense influence of the fauna on the vegetation and vice versa, etc. These islands, therefore, are ideal sites for the study of primary and secondary production in order to gain an understanding of the energy flow through the insular ecosystems.

The general ecological pattern of islands like Marion is extremely interesting, as they are exposed to the subantarctic climate and to the surrounding ocean which have an entirely different influence on the food chains of the island biota. The heavy rainfall and high humidity together with regular frost cause a fairly rapid decomposition of the basalt. The material thus formed is constantly leached through the percolation of rainwater so that the ecosystems develop in an oligotrophous direction. Such processes can be studied in detail in crater lakes and swamps which occur in the interior of the island. In great contrast to this constant depletion of minerals the narrow coast area is exposed to a constant fresh supply of these important requirements, firstly by means of salt water spray which is blown onto the land by the strong gales and secondly by the waste of the extremely numerous bird and seal populations. This enrichment of the soil leads to the other extreme of very high local salt concentrations and excreta. In his study on the vegetation of the islands Huntley made interesting observations on the response of the plant communities to these factors (chapter 7). Holdgate (1967) has discussed similar influences of the surrounding rich ocean ecosystem on the narrow coastal border of Antarctica and has produced figures on the biomass of the ecosystems concerned.

This flow of nutrients from sea to land is very apparent at some distance from the coast near the isolated colonies of Giant Petrels or the nests of other birds. During my short visit to Marion Island in 1963 the typical distribution of *Poa cookii* attracted my attention. This grass is often found near old and new nest sites especially on the downhill slope below such rookeries. It would be important to study the stimulating effect bird excreta may have on the germination or growth of this grass.

As already pointed out the general succession at some distance from the coast and in the interior of the islands leads to the development of oligotrophous bogs. Extremely interesting vegetation types are the slightly raised bogs which are covered by mosses and liverworts such as, *Rhacomitrium lanuginosum*, *Drepanocladus uncinatus*, *Campylopus arboricola* and *Blepharidophyllum densifolium* (Huntley, chapter 8). This type of bog can be compared with the raised Sphagnum bogs of the temperate and cold regions of the northern hemisphere. The analogy is very striking and the typical ecology of the ecosystem is also characterised by the low pH of the humus, the occurrence of Desmidiaceae and the many species of Nebela, which here replace the Rhizopoda species familiar in the Sphagnum bogs of the northern hemisphere (Grospietsch, chapter 37).

Much more research has to be done on the ecology of these swamps and bogs. The mires, which occur on the plains of the islands and which are overgrown by Bryophyta, *Agrostis magellanica* and some other swamp plants, also deserve more attention. It was found that the surface of many of these mires is covered by a thick gelatinous layer of Cyanophyta. These algae may be very important in the ecology of these swamps as it has been well established that one of them, *Nostoc commune*, is active in the fixation of nitrogen (Holm-Hansen, 1963).

Other interesting communites are those which are exposed to the rigour of the strong winds, such as the fjaeldmark with its hard cushions of *Azorella selago* in which the soil fauna, epiphytic grasses and mosses find protection against wind and frost. The "hamada" pavement of stone fragments between the windswept cushions is the result of long periods of up-freezing and wind erosion. Even more exposed are the higher parts of the scoria cones where no life is visible on the surface. The cryptic ecosystems of mosses, liverworts and some filmy ferns and a host of Collembola, mites, beetles and spiders live here hidden under the bigger scoria lumps (van Zinderen Bakker, Jr., 1967). The windiness and coldness of the exposed habitats is well demonstrated by the thousands of perfectly spherical brown moss balls of up to 10 cm in diameter which are found in fjaeldmark communities (van Zanten, chapter 10; Huntley, chapter 8). The slope communities, where the cover of the prostrate shrub *Acaena selago* gives protection, and the halophytic and "biotic" communities along the coast add to the ecological variety of the islands. Other interesting ecosystems occur in the littoral and intertidal zones and in pools where marine algae grow in great profusion. Their enormous biomass supplies food for a very varied fauna.

In future it will be important to make a detailed study of the food chains and webs of these communities. Many will start in the ocean where practically all the birds and seals find their source of food, but the terrestrial ecosystems also play a part. During my stay on Marion Island early in 1965, I found an interesting instance of the relationship between the marine and the terrestrial food chains. Large flocks of Dominican Gulls were concentrated on swamps between Junior's Kop and the Met Station just like the gulls which concentrate on ploughed lands. It appeared that these birds live during certain times of the year on the enormous biomass of worms and also caterpillars which are found in some types of peat. The phenomenon was further studied in detail by the botanist and ornithologist of the Expedition and as many as 1,168 worms and caterpillars were counted per square meter of peat (Huntley, chapter 8). The activity of the gulls and also sheathbills resulted in the areas on which they had foraged becoming bare and cultivated. This interference by the birds continuously causes a regression in the plant succession of the swamps.

MAMMALS AND BIRDS

During the expedition only limited attention could be given to the mammals which occur on the islands. The ornithologist van Zinderen Bakker, Jr., made a number of observations while doing his research on the avifauna (1967).

Two species of seals have been recorded. The Elephant Seal (*Mirounga leonina*) is very numerous where good landing beaches occur. Rand (1955), who made a special study of the seal population, estimated that in 1951/52 about 10,000 specimens frequented the beaches. The females come ashore only when the pups are born, between mid-September and the end of October. Thereafter they return to sea to come ashore again in January and February to moult. The bulls moult in late summer viz. in March and April.

The Fur Seal (*Arctocephalus tropicalis*) which was in danger of extermination by the fur hunters is re-establishing itself on both islands. Van Zinderen Bakker, Jr. (1967), reports three breeding populations which were found on the NW corner of Marion Island. A small isolated group was also seen during February and March on the eastern side of this island.

Killerwhales (*Orcinus orca*) were regularly seen at close quarters when they patrolled the area near the Meteorological Station during the seal pupping season and the female seal moult period. A certain bull with a broken dorsal fin could readily be recognised. A hunting pack of these marauders would search the bays very close to the shore while the big bull would stay far outside the kelp zone.

Mice must have been introduced on Marion Island accidentally, probably through shipwrecks or with food supplies. A few specimens which were studied by D. A. S. Davies belong to *Mus musculus*, the house-mouse. This species is cosmopolitan and in 1956 eleven specimens of the same species were collected on Gough Island. They also occur on Tristan (Holdgate, 1965, p. 392). The mice on Marion Island do not seem to cause much damage to plant or animal life but they have been a nuisance to expedition members by doing much damage to clothing and food, and they even nibble the hair of the oblivious man sleeping in his tent. Cats were brought to Marion Island to eradicate the mice. Van Zinderen Bakker, Jr. (1967), writes that "during the first months of our stay we were of the opinion that the cats, living under poor conditions, might be important in combatting the mice. Later on, especially during the breeding season, our experience was that the cats are widespread and take a heavy toll of the birds, particularly of the smaller species (p. 243)". Rats have, fortunately enough, not been found on the islands so far.

The number of bird species found breeding on the islands is 25, while 6 species have been seen but are non-breeding (van Zinderen Bakker, Jr., 1967). The ecology of the birds has been studied in relation to their numbers, food supply and distribution in six different physiographic and geological habitat units which could be distinguished (van Zinderen Bakker, Jr., chapter 9). During winter when the seals are at sea the shores are desolate as the Macaroni- and Rockhopper- and many of the King Penguins travel far away from the islands. The Gentoo Penguins, the population of which numbers 2,000–3,000 stay on right through the year. It is estimated that over 5 million penguins are breeding on the two islands. Two fifths of these are King Penguins, a further two million are Macaroni's and the remaining one million are nearly all Rockhoppers. These figures give an idea of the enormous biomass of sea birds living along the coasts and also of the influence of the oceanic ecosystem on the islands' food chains (van Zinderen Bakker, Jr., chapter 9). The most numerous bird species on the islands is, apparently, the Salvin's Prion (*Pachyptila salvini*) which breeds from sea level up to the highest altitude at which flowering plants occur.

These millions of birds all live directly or indirectly on the high food production of the surrounding ocean. The food web constructed for the birds is very instructive in this connection (van Zinderen Bakker, Jr., chapter 9). On a clear day flocks of birds can be seen foraging out at sea beyond the kelp zone which surrounds the island. These innumerable white specks flicker in the sunlight and return to the shore at nightfall. At this moment on a quiet evening

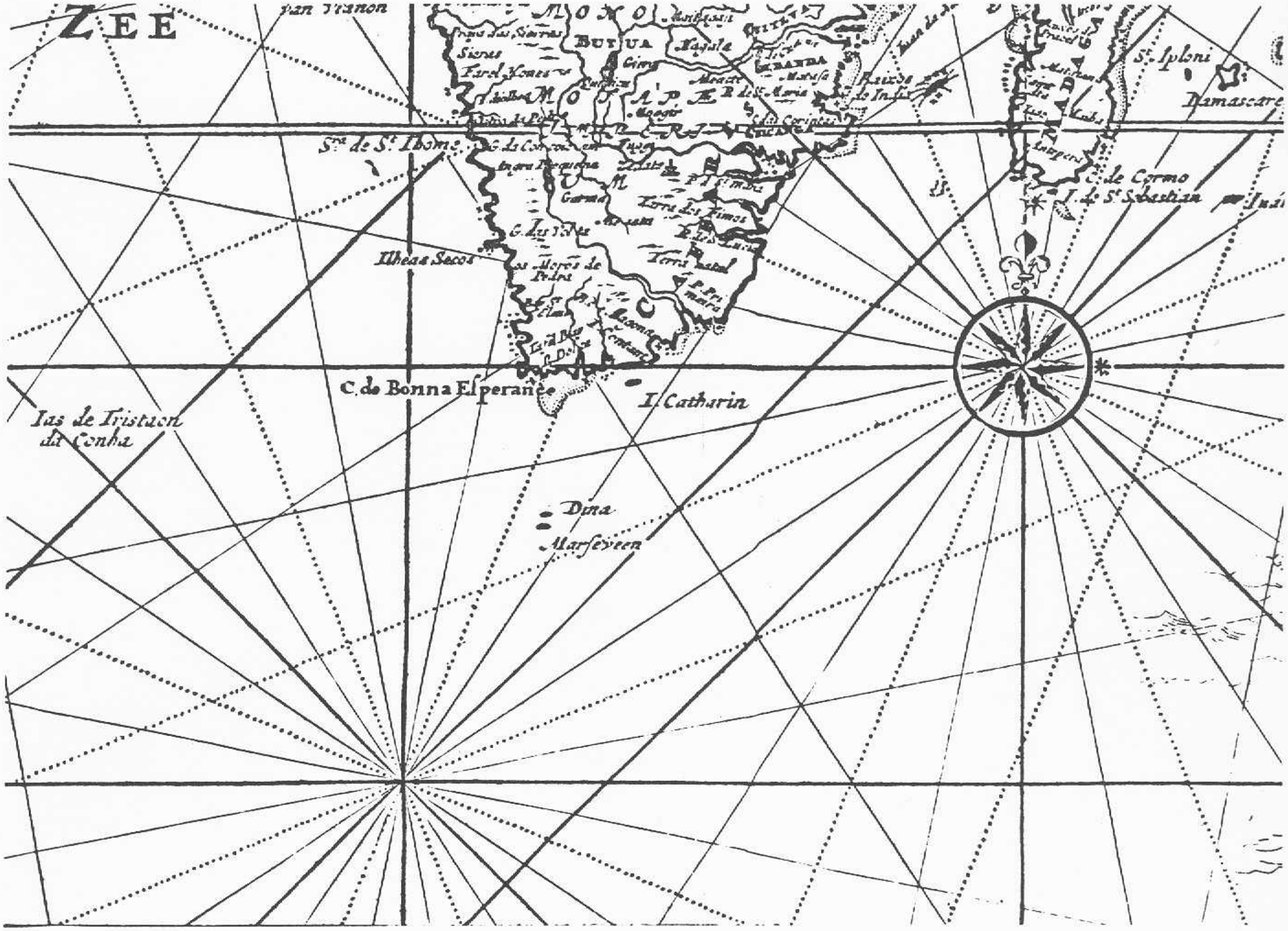
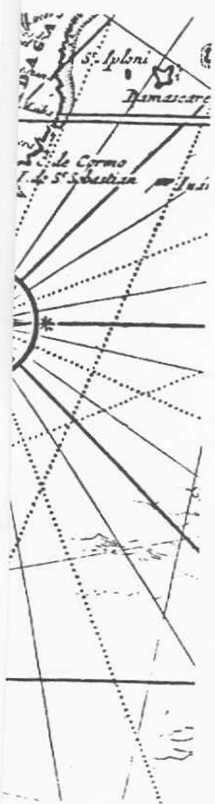


PHOTO 3: Detail of chart of the world designed and published by Gerard van Keulen (beginning 18th Century). Algemeen Rijksarchief, 's-Gravenhage, Netherlands.

»'smorgens de zon gepeild en het opkomen 16 grad. 45 min., de ware opgang is 8 gr. 32 min. en na het gebed gedaan was, zagen twee eilandekens aan bakboord van ons, des middags namen wij (de) hoogte van 41 gr. 13 min., en die eilanden lagen regt Z. en N. van malkanderen. Toen wij bij dat voorschreven eiland kwamen, gisten dat die eilanden omtrent 5 mijlen van N. van elkander (lagen); welke dat gissing maakten dat op 40 gr. 51 min. legt Noordwaarts van ons, gaven wij de naam van het eiland Dina, en dat andere daar wij bij langs zeilen en al vrij digt bij langs, omtrent een ½ van een mijl, gaven wij de naem van Maerseveen; welke legt op 41 gr. 13 min. en naer gissing op 43 gr. 40 min. (lengte); (2) zagen daar ook een mooi groot rif rondom branden, dat geweldig brandde, zagen ook 6 à 7 blinde klippen branden. Wij zeilden bij een langs, dat wel ½ mijl in zee ligt, bij dat voorschreven Maerseveen, want die klippen liggen daer veel."

PHOTO 4: The discovery of the islands Dina and Maerseveen on 4 March 1663 described by Michiel Gerritsz. Boos, first mate on board the galleon Maerseveen (Leupe, 1868, p. 244. See Introduction).

PHOTO 5: *See previous page.*



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first mate on
n (Leupe, 1868,

the atmosphere on the island changes suddenly as the raucous cries of the Skuas are replaced by the melodious sounds of the petrels which return home from their fishing grounds after their predators have disappeared from the scene. Such evenings are certainly the most lovely moments one can experience in these desolate regions. Very many of these petrels which venture in daytime to feed the young waiting in their burrows are caught by packs of Skuas and the swamps and hills are covered with the skulls and wings of these victims. One of these petrels, the South Georgian Diving Petrel, (*Pelecanoides georgicus*), makes its burrows in loose scoria slopes at altitudes above 700 m. In some of these slopes the subsoil was so much burrowed that walking was extremely difficult. This was especially the case on the higher peaks of Prince Edward Island.

The islands offer excellent opportunities for the detailed study of the behaviour of birds as is illustrated by the description of the ethology of the Gentoo Penguin and the Albatrosses by van Zinderen Bakker, Jr. (chapters 15, 16).

The influence of the enormous bird and seal populations on the soil and vegetation of the islands is profound, not only because of the excreta which enrich the wallows and the nest sites but especially because of the soil erosion they cause. The constant trampling by thousands of penguins denudes the soil and the weak peat easily gives way in the rainy climate. Deep gulleys originate in this way and in old penguin rookeries 2 m or more of the soil has washed away to the sea so that the birds live on the boulders and the bed rock. The cycles of geological and biological processes may recommence after the penguins have left the site. It is, however, known from rookeries of the Adelie Penguin on Antarctica that favourable sites may be inhabited for more than a thousand years (Harrington et al., 1958).

CONSERVATION

The subantarctic islands fall outside the region in which the Recommendations and Conventions of the twelve Treaty Powers of SCAR are effective. These measures promote the protection, scientific study and the rational use of the Antarctic biota. It is, therefore, most important that the South African Government at the time of the annexation in 1947/48 decided to declare the islands Marion and Prince Edward nature reserves in the widest sense. The exploitation of the islands had in previous years greatly impoverished the seal and penguin populations. The protection has given nature the opportunity to regenerate the wounds inflicted in the past and the islands are now truly undisturbed paradises. Contact with man has certainly caused some small changes but these are negligible compared with what has happened to the biota of other oceanic islands. Prince Edward Island, which has been more isolated, is the more natural of the two islands as can be concluded from the following:–

The only alien species of vascular plants which occurs on Prince Edward Island is *Poa annua* while the following 13 species have been introduced on Marion Island: *Alopecurus australis, Holcus lanatus, Avena satira, Festuca rubra, Poa annua, P. pratensis, Agropyron repens, Rumex acetostella, Stellaria media, Cerastium holosteoides, Sagina apetala, Plantago lanceolata* and *Hypochoeris radicata* (Huntley, chapter 8).

Intruders such as *Poa annua* can spread rapidly over wide areas as the competitive pressure is not strong in the many niches that are hardly occupied. The vegetation, which is still young and in a state of disharmony, is very vulnerable and should be protected against foreign "weeds". Several alien species have certainly been introduced by sealers, but, more freely in recent times, with the sheep and chickens and their food which are transported yearly to the island Marion. It will therefore be a great step forward if in the near future the plan can be implemented to bring carcasses in deep freeze to Marion, instead of live sheep, as food for the meteorological team.

A little greenhouse which was erected many years ago will be demolished so that direct importation of seeds and soil will be stopped. In the past a few attempts have been made to plant pines and willows round the Meteorological Station but the rigorous climate, fortunately prevented their establishment. The authorities are very concerned about preserving the islands in their present state and preventing any exploitation or interference by man. The equilibrium in the ecosystems is therefore not disturbed and is practically natural. However, the mice which abound, especially on Marion Island, form a small exception, but they seem to do little damage to plant- or animal life. The cats which were introduced to eradicate the mice, are, however, harmful to the birds, especially in the breeding season. It seems to be very difficult, if not impossible, to exterminate these marauders in a terrain which offers so many hiding places.

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