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SUBANTARCTIC ENTOMOLOGY AND BIOGEOGRAPHY[1]

By J. Linsley Gressitt[2]

CONTENTS

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2. Bishop Museum, P.O. Box 6037, Honolulu, Hawaii 96818.

Abstract: By strict climatic definition, only South Georgia, Marion—Prince Edward, the Crozet Is., Kerguelen, Heard and Macquarie, and their associated islets, are subantarctic. Each of these island groups has a very limited fauna, much smaller than that of Campbell I., which has well over 300 species of land arthropods. Each of the subantarctic islands has a somewhat distinctive fauna, although the four islands in the southern Indian Ocean have a number of elements in common, and the Heard fauna is essentially a depauperized Kerguelen fauna. The Crozet Is. have several African elements not found on the other islands. South Georgia has some southern South American groups not represented on the rest, and Macquarie has a few New Zealand elements lacking on the others. The subantarctic fauna appears to consist partly of pre-Pleistocene relicts and partly of post-Pleistocene waifs.

THE ENVIRONMENT

Significance of Biota on Subantarctic Islands

There is much that can be learned from studies of subantarctic islands. These islands can teach us fundamentals of evolution on small islands. As dating is better perfected they may teach us about the rate of evolution. With the restrictions of the hostile environment, the biota are extremely limited and thus ecosystems and food webs are remarkably simple. Because of isolation and adverse climate, some islands have been seldom visited and relatively little disturbed. Thus, among the small islands of the world, some of these in the subantarctic are the best preserved as regards the biota and natural environment (Holdgate & Wace 1961). Nevertheless, because of the severe environment and the resultant delicate balance of life, the islands are vulnerable, and disturbances in the ecosystem have caused serious changes.

Setting

The true subantarctic islands, as defined below, are widely scattered around the Antarctic continent, between 46° and 55° south latitude, in the neighborhood of the Antarctic Convergence where cold Antarctic waters sink below temperate waters (Fig. 11). They occur in three widely separated areas, near South America and the Antarctic Peninsula (South Georgia), in the southern Indian Ocean (Marion-Prince Edward, Crozet Is., Kerguelen, Heard), and south of New Zealand and Tasmania (Macquarie). South Georgia and Macquarie may be parts of the former connection between South America and New Zealand, through the Trans-Antarctic Mts., and have been said to be continental (Jeannel 1940a: 15), while the southern Indian Ocean islands have been termed oceanic. Actually, Macquarie is entirely volcanic and marine sedimentary, so it is more strictly an oceanic island, particularly in the biological sense, since it has been completely submerged at one stage, and has also probably been entirely covered by ice in the Pleistocene (Mawson 1943). Kerguelen, on the other hand, is relatively old, having fossil deposits. This and others like the Crozets and South Georgia, may be fragments left behind in the process of continental drift.

As this chapter discusses zoogeography in general for the true subantarctic islands, and as South Georgia and Heard I. are described in a general way in the first two chapters, some brief descriptions of geology, geography and other aspects are presented for the other islands below.

Definition of Subantarctic Islands

In the past, different numbers of island groups have been classified as subantarctic. In the broadest interpretations the classification has included the southern portion of South America as far north as Osorno (just north of Chiloe I., Chile), the Falkland Is., Tristan da Cunha, Gough, New Amsterdam, St. Paul, Aucklands, Campbell, Snares, Bounty, Antipodes, and islands to their south. In a recent coverage (Arnaud et. al. 1967), all of these except the Snares Is. were included. In some more restricted treatments, based largely on climatic consideration (Holdgate 1964, Wace 1965, Greene & Greene 1963), only South Georgia, Marion (& Prince Edward), Crozet, Kerguelen, Heard, and Macquarie are classified as subantarctic. The South Shetlands, South Orkneys, South Sandwich, Bouvet, Balleny and Peter Ist I. are considered as antarctic in this classification. This arrangement is fairly closely associated with the Antarctic Convergence, which varies greatly in latitude. Thus, the subantarctic islands in the restricted sense include only those islands within about 15 degrees of latitude of the Antarctic Convergence. The convergence extends farther north in the Indian Ocean, and thus the Crozet Islands may be included as subantarctic, even though they are much farther north than Campbell I., Auckland Is., Snares, Antipodes, Bounty, Falklands and

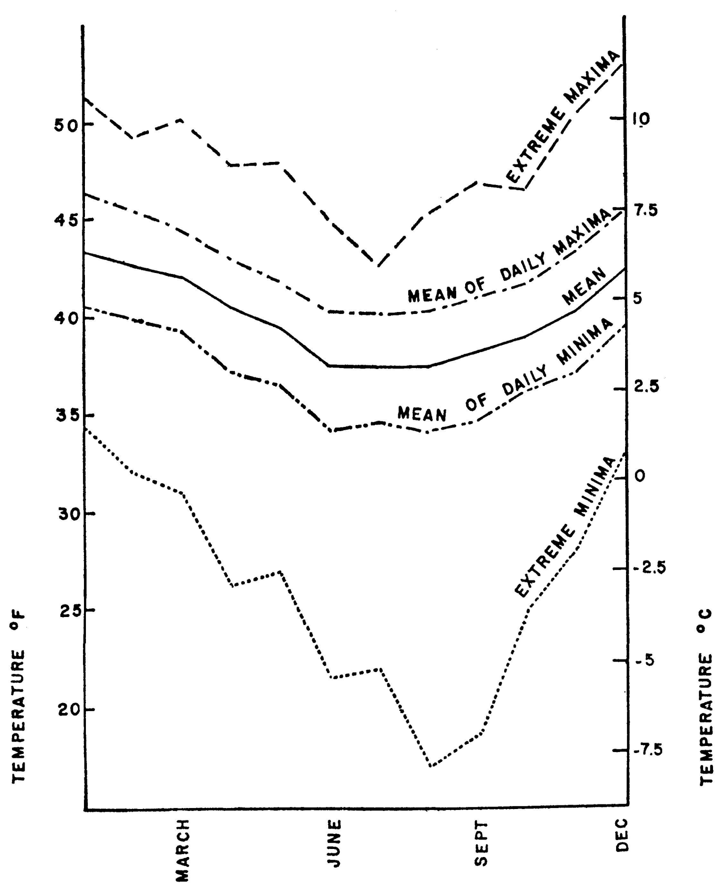

Fig. 1. Graph of temperature means for the annual cycle on Macquarie Island.

the southern tips of New Zealand and South America. All of these latter are then cool temperate but not subantarctic.

In the following discussions, special emphasis will be devoted to zoogeographical relationships of the subantarctic islands in the strict sense: South Georgia, Marion, Crozet, Kerguelen, Heard and Macquarie, although certain others may be cited for purposes of comparison.

Climatic Comparisons

Holdgate (1964: 182) presented a classification of southern areas based on range of mean monthly temperatures. This gives the following approximate arrangement, although Holdgate did not include the Crozet Is., which overlap somewhat with the temperate. All the subantarctic islands (except possibly the Crozets) are colder than the range of mean monthly temperatures permitting the existence of trees (some months above 8.5 °C mean), and no trees occur, even in the Crozets.

The subantarctic contrasts strongly with the arctic in that the former has a very limited range in annual temperature cycle, so that winter is not very greatly different from summer. Thus winters are warmer and summers cooler, in general, than in the arctic.

Table 1. Climatic classification of far southern areas.

Grouping	Area	Range of mean monthly temperatures (°C) Min.	Max.	Min.	Max.
Cool Temperate	Tristan da Cunha	11	18		
	Gough I.	9	16		
	Auckland Is.	5	12	1	18
	Campbell I.	4	9		
	Falkland Is.	2	9		
	Ushuaia, Tierra del Fuego	1	9		
Subantarctic	Crozet Is.	3	8+		
	Marion I.	3	7.9		
	Macquarie	3	7	−3	8+
	Kerguelen	2	7.8		
	South Georgia (Grytviken)	−3	+6		
	Heard I.	−2	+4		
Maritime Antarctic	Admiralty Bay, Ant. Pen.	−10	+1.5		
	Deception I., S. Shetlands	−10	+1.5	−12	+1.5
	Signy I., S. Orkney Is.	−12	+1		
	Argentine Is., Ant. Pen. (also S. Sandwich, Bouvet)	−12	0		
Continental Antarctic (fringe)	Cape Adare, N. Victoria	−26	0		
	Cape Evans, Ross I.	−26	−3	−40	0
	Little America	−40	−6		

Island Groups

South Georgia and Heard I. are described in some detail in the first two chapters of this volume. Following are some brief notes on the other islands discussed in this article—Marion, Crozet Is., Kerguelen and Macquarie—for comparative purposes.

Marion Island

Marion is the major island of a group of two islands often called the Prince Edward Is. The smaller island, Prince Edward, had not been sampled for insects until recently, and is omitted from the faunal discussion. It is separated from Marion by several times its own diameter. Marion is only about 25 by 15 km in size and is located just north of 47° S. Lat. and just west of 38° E. Long. It is thus barely south of the Crozet Is. and 725 km to the west. It is about 1280 m in altitude and is somewhat oblong in shape. The summit is a volcanic cone, and there are a number of cinder cones on the slopes. Marion and Prince Edward are twin peaks of a basaltic volcano rising from the Atlantic-Indian Ocean Ridge near its junction with the subsidiary Crozet Ridge. Alternating explosive and effusive eruptions took place from numerous vents. Glaciation and tectonic movements

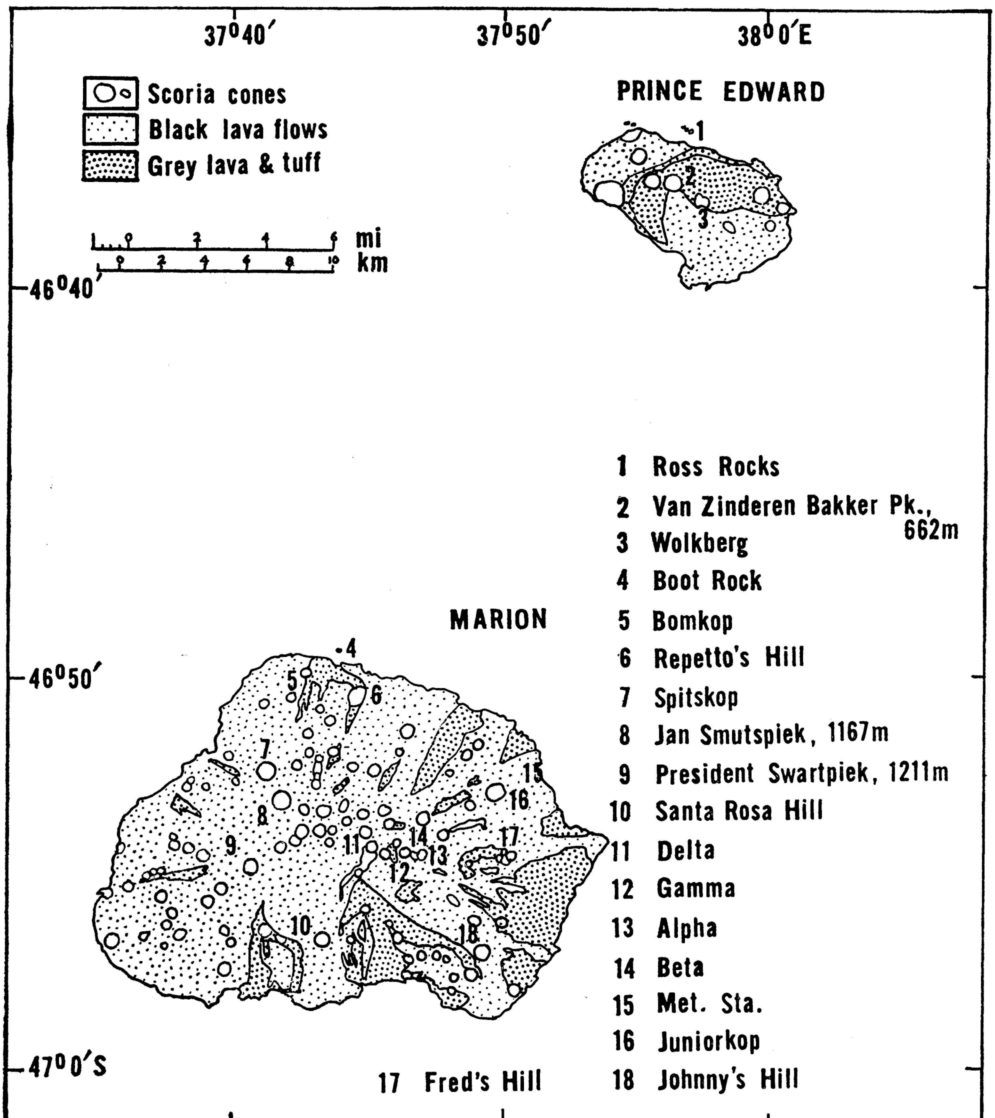

Fig. 2. Map of Marion I. and Prince Edward I.

intervened between older and younger volcanic phases. (Verwoerd 1967).

Mean annual temperature is 4.4°C; warmest month mean, 7.9°C. Rainfall is 255 cm/year. There is a very limited area of permanent ice. (Huntley 1967).

Marion may have lost most of its vegetation in the Pleistocene, and volcanic activity may have exterminated plants more recently (Zinderen Bakker, Sr 1967a). Prevalent plants on Marion are the Kerguelen cabbage (*Pringlea antiscorbutica*), *Azorella selago*, *Colobanthus kerguelensis*, *Tillaea moschata*, *Cotula plumosa*, *Poa cookii*, *Agrostis magellanicum*, *Acaena adscendens*, *Blechnum penna-marina*, *Uncinia dikei*, *Callitriche antarctica*, *Montia fontana*, *Ranunculus biternatus*, *Lycopodium saururus* and various bryophytes. There are about 8 introduced plants, including *Poa annua* and *Agropyron repens*. (Huntley 1967).

About 16,000 years ago (peat datings) Marion had a flora of *Azorella* near the coast on the partly glaciated island (last maximum glaciation). Later this was replaced by the lowland *Acaena* vegetation, followed by a grass-moss swampy vegetation. (Schalke & Zinderen Bakker, Sr. 1967).

Marion has 25 species of breeding birds and 10 non-breeding. They are all marine feeders or scavengers, and there are no passerine birds. The species are the same as on most other subantarctic isles. (Zinderen Bakker, Jr. 1967).

Crozet Islands

The Crozet Archipelago is the northernmost of the true subantarctic groups, being situated from just north to a little south of 46° S. Lat., in the area of 50–52° E. Long. Although they are distinctly farther north than Campbell I. and the Auckland Is., they have a more severe climate, being affected, like Marion, by the frigid and stormy Weddell Sea south of South Georgia.

The Crozets consist of a western and an eastern group, the former constituted by Ile aux Cochons, with a small group of islets, the Apostles, to the north, and another, the Penguins, to the south. The eastern group consists of Ile de la Possession and to its east Ile de l'Est. All the early records of insects from the Crozets related to Possession. Ile de l'Est has still not been sampled for insects, and Ile aux Cochons was first sampled in 1963–64 by Ph. Dreux (1965a,b; 1966a,b).

Ile aux Cochons is nearly round, about 9 km in diameter, and perhaps nearly 800 m in altitude. The island is entirely volcanic, and has numerous volcanic cones. There are no streams, and fresh water emerges in most cases as springs near the shores. The substrate contains much more ash and less soil than on Possession I., and Cochons is thus a younger island. Ile aux Cochons (Hog I.) got its name from some American sealers having released pigs there. After the pigs became rather wild they were exterminated by a later group.

Ile de la Possession is slightly larger than Ile aux Cochons and somewhat higher, with a peak of 934 meters. It is an older island than Ile aux Cochons, with numerous basaltic dikes and a few craters instead of numerous cones. There are a number of streams and swampy areas.

Ile de l'Est is slightly smaller than Possession, and may be the highest of the 3 main islands. It has not been explored.

The flora of these islands is similar to that of Marion I. Cochons and Possession are fairly similar to each other in vegetation and bird life, but Cochons has been less disturbed, even though it has rabbits, cats and mice on it (Dreux 1965b, 1966a, Dreux & Milon 1967). However, there apparently are differences in the insect fauna between these islands. The differences involve both relative population levels of the same species, and populations which are related but slightly different (Dreux 1965a,b, 1966a,b; Hoffmann 1966; Dreux & Voisin 1969).

Iles Kerguelen

Kerguelen and its 300 associated islets form by far the largest group of the southern Indian Ocean islands, and the area is nearly as great as that of South Georgia. Kerguelen is more southern

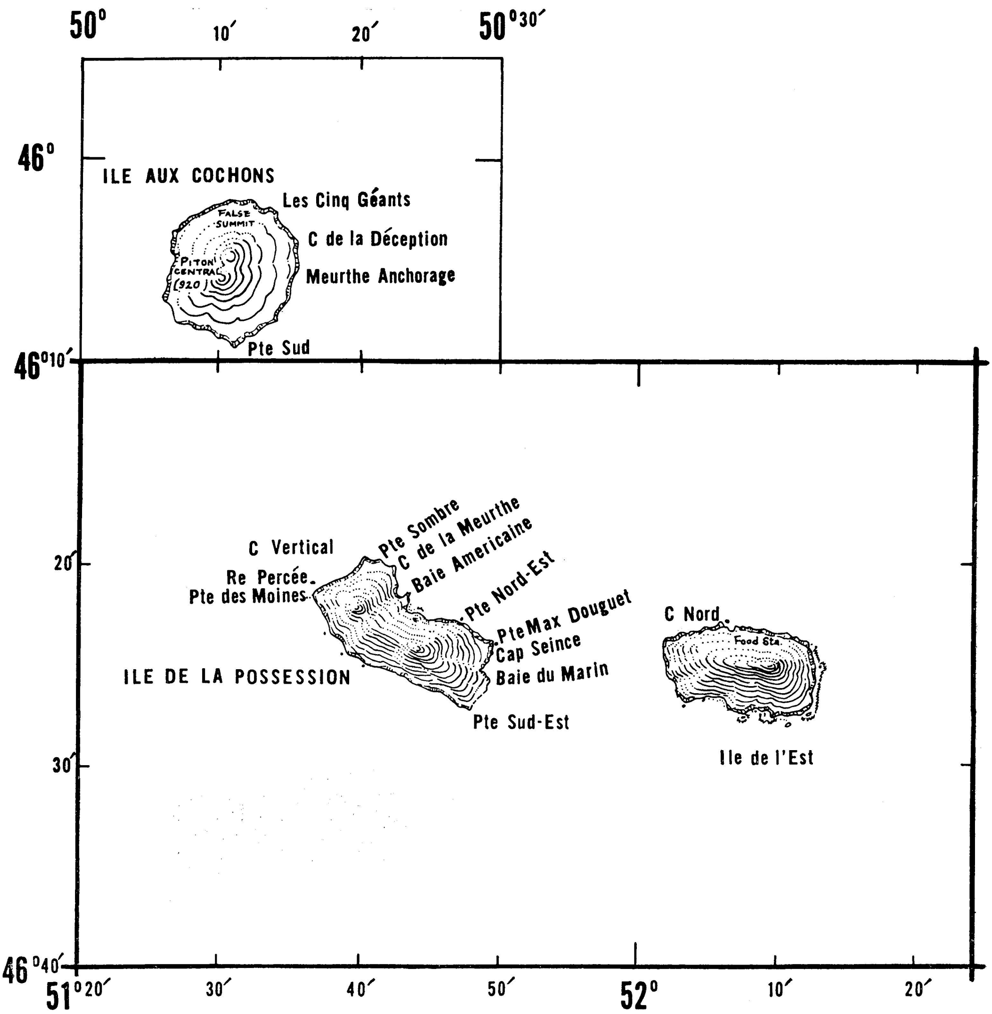

Fig. 3. Map of Crozet Is. Ile aux Cochons is displaced eastward; same scale. From H.O. 3866 (H), 1950. Apparently Possession is too narrow (see Dreux 1966a: Fig. 3).

than Marion and the Crozets, being largely south of 49° S. Lat. It is located at 69° E. Long. It is also of greater altitude, being nearly 2000 m high, and has a number of glaciers, principally in the central portion where they form an ice-cap, with some glaciers descending to the sea on both west and east sides. The NE and SE sides are cut by deep fjords, partly fringed by islets. There are many lakes and ponds, and some deep mud holes.

Kerguelen differs from Marion-Prince Edward and the Crozets in being an older island. It is principally volcanic in origin, with basaltic lava flows and dikes, but there are extensive sedimentary deposits, including abundant fossil trees, with coal and red earth. Glaciation has been extensive. The land area was probably once much greater. The fossil deposits include *Araucaria* and pollen of *Nothofagus*. There is said to be an active volcano in the SW, as well as some hot springs.

Fig. 4. Map of Kerguelen. Blank areas are largely ice covered.

Kerguelen's vegetation is similar to those of Marion and the Crozets, being dominated by *Pringlea antiscorbutica* in more protected environments, and by *Acaena* on more exposed slopes. *Azorella* and mosses are other dominant plants. The tussock grass *Poa cookii* was once far more extensive than at present. The floral affinities have been said to be more with South America than with Africa. (Greene & Greene 1963). Rabbits have greatly reduced the extent of *Pringlea* and *Poa*. (Holdgate & Wace 1961).

The birds are mostly the same as on the other subantarctic isles. As on South Georgia, there is an endemic teal (shared with the Crozets).

Macquarie Island

Macquarie is the southernmost subantarctic island in the sense that its northern tip is more southerly than the middle of South Georgia and its southern tip almost as far south as the southern tip of South Georgia. It is, however, a much smaller island, and has a much less extreme climate, lacking any permanent ice. Macquarie is located between 54° 28′ and 54° 46′ S. Lat. at 148° 50′ E. Long. It is long and narrow, N-S, and is 118 sq. km. (46 sq. miles) in area. Highest altitude

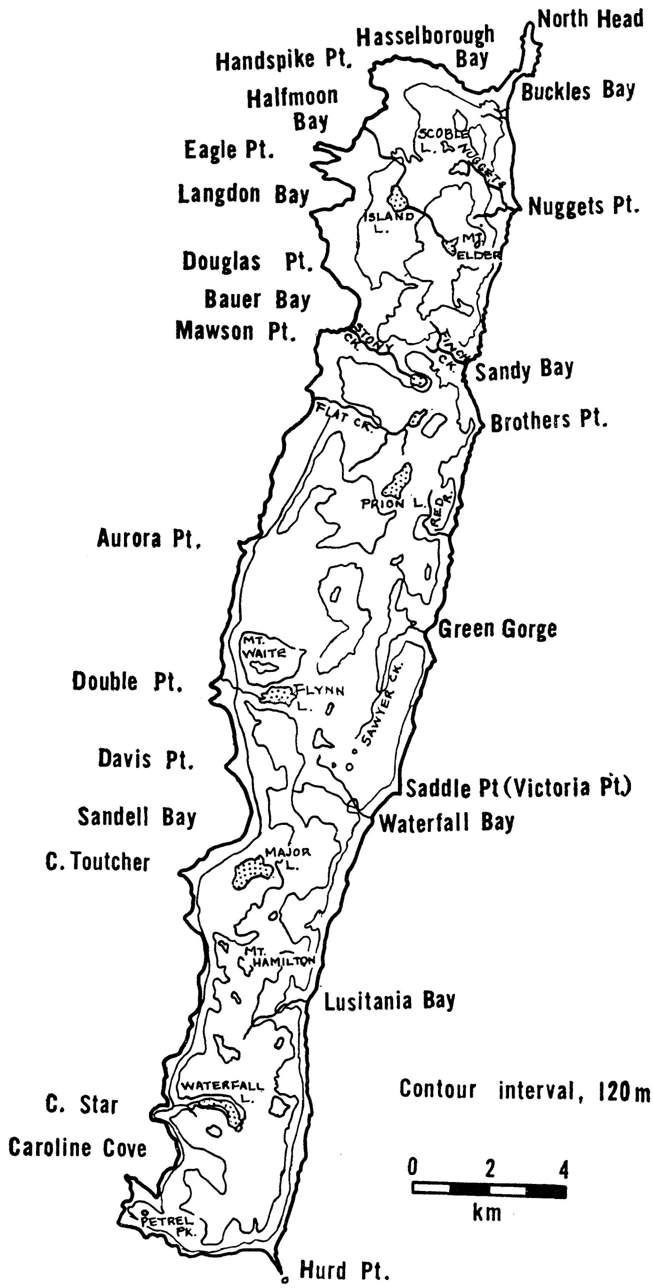

Fig. 5. Map of Macquarie I. North Head is 158°59′ E and 54°28′ S.

is only 433 meters (1,423 ft). Much of the area consists of a plateau, with hills, small lakes, tarns and streams.

Macquarie was earlier considered to be a fragment of a former larger landmass centered to the west, then eroded and partly sunken, and extensively glaciated (Mawson 1943). Recently (Varne et al. 1969) a new theory has been proposed—that Macquarie is a piece of Pliocene oceanic crust that is still being elevated. It is characterized by pillow lava, harzburgite and dikes, and may have developed by injection along the mid-oceanic ridge-axis.

Macquarie has a somewhat richer flora than do the other subantarctic isles. There are 35 species of vascular plants, dominated by *Pleurophyllum*, *Stilbocarpa*, *Acaena*, *Azorella*, *Colobanthus*, *Poa*, *Deschampsia*, *Juncus*, *Scirpus* and *Polystichum*. Mosses are abundant. (Taylor 1955, Clifford 1953).

As on the other subantarctic isles, the breeding of elephant seals and other seals is a dominant feature of the fringes, with a reducing effect on the vegetation and probably a favoring of Diptera, Collembola and some other arthropods. The usual sea birds and a duck, are present, but *Chionis* is absent. Extinct birds include a rail, a parakeet and some petrels. There are a few introduced birds, including the weka (a large rail, *Gallirallus*), the redpoll and common starling. Introduced mammals include rabbit, cat, rat and mouse. The rabbits are very abundant, and have greatly damaged and modified the vegetation, with some probable extinction of certain plants. Sheep were introduced, but were recently confined to a small number at the northern tip, north of the isthmus, and these were exterminated in 1962.

Comparisons

In comparing the ecological opportunity and likelihood of establishment upon the various subantarctic islands, a number of factors must be considered. Some of these factors tend to counterbalance others in terms of explaining the varying or similar numbers of plants, birds or insects on each island group. For instance, the larger areas of South Georgia and Kerguelen are partly offset by the fact that they are to a considerable extent ice-covered. Heard, on the other hand, is much smaller, has the most severe climate, and is almost entirely ice-covered, readily explaining its very limited flora and fauna other than sea birds. Macquarie, though small in area, has both a relatively mild climate and is relatively close to other islands and a continent. It supports the largest flora and one of the largest insect faunas. Comparing Marion, the Crozets and Kerguelen, Kerguelen is oldest but colder, while Marion is nearer Africa and South Georgia but has a young surface for glaciological and vulcanological reasons. The Crozets have the mildest climate and probably had some kind of stepping-stone connection with Africa, but are rather small and have experienced recent vulcanism. In general, therefore, glaciation and vulcanism have played a prominent role, and the biological youth of most of the islands seems apparent, from the terrestrial standpoint.

Flora and Fauna

The numbers of native plants for the various islands are shown in table 2. Jeannel (1965) considered that *Azorella* was an introduced plant on these islands, but Greene & Greene (1963) considered it native. Table 3 lists most of the birds breeding on these islands. There are only a few kinds of land snails. The few other animals are mostly microscopic.

Effect of Man and Introduced Biota

The immediate effects of Man's activites in the islands have been severe. In particular the near extermination of fur seals and to a lesser extent of elephant seals, penguins and other birds in the last century have had a long-lasting effect. The establishment of whaling and sealing camps

Table 2. Numbers of species of native higher plants on subantarctic islands
(Condensed from Greene & Greene 1963, Huntley 1967, Dreux 1964)

		S. Georgia	Marion	Crozet	Kerguelen	Heard	Macquarie
Pteridophyta							
Lycopodiaceae: *Lycopodium* (2 spp.)		1	2	2	2		1
Ophioglossaceae: *Ophioglossum* (1)		1					
Hymenophyllaceae: *Hymenophyllum* (2)			1	1	1		
Polypodiaceae: *Blechnum* (1)		1	1	1	1		1
Cystopteris (1)		1			1		
Asplenium (1)				1			
Polystichum (4)		1	2	1			1
Grammitis (2)		1	1	1	1		1
Polypodium (2)		1	1	1			
Elaphoglossum (1)			1*				
Spermatophyta-Angiospermae							
Rannunculaceae: *Ranunculus* (3)		1	1	2	3(1*)		1
Cruciferae: *Pringlea* (1)			1	1	1	1	
Cardamine (1)							1
Caryophyllaceae: *Stellaria* (1)				1			1
Colobanthus (4)		2	1	1	1	1	1
Lyallia (1)					1*		
Cerastium				1			
Sagena				1			
Portulacaceae: *Montia* (2)		1	1	1	1		1
Rosaceae: *Acaena* (4)		2(1*)	1	1	1	1	2
Crassulaceae: *Tillaea* (1)			1	1	1		1
Onagraceae: *Epilobium* (2)							2
Haloragaceae: *Myriophyllum* (1)							1
Callitrichaceae: *Callitriche* (1)		1	1	1	1	1	1
Araliaceae: *Stilbocarpa* (1)							1
Hydrocotylaceae: *Hydrocotyle* (1)							1
Umbelliferae: *Azorella* (1)			1	1	1	1	1
Polygonaceae: *Rumex* (1)				1			
Scrophulariaceae: *Limesella* (1)				1	1		
Rubiaceae: *Coprosma* (1)					1		1
Galium (1)		1		1	1		
Compositae: *Pleurophyllum* (1)							1
Cotula (1)			1	1	1		1
Juncaceae: *Juncus*		2	1	1	1		1
Rostkovia (1)		1					
Luzula (1)							1
Cyperaceae: *Scirpus* (1)							1
Uncinia (4)		1*	1*	1	1		1
Carex (1)							1
Gramineae: *Agrostis* (1)			1	1	1		1
Deschampsia (3)		1		1	1	1	2(1*)
Puccinellia (1)							1*
Poa (5)		1	1	3	2	2	2(1*)
Festuca (1)		1			1		1
Phleum (1)		1					
Alopecurus (1)		1					
Pteridophyta	17	7	9	8	7	0	4
Spermatophyta	54	17	13	23	22	8	31
Totals	71	24	22	31	29	8	35

*Endemic species.

Table 3. List of subantarctic birds (excluding infrequent visitors)

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other
Sphenisciformes: Spheniscidae							
Aptenodytes patagonica Miller	×	×	×	×	×	×	TdF,F
Pygoscelis papua (Forster)	×	×	×	×	×	×	TdF,F
P. antarctica (Forster)	×				×		A
Eudyptes c. chrysolophus Brandt	×	×	×	×	×		A,F
E. c. schlegeli Finsch						×	C,etc
E. crestatus Miller		×	×	×	×	×	C,TdF, F
Procellariiformes: Diomedeidae							
Diomedea exulans L.	×	×	×	×		×	C,Auc, etc
D. melanophris Temminck	×		×	×	×	×	C,F,NZ
D. chrysostoma Forster	×		×			×	C,
Phoebetria fusca (Hilsenberg)		×					
P. palpebrata (Forster)	×	×	×	×	×	×	C,Auc,NZ
Procellariidae							
Macronectes giganteus (Gmelin)	×	×	×	×	×	×	C,A,NZ,Auc,F
Daption capensis (L.)	×	×	×	×	×	×	C,Afr, etc
Procellaria aequinoctialis L.	×	×	×	×	×		F
P. cinerea Gmelin				×		*	NZ
Pagodroma nivea (Forster)	×				×		A
Pachyptila desolata (Gmelin)	×			×	×	×	A
P. turtur Kuhl		×					
P. salvini Mathews		×	?				
P. belcheri (Mathews)	×			×			F
P. crassirostris (Math.)					×		
Adamastor cinereus Gmelin		×					
Pterodroma macroptera (A.Sm.)		×	×	×			
P. mollis (Gould)		×					
P. brevirostris (Lesson)		×		×			
P. lessoni (Garnot)			×	×		×	NZ
Halobaena caerulea (Gmelin)	×	×	×	×	×	*?	NZ
Puffinus griseus (Gmelin)						×	NZ
Fulmarus glacialoides Smith	×						A
Hydrobatidae							
Oceanites oceanicus (Kuhl)	×			×	×		A,F
Fregetta tropica (Gould)	×				×		
F. melanogaster (Gould)			?	×			
Garrodia nereis (Gould)	×			×			F
Pelecanoididae							
Pelecanoides urinatrix exsul Salvin	×	×	×	×	×		
P. georgicus Murphy & Harper	×	×	?	×	×	*	
Pelecaniformes: Phalacrocoracidae							
Phalacrocorax atriceps georgianus Lönnberg	×						
P. a. nivalis Falla					×		
P. albiventer Lesson		×					
P. a. melanogenis (Blyth)			×				
P. a. purpurascens						×	
P. verrucosus (Cabanis)				×			
Lariformes: Stercorariidae							
Catharacta skua loennbergi (Mathews)	×	×	×	×	×	×	A,Auc,NZ

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other
Laridae							
Larus dominicanus Lichtenstein	×	×	×	×	×	×	C,Auc,NZ,F
Sternidae							
Sterna v. vittata Gmelin			×	×	×	×	A
S. v. georgiae Reichenow	×						
S. macrura Naumann					×		
S. virgata Cabanis			×	×			
Ciconiiformes: Ardeidae							
Casmarodius albus (L.)	×						TdF
Charadriiformes: Chionididae							
Chionis alba (Gmelin)	×						
C. crozettensis Sharpe			×				
C. minor Hartlaub		×		×			
C. minor nasicornis (Reichenow)					×		
Calidris fuscicollis (Vieillot)	×						
Anseriformes: Anatidae							
Anas georgicus Gmelin	×						
A. etaoni (Sharpe)			×	×			
A. superciliosa Gmelin						×	NZ
Psittaciformes: Psittacidae							
Cyanorhamphus novaezelandiae erythrotis Rsch.						*	Antipodes
Passeriformes: Anthidae							
Anthus antarcticus Cabanis	×						
Ralliformes: Rallidae							
Rallus philippensis L.						*	

* = extinct. For explanation of symbols see end of Table 6.

on the islands left permanent scars, accentuated by the slowness of the environment to recover. Debris is slow to disintegrate because of low bacterial and other decomposition rates. The long period of the existence of whaling stations in South Georgia and more recently the establishment of weather or general research stations on the other islands has caused great problems of pollution of the environment. Sealing had a great effect on Macquarie (Cumpston 1968). The animals and plants introduced by Man have caused further drastic effects. The following data are largely from Holgate & Wace (1961).

South Georgia. Rabbits (1872) failed to establish, except on Jason I. (present in 1930). Sheep, and horses (1905) were introduced but did not persist. Reindeer established and multiplied (1911-present). They have been released in two areas in the NE and are limited by glacier barriers. Rats arrived about 1800 and abound near the coast, killing smaller petrels. Fur seal, wandering albatross and teal have been greatly reduced.

Marion—Prince Edward. Marion is less disturbed than some of the other islands. It has been occupied for a weather station since 1947, but Prince Edward is almost untouched, with perhaps no introduced animals or plants. On Marion a few herbs and insects have been introduced. Sheep (1947) failed to establish. Chickens have been kept in captivity. Mice were accidentally introduced, and cats were imported to control them. The cats, though not numerous, keep the mice in check to some extent. Some alien plants, with soil, were brought in for experimental cultivation, so some soil animals may have established.

Crozet Is. Pigs were established on Ile aux Cochons before 1820 and were exterminated a few

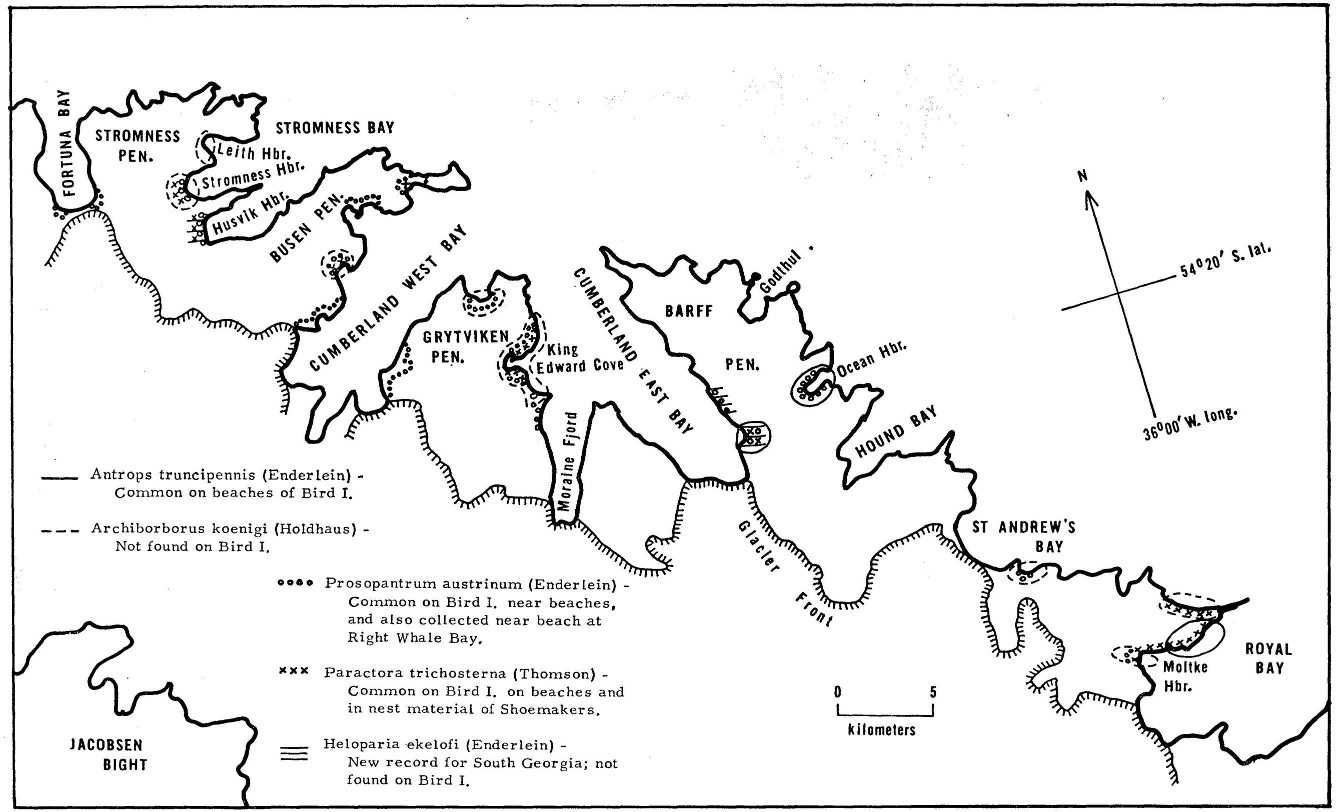

Fig. 6. North coast of part of eastern South Georgia, with ice-free peninsulas beyond the glacier fronts (including sites of main whaling stations), showing distribution of certain Diptera. The *Heloparia* might have been recently introduced.

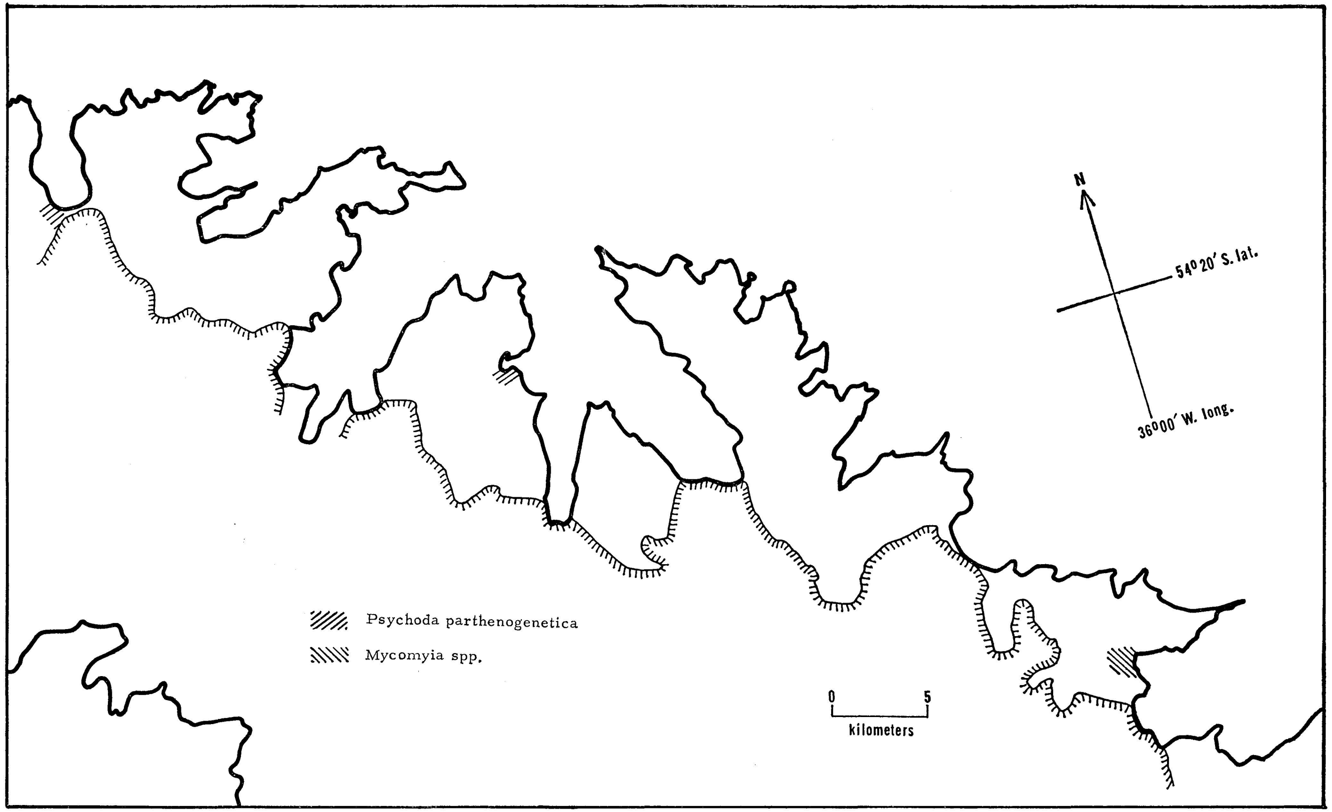

Fig. 7. North coast of part of eastern South Georgia, showing distribution of additional Diptera. (See Fig. 6 for labelling of localities).

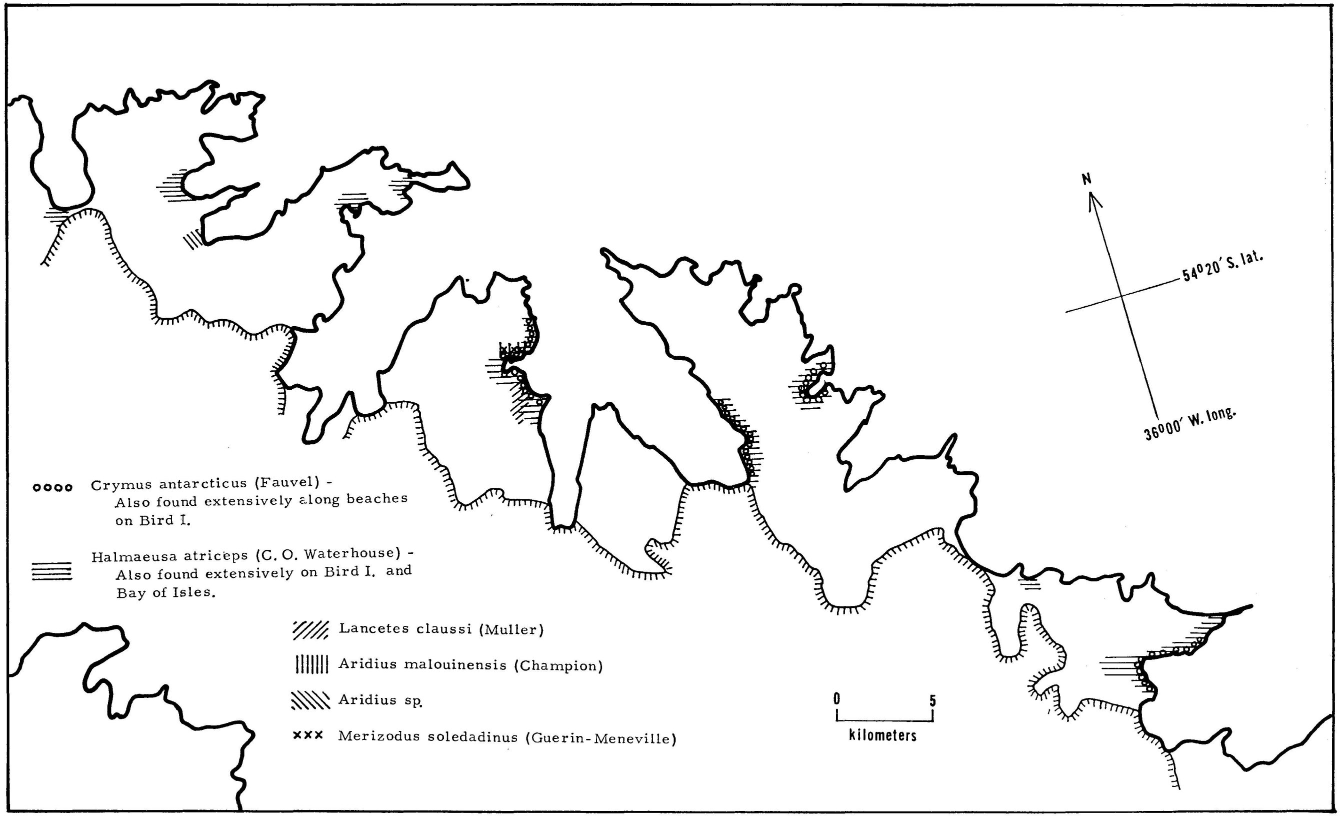

Fig. 8. North coast of part of eastern South Georgia, showing distribution of certain Coleoptera: Staphylinidae (*Crymus*, *Halmaeusa*), Dytiscidae (*Lancetes*), Lathridiidae (*Aridius*) and Carabidae (*Merizodus*). (See Fig. 6 for identification of localities).

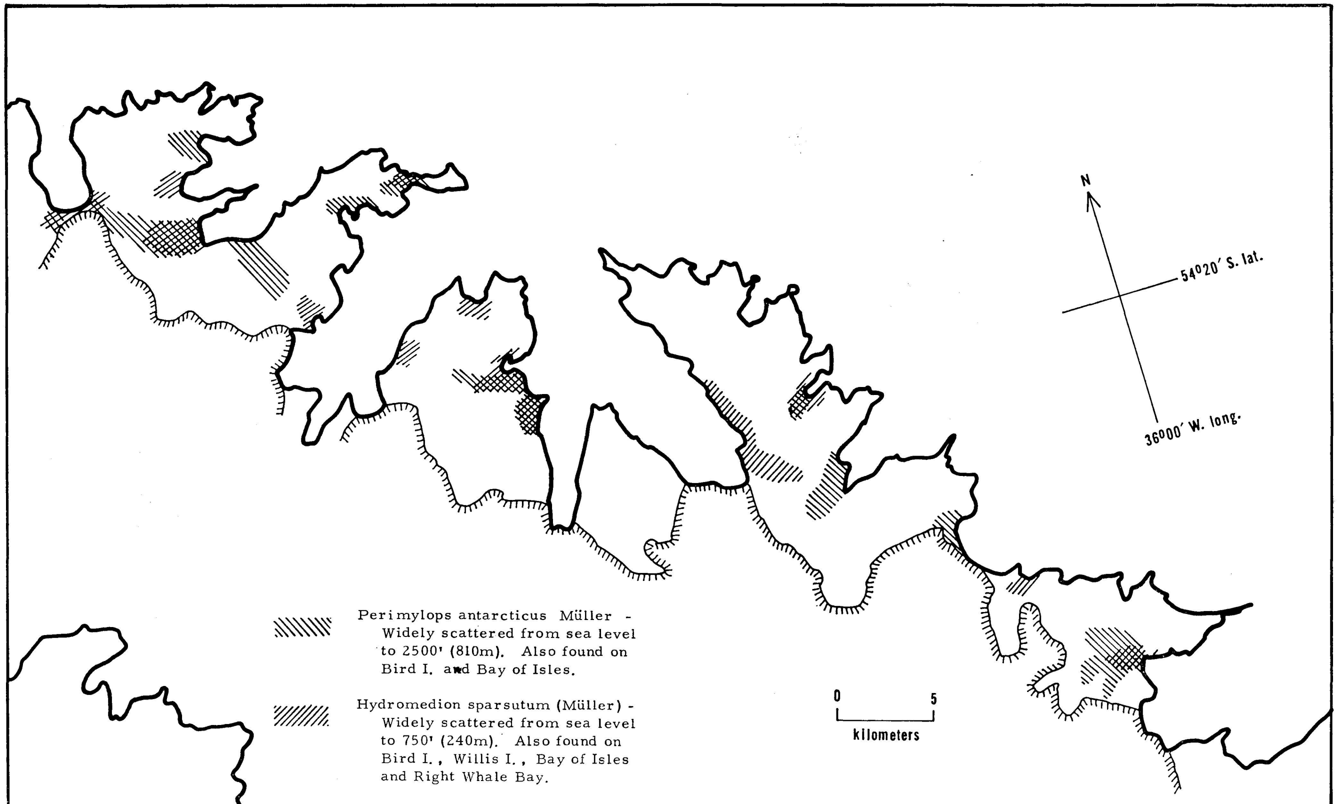

Fig. 9. North coast of part of eastern South Georgia, showing distribution of the 2 species of Perimylopidae. (See Fig. 6 for identification of localities).

decades later. Rabbits were abundant in 1873 and persisted to at least 1938, but were not seen in 1959. Goats were reported in 1875 but were absent later.

Kerguelen. Rabbits were established in 1874 and have done great damage. Sheep were imported in 1908 (Ile Longue), 1911 (Pen. Bouquet de la Grye), and 1952 (Ile Mussel). Sheep-raising was actively pursued to 1914 and between 1921 and 1932. Mules were present from 1949 to 1953. Shetland ponies, pigs and cattle have been kept around the main station. Reindeer were imported in 1955 and 1956 and may be established. Wild cats (1874), and dogs (1902?), have been reported in the past. Rats and mice have long been present.

Heard. No introduced animals or plants are known to be established.

Macquarie. Sealers established rabbits in 1880 and damage done by them has steadily increased. A small flock of sheep was present from 1947 to 1962, primarily on Wireless Hill, which lacks rabbits. Goats were established in 1947 but exterminated not long after. Some horses were present up to 1923. Dogs were present in 1821, but failed to perpetuate themselves. Cats were established before 1821 and are still abundant. They do not noticeably control the rabbits although they have reduced petrel populations. Rats are also numerous. The weka, a large rail (*Gallirallus*) was introduced from New Zealand and feeds on insects and petrel eggs and young.

THE ROLE OF TERRESTRIAL ARTHROPODS ON SUBANTARCTIC ISLANDS

The terrestrial arthropods play a prominent role in the simple ecosystems on these extreme southern islands, even though they are inconspicuous. The situation is analogous to that on small isolated islands in general, and in Antarctica, where many land animals common on continents are totally lacking.

Arthropod Habitats

The insects and other arthropods of the subantarctic islands are not very conspicuous in their occurrence. Most of the microhabitats are fairly well hidden or protected. Only a few species in South Georgia and Macquarie are flying insects, and none of those on Heard are capable of flight.

Most of the species occur hidden, except in the best of weather, among or beneath the various species of plants, as well as under rocks, bones, corpses, or in nests. Some species are very spottily distributed, as shown in Fig. 6–9. These represent well-collected areas of South Georgia.

In such environments where there are so few species, not every habitat is occupied. Also, a number of the species have occupied several microhabitats.

As an example, on South Georgia the beetle *Hydromedion sparsutum* was found as follows: Tussock grass (40 larvae; 30 adults); tussock grass debris (42; 33); *Acaena* (11; 9); *Rostkovia* (0; 2); moss (40; 18); Gentoo penguin rookery (5; 13); Wandering albatross nest (49; 5); Sooty albatross nest (0; 1); Black-browed albatross nest (13; 1); Grey-headed albatross nest (1; 0); Dove prion nest (9; 0); Giant petrel nest (3; 0); Shoemaker nest (10; 0); under rocks (45; 52); under rocks and moss (43; 80); under rocks on scree (4; 10); under stones by stream (4; 0); rock crevices nr beach (3; 4); rotting kelp and rocks on beach (11; 8); under bones, boxes, bags (18; 16); on snow (24; 23). The related *Perimylops antarctica* was found in only half as many microhabitats, not in association with nests at all, but occurred up to higher altitudes and in drier environments. The 2 species were not always both found at each locality (see Fig. 9).

In many environments there are few organisms other than arthropods and primitive plants. In other environments the sea bird and seal rookeries provide habitats for a great variety of organisms, and in others a rich herbaceous vegetation provides added microhabitats.

Important groups of animals missing or largely missing on subantarctic isles include terrestrial vertebrates, such as land mammals, land birds, reptiles, amphibians, and many others. Some groups important elsewhere, such as land mollusks, are very poorly represented on subantarctic islands. Thus, insects and their relatives are the predominant land animals on these cold islands, and constitute the main primary consumers of vegetation, as well as including the principal predators, parasites and scavengers. Almost their only non-arthropod competitors in these roles are a few nematodes and some protozoans. There are some tardigrades, copepods, annelids, planarians and rotifers, but these are inhabitants only of the ponds or very wet areas. Free-living mites and Collembola make up a large fraction of the fauna, taxonomically, and also in terms of biomass, at least on the more southern isles.

Rookeries. Although land birds and land mammals are conspicuously lacking, a very important habitat for various arthropods consists of the rookeries of sea birds and to a much lesser degree the rookeries of marine mammals, where trampling is a severe factor detrimental to the arthropods. The insects and their relatives inhabiting the rookeries include the various parasitic groups such as the biting lice on birds and the sucking lice on seals, and the fleas, parasitic mites and ticks associated with the birds or their nests. These make up a considerable fraction of the species. Parasitic flies may be lacking on the true subantarctic islands, though there are a few records from some of the southern cool temperate islands. In addition to the parasites, great numbers of other arthropods inhabit the rookery areas. These include the various scavenger groups and others not usually considered scavengers, but merely present because of greater protection afforded in one way or another by the rookery. Some of these are phytophagous insects. Among the inhabitants of rookeries are many of the species of Diptera and Coleoptera, as well as many of the free-living and saprophytic, carrion-feeding, and phytophagous mites and others. The Collembola also are usually much more abundant in the areas of rookeries, than otherwise.

In comparing subantarctic environments with Arctic and subarctic regions, a very conspicuous difference is the almost complete lack of migratory or resident shore and land birds in the subantarctic. Such predators, as well as grazers such as lemmings, reindeer or caribou, are important in food cycles in the northern regions and quite lacking in the southern islands. Also, various types of soil fauna are much poorer in representation in the subantarctic than in the arctic.

Shores. Another important environment for arthropods is the seashore, including beaches, shingle, rocks, inlets, boulders behind beaches, etc. Some of the species, particularly certain Acarina, Collembola, Coleoptera and Diptera are littoral in various degrees. Some of them pass considerable periods in the inter-tidal zone. Others, such as the kelp flies and staphylinid beetles, breed in accumulations of kelp on the beaches or rocky shores.

Seal carcasses and bird carcasses also provide an important niche for various beetles and flies.

One of the conspicuous environments of the flatter coastal strips is that of seal wallows. These may be in pools, small depressions, stream-beds or between tussocks. Wallows of elephant seals, in particular, are most notable. Depressions of various depths, including the spaces between Poa tussocks, and ponds, are occupied by these huge animals and become heavily polluted. Usually the pollution from feces and urine is too strong to permit insect life, but some Diptera may develop on the fringes of such areas.

Other habitats. Other than the rookeries, littoral and other shore and vertebrate-related microhabitats, the remainder consist mainly of plant environments. Considerable areas of ice-free land are covered with mat or cushion plants. Two dominant types are *Colobanthus* in lowland and shore areas, and *Azorella* away from the coast, as well as mosses and lichens, the latter dominating at higher altitudes. Feldmark (partial ground cover in strips parallel to prevailing winds at upper extremes of vegetation) may consist of lichens, mosses and *Azorella* or other low herbs. Various grasses occur at medium and lower altitudes, forming lush tussock growth in lower and more favorable environments, where rabbits, sheep or other introduced herbivores are scarcer or lacking. The rich tussock growth, together with more luxuriant herbaceous growth, where persisting, harbors most of the purely plant-related insects. Among the more important herbs is *Acaena*, on all isles but dominant on South Georgia. *Pringlea* is on the South Indian Ocean islands; *Pleurophyllum* and others are only on Macquarie. *Ranunculus* is on all but Heard, *Azorella* on all but South Georgia. and *Colobanthus* on all. Sedges and *Juncus* are on most but not on Heard, with *Rostkovia* only on South Georgia. (See Table 2).

Food webs

The food chains are fairly simple, consisting in the main of primary consumers and scavengers with only a few predators or parasites. The remainder of the fauna is associated with vertebrates and their nests with direct and simple relationships. The relationships are indicated simply in Fig. 10. More details are presented in Table 4. The points to be stressed are that predators and parasitoids (those parasitic on arthropods) are few in number of species and also limited in occurrence. Carabids and staphylinids are both absent from some islands, and the carabids are mostly of very limited occurrence on islands where they are present. The parasitoids have only been found on a few occasions. Also very significant is the small number of species which are primary feeders on vascular plants. Lepidoptera are absent from some islands and phytophagous Coleoptera are absent from others. South Georgia has neither. Other feeders on higher plants are lacking. Thus, aside from the obligatory parasites of birds and seals (Mallophaga, Anoplura, Siphonaptera and certain Acarina), the greater part of the arthropod fauna consists of general scavengers, algivores

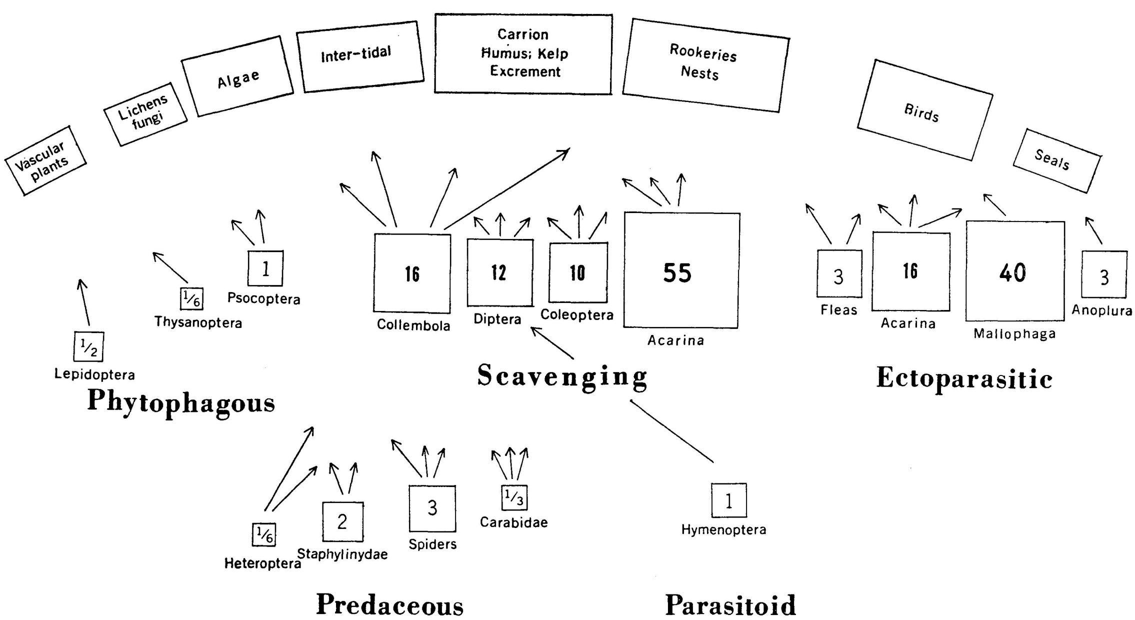

Fig. 10. Diagrammatic food web for an average subantarctic island. Sizes of squares very roughly in proportion to number of species involved. Numbers in squares represent average number of species per isle.

Table 4. Important microhabitats with principal occupant groups.

	Algae	Lichens	Moss	Tussock	Cushion plants	Herbs	Under rocks	Rotting kelp	Herb/Grass litter	Ectoparasites	Ponds, streams	Intertidal	Excrement, animal debris	Birds nests	Carcasses
Araneida (16)				×	×	×	×		×						
Mesostigmata (37+)				×	×	×				×			×	×	×
Metastigmata (2)										×				×	
Prostigmata (28)	×	×	×	×	×	×	×		×				×	×	×
Astigmata (24)				×	×	×				×			×	×	×
Cryptostigmata (35)	×	×	×	×	×	×	×		×			×	×	×	×
Collembola (39)	×	×	(×)	×	×	×	×		×			(×)	×	×	×
Psocoptera (3)				×	(×)	×			×						
Thysanoptera (1)				×		×			(×)						
Mallophaga (105)										×					
Anoplura (5)										×					
Hemiptera															
Homoptera (2)				×		×			×						
Heteroptera (1)			×				×		×						
Lepidoptera															
Tineidae (1)						×									
Yponomeutidae (1)				×											
Pyralidae (1)			×		×										
Coleoptera															
Carabidae (4)				×		×	×		×			×			
Dytiscidae (1)											×				
Staphylinidae (8)				×	×	×	×	×	×			×	×	×	×
Lathridiidae (1)					×										
Curculionidae (26)				×	×	×	×								
Diptera															
Psychodidae (2)						×			×		×		×	×	×
Trichoceridae, Tipulidae (3)				×	?	×					×				
Sciaridae (6)						×								×	
Chironomidae (9)				×		×					×	×	×		
Coelopidae (5)					×			×					×		×
Dolichopodidae (1)					×								×		
Ephydridae (3)															
Helcomyzidae (3)															
Helomyzidae (1)															
Pallopteridae (1)															
Micropezidae (1)															
Carnidae (1)				×		×							×		
Sphaeroceridae (5)															
Siphonaptera (6)										×					
Hymenoptera (3)				×	×	×								×	

(16) Total number of spp.
(×)—In habitat, but rare and/or not necessarily feeding.

and some mites of uncertain, but probably general, food habits.

Limiting Factors

In general, abiotic and intra-specific factors seem to prevail on these isles, and some of the following are of minimal significance.

Predation: Probably one of the reasons populations of arthropods may attain very high densities is the scarcity of predators. Spiders and staphylinid beetles are almost the only predators of insects present. Carabid beetles are absent from Heard and Macquarie and are represented by only a few species on the other islands. Because of the near lack of land birds, there are almost no avian predators of insects. The South Georgian pipit, the introduced weka (rail) on Macquarie, and the teal, on most islands, are perhaps the only exceptions. Centipedes and many other predatory arthropods are lacking.

Parasitism: Parasitoid insects (those parasitizing other insects) are also apparently very few in number, with no more than one or two species of parasitic wasp from a single island. There possibly are no flies which parasitize insects.

Population fluctuation: There is considerable evidence of great fluctuations in populations of arthropods. Local fluctuation among various flies (including Coelopidae) and carrion beetles (Staphylinidae) on Macquarie is partly related to the amount of kelp washed up on beaches and the number of elephant seal carcasses available. These are again partly related to season of year, and different parts of an island's shore-line, as well as the occurrence of specially stormy weather. There is also a relationship to the breeding cycles of the various birds and of the elephant seal, both largely in the warmer season between October and March. What other factors may be involved are not well understood. Dreux & Voisin (1969) indicated great fluctuations in beetle populations on Possession I. (Crozets), and commented on relevance of low populations to rapid evolution. They noted the following:

Amblystogenium pacificum—Generally abundant.

Temnostega antarctica—Abundant in April-May, moderately abundant otherwise.

Staphylinidae—Always abundant.

Pseudeuplectus antarcticus—Generally abundant.

Meropathus randi—Abundant 20-Jan.-15 Feb., 16–30 Aug.; rare otherwise.

Christensenia antarctica (*Neocanonopsis dreuxi*)—Always rare.

Bothrometopus fasciatus—Abundant in 1962; rare in 1966.

Dusmoecetes richtersi—Most abundant weevil in 1966; not so in 1962.

Seasonal cycles: On Macquarie I., of over 100 species, Watson (1967: 85) found only 6 which seemed to demonstrate clear seasonal cycles. This is a reflection of the rather slight seasonal climatic variation. The 6 species follow:

Genus 1 (Cercomegistidae)—Immatures uncertain; adults Oct.-Apr. only (?)

Scoparia mawsoni—Larvae all year; pupae Oct.-Feb.; adults Nov.-Mar.

Erioptera p. macquariensis—Larvae Dec.-Oct.; pupae Oct.-Nov.; adults Nov.-Apr.

Halirytus macquariensis—Larvae all year; pupae all year (?); adults Nov.-Apr.

Ephydrella macquariensis—Larvae Dec.-Oct.; pupae Oct.-Nov.; adults Nov.-Apr.

Schoenophilus pedestris—Larvae all year; pupae (?); adults Oct.-June.

In South Georgia, which has a more rigorous climate, more seasonality is evident. Clagg collected for 15 months, nearly 12 months of which he spent on Bird I. Some clearer examples of seasonal cycles are the following. Failure to find larvae in winter is related to snow cover.

Staphylinid beetles—Larvae Sept.-July; adults Oct.-July.

Hydromedion sparsutum—Larvae Sept.-July (1st instar, Nov.-Apr.); pupae Dec.-Mar.; adults Sept.-July.

Perimylops antarcticus—Larvae Sept.-July; adults Nov.-Apr.

Chironomid midges—Adults Oct.-early June.

Paractora trichosterna—Adults Jan.-June.

Antrops truncipennis—Adults Oct., Jan.-July.
Archiborborus koenigi—Adults Nov.-Apr.

FAUNAL REPRESENTATION

The true subantarctic islands have very limited faunas. In other climates the poor representation would be considered partial evidence of oceanic nature of the islands, but in the severe subantarctic climate this cannot be taken for granted. Although Antarctica is a continent, and in spite of now being known to have supported extensive biota in earlier periods and to have had connections with other continents, it presently has a very limited terrestrial fauna. This is clearly related to the present severe climate and to the more extensive ice cover of the Pleistocene.

Comparison of Subantarctic with Antarctic, Arctic and Cool Temperate

Antarctica proper (including South Shetland, South Sandwich and South Orkney Is., Bouvet, Balleny Is., Scott I. and Peter 1st I.) has only 76 known terrestrial free-living arthropods (21 true insects including Collembola) (Gressitt et al. 1967), but Campbell I. has over 300 (Gressitt et al. 1964). Each of the true subantarctic islands has between 26 and 100 known free-living terrestrial species (see Table 5). Thus these islands appear to resemble Antarctica in faunal size and to stand apart from the cool temperate islands to their immediate north, such as the Falklands, Campbell and Aucklands, and from the southern tip of South America, which spans the range of latitude of the true subantarctic islands. Cape Horn is at about the same latitude (55°) as the southern tips of South Georgia and Macquarie, the two southernmost subantarctic islands.

There are many similarities between the arctic tundra environment and the subantarctic islands. In general, the subantarctic islands are more mountainous, with more sea cliffs, with more glaciers reaching the sea, a more severe climate in mid-summer, but less severe in winter, and with more uniformly stronger winds. Furthermore, there are far fewer species of plants and insects in the subantarctic, with no woody plants at all. Also, there is a higher percentage of flightless species of insects of normally winged groups. As to faunal makeup, a few insect groups found on some subantarctic isles may be lacking in the most extreme Arctic environments (Gressitt 1967: 22), but in general there are more orders and families represented in the average Arctic environments (Downes 1964). This is true even in far northern areas such as northern Ellesmereland and northern Greenland, as well as at Pt. Barrow at the northern tip of Alaska. In particular, there are many more families and species of Lepidoptera, Diptera and Hymenoptera in most Arctic areas than on any subantarctic island. A conspicuous fact in the subantarctic is that competition between species and between major groups, as well as predation and parasitism, are greatly reduced. In other words, the subantarctic fauna is much more disharmonic, with many important groups totally lacking and others lacking from individual islands. The absence of weevils from South Georgia and Macquarie, of Psocoptera and Lepidoptera from South Georgia, of carabids from Heard and Macquarie, and of staphylinids, Psocoptera and Hymenoptera from Heard are only a few examples. The lack of many other important families of insects, just as of plant families, is conspicuous.

Probably the most important reasons for the great differences between arctic and subantarctic are the insular isolation of the latter since Pleistocene glacial maximum preventing land migration back towards the polar area as was possible in the arctic, together with the cooler subantarctic summers and continuous strong and cool circum-antarctic winds which restrict natural immigration. Thus, the subantarctic fauna probably consists of a few relicts plus a majority of waifs which arrived at random, rather than the biota moving together as the ice receded, as in the arctic.

The antarctic fauna differs from the subantarctic in being still less harmonic. Although there

Table 5. Relative representation of species of terrestrial arthropod groups on subantarctic islands, compared to Antarctica and Campbell I.[1]

	Antarctic	SUBANTARCTIC						Campbell[2]
		S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	
Symphyla				1				1
Pseudoscorpionida				1				2
Opiliones				1				2
Araneida		4	2	7	2	1	3	16
Acarina parasitic	11	16	2	2	7	6	2	2+
Free-living	55	51	1	23	11	10	49	69
Insecta								
Collembola	19	16	7*	7	17	7	19*	46
Mallophaga	40	35	3	4	19	17	38*	25
Anoplura	4	1				1	1	3
Psocoptera			1	1	1		1	3
Thysanoptera		1		1			1	1
[Hem.-Homoptera		2	4	1			2]	11
Hem.-Heteroptera				1				
Lepidoptera			2	2	2	1	1	29
Coleoptera	?	7	10	23	14	5	5	42
Diptera	2	13	5	12	11	3	12	81
Siphonaptera	1	1	1		2	2	5	3
Hymenoptera		1	1	1			2	9
Total	130	148	39	87	86	53	140	(350)
Free-living Insecta	21	41	30	48	45	16	43	(222)
Free-living other arthrop.	55	55	3	33	13	11	52	(94)
Parasitic Acarina & Insecta	56	53	6	6	28	26	45	(34)

1. The numbers, particularly for Acarina and Mallophaga, do not present a balanced picture because of unequal sampling and reporting to date.
2. Numbers only for groups found on true subantarctic islands.
*Estimates, partly unstudied. Square brackets, Homoptera, indicate established but probably not native.

are almost the same number of species known from Antarctica as from South Georgia or Macquarie, the former belong to fewer orders, particularly of those of the true insects. As will be seen from Table 5, there are no spiders, Psocoptera, Thysanoptera, Hemiptera, Lepidoptera or Hymenoptera in Antarctica, and the presence of Coleoptera on the antarctic fringe is somewhat questionable. These voids in most of the higher insects are balanced by good representation of mites and parasitic insects in Antarctica. This indicates that primitive arthropods are more tolerant of low temperatures and of saline and simple environments, and partly for the same reasons are more subject to dispersal by air currents, by sea and by sea birds.

Comparing the true subantarctic isles with adjacent cool temperate isles such as Campbell, a strong contrast is apparent. The same may be said for the Falkland Is. Table 5 demonstrates that Campbell has more than twice as many species as any subantarctic island. Also, not shown in the table, Campbell possesses Chilopoda, Diplopoda, Plecoptera, Orthoptera, Trichoptera and native Homoptera, besides many families of various orders lacking in the subantarctic. One exception is the presence of Heteroptera on the Crozets though apparently absent from Campbell. The contrast in the higher orders, again, is extreme. Campbell has 4 times as many species of Coleoptera, over 9 times as many Diptera and Hymenoptera and 22 times as many Lepidoptera, as the average for subantarctic isles. Probably the main reasons for these differences, with almost no change in latitude, relate to slightly milder climate, greater proximity to New Zealand, and a more continental geological history suggesting much larger Tertiary fauna and more surviving relicts with less complete ice cover in the Pleistocene.

Representation on the Various Island Groups

Perusal of the table of arthropod species (Table 6) recorded from the various islands under consideration may give a partly wrong impression of relative representation. For the Acarina, in particular, it more nearly reflects the relative state of collecting or study of collections. South Georgia and Macquarie have obviously been rather thoroughly collected. Heard Island, though as yet insufficiently collected, undoubtedly has the poorest fauna. Perhaps the Heard fauna may be not more than one-third as rich as that of Macquarie. This could be related to greater isolation, colder climate and very limited areas for colonization. When recent collections from Marion, Prince Edward and the Crozet Is. (Cochons and Possession) are fully reported, we shall have a more balanced view of the faunal representation.

For the true insects, the records as indicated are more balanced and complete, although additions for Marion I. will be forthcoming, and a few more for the Crozets. From the Collembola through the Hymenoptera, the totals for the various islands are given in Table 5.

These figures in Table 5 and the subtotals in the list of species (Table 6), include some being newly described or recorded from Marion and Prince Edward (by Dreux or others) and a few records from the Crozets (by Davies or others), even though these are not named on the list. I am grateful to Prof. Dreux and Dr Davies for kindly putting this information at my disposal.

In this section, and in the following section on groups of arthropods, discussion and statistics will concern only those species thought to be natural residents of these islands, and will exclude those thought to have been carried to the islands by man. Most of the comparative remarks will concern the true insects (including Collembola), since the mites are so unequally known.

South Georgia: This may be the second or third richest subantarctic fauna. Though the largest and in some senses least isolated of these islands, it is also the second coldest and the second most extensively ice-covered. Although the total number of arthropods listed for South Georgia is the largest in the list, this probably represents more thorough collecting for mites and certain parasitic groups, as the number for true insects is less than for the Crozets and Macquarie. Thirty-seven species of free-living true insects (including Collembola) are now known from South Georgia. Of these, 7 are in common with the Falklands, 8 with southern South America, 3 with Antarctica, and only 1 with South Indian Ocean islands. Quite a few of the mites are in common with southernmost South America or Antarctica. On the generic level there is more in common between the several areas, including South America and South Indian Ocean islands.

Marion and Prince Edward: Previously only 25 species of insects have been recorded from Marion, and none from Prince Edward. The South African Biological-Geological Expedition to Marion and Prince Edward Islands (Jan.-Mar. 1965) collected extensively on both Marion and Prince Edward, and the report to be published will include a number of additional new and interesting records. Prof. Dreux, of Paris, has indicated to me (pers. comm.) that he or others are describing or recording several additional species, some of which are already known from the Crozets, and a few of which are new species.

Of Marion's 25 species, 8 are endemic, 4 occur also on the Crozets and Kerguelen, 4 additional on the Crozets and 1 additional on Kerguelen. Another occurs also on Crozets, Kerguelen and Heard, another on these plus Macquarie. One extends from the Falklands to the Crozets through

Table 6. List of subantarctic arthropods.

The following list is based upon data in this volume, or earlier published data. Additional species and records are in press elsewhere, or shortly will be, mainly relating to reporting of new collections from Marion and Prince Edward islands and the Crozet Is. Some information on the new collections has kindly been supplied to me by Ph. Dreux and Lewis Davies. The new records are not indicated in the following list, but are partly included in the total numbers recorded, both in this table and the preceding one.

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
ARANEIDA								
Micryphantidae								
Notiomaso australis (Banks, 1914)	×							
Perimaso grytvikensis Tambs-Lyche, 1954	×							
Micromaso flavus Tambs-Lyche, 1954	×							
***Neomaso claggi* Forster	×							
Micryphantidae or Linyphiidae								
Ringina antarctica (Hickman, 1939)			×					
R. crozetensis Tambs-Lyche, 1954			×					
Porrhomma antarctica Hickman, 1939		×		×				
Linyphiidae								
Mynoglenes marrineri Hogg, 1909						×	C,Auc	
M. insolens Simon, 1905						×	Auc	
Agelenidae								
Myro kerguelenensis Cambridge, 1876			×	×	×	×		
M. jeanneli Berland, 1947			×					
M. paucispinosus Berland, 1947		×	×					
Muizenbergia crozetensis (Hickman, 1939)			×					
Symphytognathidae								
Crozetulus minutus Hickman, 1939			×					
OPILIONES								
Triaenonychidae								
("*Nuncia*") *unifalculata* (Enderlein, 1909)			×					
PSEUDOSCORPIONIDA								
Austrochthonius insularis Vit.-di Castri, 1969			×					
ACARINA								
MESOSTIGMATA								
Parantennulidae								
***Davacarus gressitti* Hunter	×		×					
Laelapidae								
Ayersacarus gelidus Hunter, 1964						×		
A. plumapilus Hunter, 1964						×	C,Auc	
A. tilbrooki Hunter, 1967	×						SS	
A. strandtmanni Hunter, 1964						×		
Androlaelaps pachyptilae (Zumpt & Till, 1956)	×		×		×	×	C,Auc	
Eulaelaps mawsoni Womersley, 1937						×		
***Stevacarus claggi* Hunter	×							
S. evansi (Hunter, 1964)	×					×		
Pachylaelaps macquariensis Womersley, 1937						×		
Eviphididae								
**Thinoseius hirschmanni* Hunter	×							
**T. katherinae* Hunter	×							

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
Digamasellidae								
Dendrolaelaps dargi Hirschm, 1966						×		
D. schusteri Hirschm., 1966						×		
D. watsoni Hirschm., 1966						×		
**Digamasellus templei* Hunter			×		×			
Rhodacaridae								
Gamasellus watsoni Hirschm., 1966						×		
G. rykei (Hunter, 1967)	×		×				SS	
G. jeanneli André, 1947				×				
G. racovitzai (Trouesart, 1903)	×						A	
**G. gressitti* Hunter	×							
G. crozetensis Richters, 1907			×					
G. (*Hydrogamasellus*) *macquariensis* Hirschm., 1966						×		
G. (*H.*) *antarcticus* (Trgdh., 1908)	×		×			×	A	
G. (*H.*) *schusteri* Hirschm., 1966						×		
Asca crozetensis Richters, 1907			×					
?Neoparasitidae								
Hydrogamasus (*Austrophydrogam.*) *watsoni* Hirsch., 1966	×					×		
Gamasiphis crozetensis (Richters, 1907)			×					
G. watsoni Hirschm., 1966						×		
Neoparasitus crozetensis Richters, 1907			×					
Veigaiidae								
Cyrthydrolaelaps watsoni Hirschm., 1966	×					×		
C. sp.			×					
**Veigaia claggi* Hunter	×							
**Gamasolaelaps arenosus* Hunter	×							
Parasitidae								
Parasitus sp. Richters, 1907			×					
Eugamasus (5 spp.)						×		
Blattisocidae								
Iphidozercon sp. Lindquist (Watson, 1967)						×		
Ameroseiidae								
Ameroseius sp. Chant & Lind. (Watson, 1967)						×	C	
Halarachnidae								
Halarachne miroungae Ferris, 1925	×			×			A, N.Amer.	*Mirounga leonina* *Pygoscelis papua*
Rhinonyssidae								
Rhinonyssus rhinolethrum (Trst., 1895)	×							*Anas georgicus*
R. schelli Fain & Hyl., 1963	×						A	*Pygoscelis papua*
Uropodidae								
Piracarus crozetensis Richters, 1907			×					
Uropoda spp.	×		×			×		
Opisthope crozetensis Richters, 1907			×					
Polyaspididae								
n. gen., n. spp.			×			×		
Cercomegistidae								
?*Celaenogamasus* sp.						×		

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
METASTIGMATA								
Ixodidae								
Ixodes kerguelenensis André & Col.-Bel., 1942	×	×	×	×	×	×	C S.Aust C.Pac	*Procellaria, Pachyptila, Pelecanoides*
I. uriae (White)	×	×	×	×	×	×	Aust Chile NZ, A, Arctic	*Diomedea, Phoebetria, Pachyptila*
PROSTIGMATA								
Eupodidae								
Eupodes minutus (Strandtmann, 1967)	×						A,SS	
E. sp.						×		
Protereunetes sp.						×		
Halotydeus sp.						×		
Penthalodidae								
**Stereotydeus reticulatus* Strandtm.	×							
**S. longipes* Strandtm.	×							
Rhagidiidae								
Rhagidia gerlachei (Trst., 1903)	×						A,SSh	
R. leechi Strandtm., 1963	×						A,SSh	
R. macquariensis Womersley & Strandtm., 1963						×		
R. kerguelenensis (Cambridge, 1876)			×	×			St.Paul	
Pyemotidae								
**Bakerdania rugosa* Cross	×							
**B. equisetosa* Cross	×							
B. sp.	×							
B. tripartitus (Cross, 1964)						×		
Tydeidae								
Tydeus tilbrooki Strandtm., 1967	×						A,SSh, SO	
T. antipodus Womersley, 1937						×		
Pachygnathidae								
Nanorchestes antarcticus Strandtm., 1963							Bouvet A,SSh,SS, C,SO	
Tarsonemidae								
Disparipes antarcticus Richters, 1907			×		×			
Ereynetidae								
Ereynetes macquariensis Fain, 1962	×					×		
Ereynetoides watsoni Fain, 1962						×		
Erythraeidae								
Genus nr *Neosmaris*	×							
Bdellidae								
**Bdellodes* (*Bdellodes*) *georgianensis* Wallace	×							
B. (B.) sp.	×							
B. (*Hoploscirus*) *macquariensis* Atyeo, 1963						×		
B. (*H.*) *watsoni* Atyeo, 1963						×		
**B.* (*H.*) *rhachia* Wallace	×							
Spinibdella antarctica (Trgdh, 1907)	×							
Bdella pallida Cambridge, 1876			×	×				
B. antarctica Trgdh, 1907	×							

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
Halacaridae								
Isobactrus sp.						×		
ASTIGMATA								
Pterolichidae								
Thecarthra theca (Megnin & Trt., 1884)					×		Wide	*Sterna*
Proctophyllodidae								
Alloptes aschizurus Gaud, 1952				×	×		SSh, A	*Chionis*
A. chionis Atyeo & Pet., 1967					×		A	*Chionis*
A. obtusolobus Dubinin, 1951	×						A	*Larus dominicanus*
Echinacarus rubidus (Trt, 1886)	×						S.Cont's.	*Diomedea*
E. petaliferus (Trt, 1898)	×						"	*Diomedea*
**Brephosceles gressitti* Atyeo & Pet.	×							*Diomedea chrysostoma*
B. marginiventris (Trt., 1899)	×							*Macronectes*
**B. diomedei* Atyeo & Pet.	×							*Diomedea*
Oxyalges incertus (Gaud, 1952)				×			S. Ocean	*Pelecanoides georgicus*
O. cardiurus Gaud & Atyeo, 1966						×	F, SO	*Pachyptila*
Analgidae								
Leptosphyra antarctica (Gaud, 1952)				×				*Pelecanoides georgicus*
L. sp.							F	*Chionis alba*
Diomedacarus gigas (Trt, 1895)	×						S.Atl., *N.*Pac.	*Diomedea*
Avenzoariidae								
Avenzoaria calidridis (Oudemans, 1904)	?							*Calidris fuscicollis*
Megninia antarctica Gaud, 1952				×				*Pelecanoides georgicus*
Promegninia pedimana (Trt, 1899)	×							*Diomedea*
Zachvatkinia nr. *hydrobatidii*	×							*Oceanites*, *Pagodroma*, *Fregetta*
Scutomegninia phalacrocoracis (Dub. & Dub., 1940)	×							*Phalacrocorax atriceps*
Acaridae								
Calvolia sp.						×		
Saproglyphidae								
***Neocalvolia claggi* Hughes	×							
Hyadesidae								
Hyadesia sp. ?*uncinifera* Megnin, 1889						×		
H. kerguelenensis Lohmann, 1908				×				
Algophagus antarcticus Hughes, 1955					×			
Carpoglyphidae								
Carpoglyphus sp.						×		
Anoetidae								
Histiostoma sp.						×		
Dermoglyphidae								
Thecarthra incerta Gaud, 1952				×				*Pelecanoides georgicus*
Torynophora saxorum (Studer, 1879)				×				
CRYPTOSTIGMATA (Oribatei)								
Palaeacaridae								
Andacarus watsoni Travé, 1964						×		
Brachychthoniidae								
Liochthonius mollis (Hammer)	×						A,S.Am.	

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
Holonothridae								
Eobrachychthonius oudemansi (van der Hammen)	×						S.Am.	
Holonothrus foliatus Wallwork, 1963						×		
Camisiidae								
Platynothrus skottsbergii expansus Wallw., 1966	×						P.s.-S.Am.	
Camisia segnis (Hermann)	×							
Malaconothridae								
* *Trimalaconothrus flagelliformis* Wallw.	×							
Metrioppidae								
Macquarioppia striata Wallw., 1963				×	×	×		
Oppiidae								
Oppia crozetensis (Richters, 1907)	×		×			×	SS, S.Am.	
**O. scotiae* Wallw.	×							
**Globoppia intermedia longiseta* Wallw.	×				×		G.i.-SS, S.Am.	
Podacaridae								
Halozetes marinus (Lohmann, 1908)	×			×		×	SO. St. Paul	
H. intermedius Wallw., 1963						×		
**H. littoralis* Wallwork	×							
H. b. belgicae (Michael, 1903)	×				×		A,S.Sh.,SS, S,Ork.	
H. b. brevipalis Wallwork, 1963					?	×		
H. crozetensis (Richters, 1907)			×	×	×	×		
H. macquariensis (Dalenius, 1958)						×		
**Alaskozetes antarcticus intermedius* Wallwork	×						Bouvet	
A. antarcticus subsp.?		×	×					
A. antarcticus grandjeani (Dalenius, 1958)					×	×		
Podacarus a. auberti Grandjean, 1955				×	×	×		
P. auberti occidentalis Wallwork, 1966	×							
**Antarcticola georgiae* Wallwork	×							
Ceratozetidae								
Antarctozetes crozetensis (Richters, 1907)			×	×				
Edwardzetes elongatus Wallwork, 1966	×							
Magellozetes antarcticus (Michael, 1895)	×						A,S.Am.	
Scotiazetes bidens Wallwork, 1966	×							
Porozetes polygonalis quadrilobatus Wallw., 1966	×						(P.p.-TdF)	
Mycobatidae								
Cryptobothris monodactyla Wallwork, 1963						×		
Neomycobates tridentatus Wallwork, 1963						×		
Parakalummidae								
Sandenia georgiae (Oudemans, 1914)	×							
Porokalumma rotunda (Wallwork, 1963)						×		
Haplozetidae								
Totobates anareensis (Dalenius, 1958)						×		
T. elegans (Hammer, 1958)						×	C, Andes	
?*Oribata gaussi* Richters, 1907			×					
COLLEMBOLA								
Onychiuridae								
Tullbergia mixta Wahlgren, 1906						×	SSh	

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
T. antarctica Lubbock, 1876			×	×	×			
**T. templei* Wise					×			
T. bisetosa Börner, 1902	×	×		×	×	×	F, TdF	
Dinaphorura spinosissima Wahlgen, 1906				×			TdF	
Hypogastruridae								
Hypogastrura antarctica Salmon, 1962						×	SSh	
H. viatica (Tullberg, 1872)	×			×		×	SSh, TdF Cosmop.	
**Xenylla claggi* Wise	×							
Neanuridae								
Setanodosa steineni (Schäffer, 1891)	×							
Friesea grisea (Schäffer, 1891)	×						A, SSh	
**F. tilbrooki* Wise	×							
F. jeanneli Denis, 1947				×				
F. multispinosa Denis, 1947				×				
F. nigroviolacea Enderlein, 1909				×				
Isotomidae								
Cryptopygus antarcticus Willem, 1901	×			×	×	×	A,SSh,SO, SS, Bouvet TdF	
**C. subantarcticus* Wise	×							
C. reagens Enderlein, 1909			×	×	×			
C. tricuspis Enderlein, 1909				×				
C. caecus Wahlgren, 1906	×			×			SSh, S.Afr. SW S.Am., C.	
**Parafolsomia quadrioculata* Wise	×							
Sorensia subflava Salmon, 1949 (*S. dreuxi*)	×		×		×	×	C, Auc	
**S. atlantica* Wise	×							
S. punctata (Wahlgren, 1906)		×		×			F,TdF,S. Patag.	
Setocerura georgiana (Schäffer, 1891)	×						TdF	
Isotoma sp.	×					×		
Proisotoma pallida (Moniez, 1894)			×				Brazil	
Spinocerura dreuxi Del. Deb. & Mass., 1966			×					
Parisotoma octooculata (Willem, 1901)	×			×	×	×	A,SSh,SO Auc,C	
P. boerneri (Enderlein, 1903)			×	×			C,Auc	
Entomobryidae								
Lepidocyrtus cyaneus cinereus Folsom, 1924						×	C,NZ,N.Am	
Lepidobrya mawsoni (Tillyard, 1920)						×	C	
Sminthuridae								
**Sminthurinus jonesi* Wise	×							
S. granulosus Enderlein, 1909			×					
S. kerguelensis Salmon, 1964				×		×		
Katianna banzarei Salmon, 1964						×		
K. kerguelenensis Denis, 1947				×				
Metakatianna gressitti Salmon, 1964						×		
Polykatianna davidi (Tillyard, 1920)						×		
MALLOPHAGA								
Menoponidae								
Actornithophilus pauliani Seguy, 1954		×		×	×			*Chionis minor*
A. piceus (Denny, 1842)								*Larus dominicanus*

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
Ancistrona procellariae (Westw., 1874)								*Daption capense*
A. sp. (Piaget, 1880)								*Fulmarus glacialoides Pachyptila forsteri, P. desolata*
A. sp.						×		*Halobaena caerulea, Thalassoica antarctica, Procellaria aequinoctialis, P. nivea*
Austromenopon affine (Piaget, 1890)	×						A	*Diomedea exulans, D. chrysostoma*
A. ossifragae (Eichler, 1949)				×				*Macronectes giganteus*
A. daptionis (Eichler, 1949)							A	*Daption capense, Pagodroma nivea*
A. brevifimbriatum (Piaget, 1880)							A	*Fulmarus glacialoides*
A. stammeri Timmermann, 1963								*Pachyptila belcheri, P. turtur*
A. oschei Timmermann, 1963							A	*Thalassoica antarctica*
A. longithoracicum (Piaget, 1880)								*Adamastor cinereus*
A. paululum (Kell. & Chapm., 1899)								*Puffinus griseus*
A. elliotti Timm., 1954	×							*Pelecanoides urinatrix exsul*
A. fuscofasciatum group					×			*Catharacta skua*
A. transversum (Denny, 1842)								*Larus dominicanus*
Eidmanniella pellucida (Rudow, 1869)								*Phalacrocorax albiventer*
Holomenopon sp.								*Anas acuta, A. superciliosa*
Longimenopon galeatum Timm., 1957						×	SO	*Pelagodroma marina, Pachyptila desolata*
Piagetiella caputincisa (Eichler, 1950)	×						A,SO	*Phalacrocorax atriceps, P. albiventer*
Trinoton querquedulae (Linn., 1758)								*Anas acuta, A. superciliosa*
Philopteridae								
Anaticola crassicornis (Scopoli, 1763)								*Anas acuta*
A. sp.	×							*Anas georgicus, Chloephaga leucoptera*
Anatoecus dentatus (Scopoli, 1763)	×					×		*Anas acuta, A. superciliosa*
A. icteroides (Nitzsch, 1818)	×					×		*Anas acuta, A. superciliosa*
A. sp.	×							*Anas georgicus*
Austrogoniodes brevipes (Giebel, 1816)				×				*Aptenodytes patagonica*
A. mawsoni Harrison, 1937							A	*A. forsteri*
A. gressitti Clay, 1967	×						A,SSh	*Pygoscelis papua, P. antarctica, Eudyptes chrysolophus*
A. keleri Clay, 1967							SSh	*P. papua, Eudyptes crestatus, E. chrysolophus*
A. macquariensis Harrison, 1937	×				×	×	SSh	*P. papua, P. antarctica, Eudyptes*

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
								crestatus, *E. chrysolophus*, *E. pachyrhynchus*
A. *antarcticus* Harrison, 1937							A	*P. adeliae*
A. *bifasciatus* (Piaget, 1885)							A	*P. adeliae*
A. *concii* (Kéler, 1952)			×		×			*Eudyptes crestatus*, *E. chrysolophus*, *E. pachyrhynchus*
A. *cristati* Kéler, 1952			×		×	×		*E. crestatus*, *E. chrysolophus*, *E. ch. schlegeli*
A. *hamiltoni* Harrison, 1937						×		*E. crestatus*, *chrys. schlegeli*, *E. pachyrhynchus*
A. *bicornutus* (Kéler, 1954)					×			*Eudyptes chrysolophus*
A. *demersus* Kéler, 1952								*E. chrysolophus*
A. ?*strutheus* Harrison, 1915						×		*E. chryso. schlegeli*
A. *waterstoni* (Cummings, 1914)						×		*E. pachyrhynchus sclateri*
Bedfordiella simsi Timm., 1961								*Pachyptila forsteri*
B. *unica* Thompson, 1937								*Pterodroma brevirostris*
Docophoroides brevis (Dufour, 1835)	×		×	×		×	SSh	*Diomedea exulans*
D. *harrisoni* Waterston, 1917							SSh	*D. melanophris*, *D. chrysostoma*
D. *simplex* (Waterston, 1914)	×						A	*D. melanophris*, *D. chrysostoma*, *Procellaria aequinoctialis*
D. *murphyi* (Kellogg, 1914)	×			×		×	A	*Phoebetria palpebrata*, *Macronectes giganteus*
Episbates pederiformis (Dufour, 1835)	×							*Diomedea exulans*
Haffneria grandis (Piaget, 1880)	×			×	×	×	A,SSh	*Catharacta skua*
Halipeurus falsus pacificus Edwards, 1961								*Pelecanoides u. urinatrix*
H. *heraldicus* Timm., 1960				×				*Pterodroma mollis*
H. *turtur* Edwards, 1961						×		*Pachyptila desolata*
H. *pelagicus* (Denny, 1840)								*Oceanites oceanicus*, *Fregetta tropica*
H. *diversus* (Kellogg, 1896)						×		*Puffinus griseus*
H. *procellariae* (Fabr., 1775)				×		×		*Pterodroma macroptera*, *P. lessoni*, *P. mollis*
Harrisoniella hopkinsi Eichler, 1952	×						SSh	*Diomedea exulans*, *Macronectes giganteus*
H. *ferox* (Giebel, 1867)	×							*D. melanophris*
H. *chilensis* Carriker, 1964								*Fulmarus glacialoides*
"*H.*" *grandis* (Piaget, 1880)	×					×		*Catharacta skua*
Naubates fuliginosus (Taschenb., 1882)	×			×		×	A	*Diomedea exulans*, *Phoebetria fusca*, *P. palpebrata*, *Adamastor cinereus*, *Procellaria aequinoctialis*

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
N. prioni (Enderlein, 1908)	×			×	×	×		*Pachyptila belcheri, P. forsteri, P. desolata, P. turtur*
N. testaceus (Taschenb., 1882)								*Daption capense*
N. clypeatus (Giebel, 1874)				×	×			*Halobaena caerulea*
N. pterodromi Bedford, 1930								*Pterodroma macroptera*
N. heteroproctus Harrison, 1937						×		*P. macroptera, P. lessoni*
Nesiotinus demersus Kellogg, 1903	×					×		*Aptenodytes patagonica*
Paraclisis hyalina (Neumann, 1911)	×					×		*Diomedea exulans*
P. diomedeae (Fabr., 1775)	×	×		×		×	A,SSh	*D. melanophris, D. chrysostoma, Phoebetria fusca, P. palpebrata, Fulmarus glacialoides, Pachyptila forsteri*
P. obscura (Rudow, 1869)	×			×		×	A,SSh	*Macronectes giganteus*
Pectinopygus turbinatus (Piaget, 1890)	×					×	A,SO	*Phalacrocorax atriceps, P. albiventer*
Pelmatocerandra enderleini Eichler, 1949	×				×			*Pelecanoides georgicus*
P. setosa (Giebel, 1876)	×			×	×	×		*P. ?georgicus, P. urinatrix exsul*
Perineus concinnoides Kéler, 1957	×							*Diomedea exulans*
P. circumfasciatus Kéler, 1957	×					×	A	*D. melanophris, D. chrysostoma, Phoebetria palpebrata, Macronectes giganteus*
P. nigrolimbatus (Giebel, 1874)							A,SSh	*Daption capense, Fulmarus glacialoides*
Philoceanus robertsi (Clay, 1940)							A	*Oceanites oceanicus*
P. fasciatus (Carriker, 1958)							SS,SO	*Fregetta tropica*
P. garrodiae (Clay, 1940)				×				*Garrodia nereis*
Pseudonirmus gurlti (Taschenb., 1882)	×					×	A,SSh	*Daption capense*
P. lugubris (Taschenb., 1882)							A,SSh	*Thalassoica antarctica*
P. charcoti (Neumann, 1907)	×						A,SSh,SO	*Pagodroma nivea*
Quadraceps ornatus antarcticus Timm., 1952	×						A,SO	*Chionis alba*
Q. o. fuscolaminulatus (End., 1908)	×					×		*Larus dominicanus*
Q. vaginalis Timmerm.		×			×			*Chionis minor*
Q. alpha (Kellogg, 1914)							A	*Catharacta skua*
Q. punctatus sublingulatus Timm., 1952								*Larus dominicanus*
Q. houri Hopkins, 1949							SSh	*Sterna vittata*
Q. sellatus (Burmeister, 1838)								*S. vittata*
Saemondssonia gaini (Neumann, 1913)	×						A	*Macronectes giganteus*
S. stammeri Timm., 1959							A,SSh	*Daption capense*
S. bicolor (Rudow, 1870)							A,SSh,SO	*Fulmarus glacialoides*
S. pterodromae Timm., 1959					×	×		*Halobaena caerulea, Pterodroma brevirostris*

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
S. desolata Timm., 1959							A	*Pachyptila forsteri, P. belcheri, P. desolata, P. turtur*
S. enderleini (Eichler, 1949)								*Pterodroma mollis*
S. nivea Timm., 1956	×						A,SO	*Thalassoica antarctica, Pagodroma nivea*
S. marina Timm., 1956							A	*Oceanites oceanicus*
S. nereis Timm., 1950								*Garrodia nereis*
S. australis Timm., 1955			×	×	×			*Chionis minor*
S. stresemanni Timm., 1949				×	×	×	A,SSh	*Catharacta skua*
S. lari (O. Fabr., 1780)	×				×	×	A,SSh,SO	*Larus dominicanus*
S. sternae (Linn., 1758)								*Sterna vittata*
S. lockleyi Clay, 1949	×			×	×		A,SSh	*Sterna vittata, S. virgata, S. macroura*
S. sp.						×		*Pterodroma lessoni*
Trabeculus heteracanthus (Waterston, 1912)								*Macronectes giganteus*
T. hexacon (Waterston, 1914)	×					×	A	*Adamastor cinereus, Procellaria aequinoctialis, Puffinus griseus*
T. schillingi Rudow, 1866				×		×		*Pterodroma macroptera, P. lessoni, P. mollis*
ANOPLURA								
Echinophthiridae								
Antarctophthirus microchir Trou. & Neum., 1888							C	*Phocarctos hookeri*
A. ogmorhini Enderl., 1906						×	A	*Leptonychotes weddelli, Hydrurga leptonyx*
A. lobodontis Enderl., 1906							A	*Lobodon carcinophagus*
A. mawsoni Harrison, 1937							A	*Ommatophoca rossi*
Lepidophthirus macrorhini Enderl., 1904	×				×	×	A	*Mirounga leonina*
PSOCOPTERA								
Elipsocidae								
Antarctopsocus jeanneli Badonnel, 1947		×	×				(Cochons)	
Philotarsidae								
Austropsocus insularis Smithers, 1962						×	C	
Psoquillidae								
Rhyopsocus eclipticus Hagen, 1876				×				
THYSANOPTERA								
Thripidae								
Physemothrips chrysodermus Stannard, 1962						×		
HEMIPTERA-HETEROPTERA								
Enicocephalidae								
Phthirocoris antarcticus Enderlein, 1904			×					
LEPIDOPTERA								
Tineidae								
Pringleophaga kerguelensis Enderlein, 1905		×	×	×				
Yponomeutidae								
Embryonopsis halticella Eaton, 1876 (*P. heardensis*)		×	×	×	×			

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
Pyralidae								
Eudoria mawsoni (Womersley & Tindale, 1937)						×		
COLEOPTERA								
Carabidae (Trechinae)								
Merizodus soledadinus (Guerin-Men., 1832)	×			(×)			F,TdF N to 52°	
Temnostega antarctica Enderlein, 1905			×					
Amblystogenium p. pacificum Putzeys			×				(Possession)	
A. p. dreuxi Jeannel			×				(Cochons)	
Dytiscidae								
Lancetes claussi (Müller, 1884)	×							
Staphylinidae								
Omaliomimus albipenne (Kiesenwetter, 1877)						×	C,Auc	
O. venator (Broun, 1909)						×	C,Auc	
Stenomalium helmsi (Cameron, 1945)						×	NZ	
S. sulcithorax (Broun, 1880)						×	NZ	
Antarctotachinus crozetensis Enderlein, 1909			×					
Halmaeusa antarctica Kiesenwetter, 1877						×	Auc	
H. atriceps (C.O. Waterhouse, 1875)	×	×	×	×				
Crymus antarcticus Fauvel, 1904	×							
Pselaphidae								
Pseudeuplectus antarcticus Enderlein, 1909			×					
Hydraenidae								
Meropathus randi Jeannel, 1953		×	×					
M. chuni Enderlein, 1901				×	×			
Lathridiidae								
Aridius malouinensis (Champion, 1918)	×						F	
Byrrhidae								
?*Pedilophorus* sp.						×		
Perimylopidae								
Perimylops antarcticus Müller, 1884	×							
Hydromedion sparsutum (Müller, 1884)	×							
Curculionidae								
Canonopsis sericeus C.O. Waterhouse, 1875				×	×			
Christensenia antarctica Brinck, 1945 (= *Neocanonopsis dreuxi* Hoffmann, 1964, **New Synonymy**)			×				(Possession)	
C. suorum (Hoffmann, 1966), n. comb.			×				(Cochons)	
Antarctonesiotes gracilipes C.O. Waterhouse, 1875			×	×	×		(Possession)	
A. tenuicornis Jeannel, 1940				×				
A. dreuxi Hoffmann, 1966		×	×				(Cochons)	
A. elongatus Jeannel, 1953		×						
Bothrometopus fasciatus Jeannel, 1940		×	×	×			(Possession)	
B. variabilis Hoffmann, 1966			×				(Cochons)	
B. randi Jeannel, 1953		×						
Mesembriorhinus brevis (C.O. Waterhouse, 1875)			×	×	×			
M. parvulus (C.O. Waterh., 1885)		×						

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
M. eatoni (C.O. Waterh., 1879)		×	×	×				
Ectemnorhinus (s.str.) *viridis* G.R. Waterhouse, 1853				×				
E. (s.str.) *grisescens* (Enderlein, 1909)					×			
E. (s.str.) *curtus* Jeannel, 1940				×				
E. (s.str.) *drygalskii* Enderl., 1909				×				
E. (s.str.) *angusticollis* C.O. Waterh., 1875				×				
E. (*Dusmoecetes*) *geniculatus* Jeannel, 1940			×					
E. (*D.*) *richtersi* Enderlein, 1904			×					
E. (*D.*) *similis* C.O. Waterh., 1885		×						
E. (*D.*) *marioni* Jeannel, 1940		×						
Xanium vanhoeffenianum Enderlein, 1904			×				(Possession)	
X. crozetense Enderlein, 1904 (*desolationis* Jean.)			×	×				
X. a. affinis Hoffmann, 1966			×				(Cochons)	
X. a. possessionensis Hoffmann, 1966			×				(Possession)	
DIPTERA								
Trichoceridae								
Trichocera maculipennis Meigen, (*Palaeopetaurista dubitata* Seg.)				×			Wide	
T. regelationis (Linnaeus, 1758)	×						Wide	
Tipulidae								
Erioptera (*Trimicra*) *pilipes macquariensis* Alexander, 1962						×		
Sciaridae								
?)*Sciara womersleyi* Séguy, 1940				×				
?)*S. jeanneli* Séguy, 1940				×				
Lycoriella auberti (Séguy, 1940), n. comb.				×				
L. (s. str.) *caesar* (Johannsen, 1929)	×						Ontario	
Bradysia sp.	×							
B. watsoni Colless, 1962						×		
Psychodidae								
Psychoda parthenogenetica Tonnoir, 1940	×		(×)	×		×	Europe, Japan, Korea, C, NZ, S. Austral., Juan Fernandez	
P. surcoufi Tonnoir, 1922						×	C, NZ, Austral.	
Chironomidae								
Parochlus steineni (Gercke, 1889)	×						SSh, S.Am.	
"*Eretmoptera*" *murphyi* Schaeffer, 1914	×							
Limnophyes pusillus Eaton, 1875		×						
L. sp.	×							
Halirytus macquariensis Brundin, 1962						×		

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
H. amphibius Eaton, 1875			×	×				
Microzetia mirabilis Séguy, 1965			×				(Possession)	
Protobelgica albipes Séguy, 1965			×				(Possession)	
Smittia sp.						×		
Simuliidae								
Crozetia crozetense (Womersley, 1937)			×					
Mycetophilidae								
Mycomya sp. nr *bifida* Freeman	×						bifida: S'n S. Am.	
Unidentified sp.			×					
Coelopidae								
Apetenus litoralis Eaton, 1875		×	×	×				
A. watsoni Hardy, 1962						×		
Coelopa (*Coelopella*) *curvipes* Hutton, 1902 (? = *asymmetrica* End.)						×	Auc., NZ, Chatham	
C. (*Fucomyia*) *nigrifrons* Lamb, 1909						×		
Listriomastax litorea Enderlein, 1908			×	×				
Ephydridae								
Ephydrella macquariensis (Womersley, 1937)						×		
Amalopteryx maritima Eaton, 1875			×	×	×			
Helcomyzidae								
Paractora jeanneli Séguy, 1940		×						
P. dreuxi Seguy			×					
P. trichosterna (Thomson, 1868)	×						TdF, F	
Helomyzidae								
Prosopantrum austrinum Enderlein, 1912	×							
Pallopteridae								
Heloparia ekeloefi Enderlein, 1912	×						F	
Micropezidae								
Calycopteryx moseleyi Eaton, 1874				×	×			
Carnidae								
Australimyza macquariensis (Womersley, 1937)						×		
Dolichopodidae								
Schoenophilus pedestris Lamb, 1909						×		
Sphaeroceridae: Leptocerinae								
Anatalanta aptera Eaton, 1875				×	×			
A. crozetensis Enderlein, 1908			×					
Antrops truncipennis Enderlein, 1909	×						TdF	
Siphlopteryx antarctica Enderlein, 1908			×					
Archiborborus koenigi Holdhaus, 1931	×							
Leptocera pauliani Seguy, 1954				×				
SIPHONAPTERA								
Ceratophyllidae								
Nosopsyllus fasciatus (Bosc, 1800)						×	Wide	*Rattus rattus*
Pygiopsyllidae								
Notiopsylla kerguelensis (Taschenberg, 1880)	×			×	×	×	Snares	*Procellaria aequinoctialis* *Prion banksi* *Macronectes giganteus* *Puffinus griseus* *Pterodroma lessoni*

	S. Georgia	Marion	Crozets	Kerguelen	Heard	Macquarie	Other	Hosts
								Pelecanoides urinatrix
N. *enciari* Smit, 1957						×	Auc, Antipodes, Snares	*Pterodroma lessoni*
Rhopalopsyllidae								
Parapsyllus m. magellanicus Jordan, 1938							F,TdF?	*Macronectes giganteus* *Pachyptila desolata* *Catharacta skua* *Phoebetria palpebrata*
P. *m. heardi* de Meillon, 1952		×		×	×	×		*Daption capensis* *Phalacrocorax*, *Eudyptes*, *Pterodroma*, *Halobaena*
P. *cardinis* Dunnet, 1961						×		*Pachyptila desolata* *Pterodroma lessoni* *Macronectes giganteus*
HYMENOPTERA								
Mymaridae								
***Notomymar aptenosoma* Doutt & Yoshimoto	×							
Diapriidae								
Antarctopria latigaster Brues, 1920						×	C	
Eucoilidae								
Kleidotoma icarus (Quinlan, 1964)			×					
Totals	148	39	87	86	53	140		

A = Antarctica; Auc = Auckland Is.; Aust = Australia; C = Campbell I.; F = Falkland Is.; NZ = New Zealand; SO = South Orkney Is.; SS = South Sandwich Is.; SSh = South Shetland Is.; TdF = Tierra del Fuego

Possession and Cochons in parentheses indicate apparent different representation in Crozet Is. fauna.

South Georgia and Marion, and another on all subantarctic islands. So far, no genera are reported from Marion which do not also occur in South Georgia or the Crozets or Kerguelen. Eleven genera are in common with South Georgia and 23 are in common with the Crozets and/or Kerguelen.

Crozet Islands: For insects proper these islands possess 42 species, of which 38 are native and 21 are endemic. Of the endemic species, 5 have their closest relatives in Africa (some on high African mountains). Most of the rest have primarily or exclusively subantarctic relationships.

According to Jeannel (1965) and Dreux (1966a,b), the island groups of Marion (Prince Edward), Crozet, Kerguelen and Heard should form a local zoogeographical province. There are 25 species which are found on at least 2 of these. Four species are limited to Crozets and Kerguelen. Three occur on Marion, Crozets and Kerguelen only. Only 2 species found on Heard are not known from Kerguelen or Crozets also. Among the parasitic mites, some species are described in this volume from Heard I., but it is unlikely that they are restricted to the island since their hosts also occur elsewhere. Marion, Crozets and Kerguelen do each have some species of true insects restricted to a particular group, notably so with the Crozets. Some, even, are known only from a single island, as with Ile des Cochons and Ile de la Possession of the Crozets. There are indications of separate speciation on Cochons and Possession, with sister forms on the 2 islands, sometimes apparently at the species level and sometimes at the subspecies level. The Crozets appear both to be the richest group of the South Indian Ocean Islands and to have the highest rate of species endemicity (about 50%). Twenty-one species are in common with Kerguelen, 13 with Marion, 13 with Heard, 10 with South Georgia and 8 with Macquarie (excluding Mallophaga). Of the genera, 20 are not found on other subantarctic islands, 33 are on other subantarctic isles; 17 occur on South Georgia and 12 are on Macquarie.

Kerguelen: There are 38 species of true insects recorded from Kerguelen (including Collembola). Of these, 13 are apparently endemic, 14 occur also on the Crozets, 11 also on Heard, 7 (or more) on Marion, 4 on Macquarie and 6 on South Georgia. Even more species may be determined to be in common with the Crozets, Marion or Heard. This would reduce the apparent endemicity. It could also partly confirm the theory that the fauna of these islands was forced north in the Pleistocene (to St. Paul and Amsterdam I., or to larger land masses of which those islands are relics), and then back south again after the Pleistocene.

Kerguelen is well known for having a unique fauna with a high percentage of specialized and flightless insects. However, it was better investigated at an earlier date than were Marion and the Crozets. Actually a number of the conspicuous forms, like the flightless moths and some of the flies are in common with, or very closely related to species on Marion and the Crozets. Thus the endemism (34%) is not particularly high. Generic endemism is very low. Sixteen genera are in common with South Georgia, 17 with Marion, 23 with the Crozet Is., 13 with Heard and 18 with Macquarie; at least 4 occur also on Antarctica.

Heard Island: Heard is the poorest of the true subantarctic islans, being one of the smallest, as well as the coldest and most extensively ice-covered. It is probably the only one with a still active volcano. Only 16 free-living species of true insects are known from Heard. Of these, 5 occur also on South Georgia, 3 (or more) on Marion, 8 on the Crozets, 13 on Kerguelen and 6 on Macquarie. The 3 species not in common with Kerguelen are 2 Collembola (the new *Tullbergia* and *Sorensia subflava*) and 1 of the Kerguelen-related weevils.

Heard is the only major island without any species capable of flight. Also, it may have only 1 or 2 endemic species of true insects. Possibly all, or at any rate nearly all, of the insects on Heard came from Kerguelen. Air transport is a possibility, but direct land connection in the past, or at least greater proximity to a larger Kerguelen cannot be ruled out. In any case, the surface of Heard is much younger than that of Kerguelen, and may or may not have been involved in the evolution of the weevils, moths and others endemic to the 4 groups of southern Indian Ocean islands.

Macquarie Island: Macquarie is one of the 2 southernmost subantarctic islands, although it is north of the Antarctic Convergence. It is one of the 2 groups without glaciers. It is an old eroded island, possibly a remnant of a former much larger land mass, and was glaciated during the Pleistocene. Another theory is that it is a raised portion of the mid-ocean ridge. It is much lower in altitude than South Georgia and Heard, and lacks distinct volcanic cones like those on Marion, Kerguelen, Crozets and Heard. The fauna of Macquarie is slightly smaller than those of Crozets and Kerguelen for true insects, and is about as large as that of South Georgia. Forty native species of these are recorded, of which about 25 are endemic; 4 Collembola are in common with South Georgia, perhaps 2 or more of these are in common with Marion, 1 or more with the Crozets, 4 Kerguelen and 4 with Heard. Most of these involve the same Collembola. Probably more species are in common among the mites. In the oribatoids, 2 are in common with South Georgia, 2 with the Crozets, 4 with Kerguelen and 4 with Heard. Macquarie's relationships are more closely with Campbell I. and the Aucklands, with 9 species in common with the former and at least 5 with the

Fig. 11. Map of the antarctic area, showing the subantarctic islands: South Georgia and Heard situated just south of the Antarctic Convergence, and Marion—Prince Edward, Crozet, Kerguelen and Macquarie located north of the Convergence, which is the line at which the cold antarctic surface waters sink beneath the warmer temperate waters.

latter. At least 3 are in common with New Zealand. Of spiders, 1 is in common with Campbell and 2 with the Aucklands, and the third with Crozets, Kerguelen and Heard.

Numbers of Species

Island area and topography: In these extreme southern environments, some of the usual principles relating to the number of species which an area can support do not apply. For the true subantarctic islands, there is almost no correlation between area of island and number of species supported. There is also no correlation between altitude range and number of species. In fact, two of the smallest groups, Macquarie and Crozet, have among the largest number of species, and these two island groups are relatively low in altitude. Heard, with almost the greatest altitude range, has the smallest number of species. South Georgia (greatest altitude range) and Kerguelen, both with by far the greatest areas, hardly have larger numbers of species, respectively, than Macquarie and Crozets. Thus, the question of the odds against successful establishment, and of extinction or survival of relicts from earlier larger land-masses, seem to override other considerations. Also, either the environment does not favor proliferation of species, or there has not been time enough since the maximum glaciation of the Pleistocene which must have at least greatly reduced the number of species, or the selective biotic factors are largely absent.

Further field work will probably not weaken the above statements because South Georgia, Kerguelen and Macquarie have been rather thoroughly investigated. More species will be forthcoming from Marion and the Crozets, and this will accentuate the contrasts, as those two are among the smallest and lowest islands.

As pointed out by van Balgooy (1969) in regard to diversity of insular floras, numerical data cannot be uniformly applied without consideration of other factors (see also MacArthur & Wilson 1967).

Table 7. Lack of relationship of area, altitude and numbers of species (Islands arranged in order of decreasing size)

			Numbers of species of free-living insects (Orders arranged in usual order of increasing no. of world species, left to right)							
	Area sq. km.	Altitude meters	Pso-copt.	Thy-sanopt.	Col-lem.	Het.	Hym.	Lep.	Dipt.	Col.	Total
South Georgia	3755	2934	–	–	16	–	1	–	13	6	36
Kerguelen	3626	1960	1	–	17	–	–	2	11	14	45
Heard	375	2750	–	–	7	–	–	1	3	5	16
Marion	297	1232	1	–	7	–	1	2	5	10	26
Crozets	233	934	1	–	15+	1	1	2	11	22	53
Macquarie	119	433	1	1	19	–	2	1	12	6	42

Notes: Some of the figures for numbers of species on Marion include estimates of those from the recent expedition still being studied. The altitude given for the Crozet Is. is the highest (Possession) of those islands collected to date only. Isle de l'Est rises to about 1200 m, but has not yet had its insect fauna sampled. Area for Crozets also ignores Isle de l'Est. The failure of the numbers of species of the various orders to increase regularly from left to right demonstrates the faunal disharmony. Discrepancies between this table and Table 5 relate to exclusion of all introduced species from this table.

Table 8. Numbers of species of free-living insects in relation to climatic position of islands (islands in sequence colder to warmer)

	No. of orders native	No. of orders introd.	Total No. of species
Heard	4	–	16
South Georgia	4	2	36
Kerguelen	5	–	45
Macquarie	7	1	42
Marion	6	1	26
Crozet Is.	7	1	53

Note: From this arrangement, it appears that the situation with Marion I. is inconsistent. For even though small in area (it is larger than Macquarie), since it has a milder climate than Macquarie, one would expect it to have more species. Another consideration is that it is younger than Macquarie and Kerguelen. Also, from the standpoint of populating by west wind drift, the gap to westward of Marion is the greater gap in the series South America-Falklands-South Georgia-Marion-Crozet-Kerguelen-Heard.

Southernmost extensions of insect families: Because of erratic representation on the different subantarctic islands, different islands possess the southernmost known occurrences of various families. As Macquarie is both southernmost and one of the richest, it boasts the southernmost extensions of the largest number of families—about 20 excluding mites (disregarding South America).

Faunal Notes on Arthropod Groups

Araneida: A number of the spider genera appear to be endemic to the subantarctic, but insufficient comprehensive studies have been made. A few genera such as *Porhana* are widespread and this genus occurs largely in the Northern Hemisphere. *Myro* is entirely far southern, occurring also in Chile, South Africa, Tasmania, and New Zealand. *Crozetulus* is similar to a species of *Risadonius* in Tasmania. *Meuizenbergia* has an African species as its type. "*Nuncia*" *unifalcata* is not a *Nuncia* (which is restricted to New Zealand), but may belong to an Australian or African genus. Possibly most of the species are relicts rather than having been transported by air currents (Forster, pers. comm.). (See Fig. 12).

Acarina: Not many conclusions can be drawn regarding the zoogeography of the mites, because they are so unequally known and so imperfectly known from nearby continents. In general, quite a number seem to be widely distributed, or appear to represent closely related species on the various islands. It may be safe to assume that a number of them have been carried by some of the wide-ranging birds which fly from one subantarctic island to another. On South Georgia there is a strong South American element and a lesser endemic element. Wallwork (1963) believes that the fauna of Macquarie indicates earlier connections with South America through West Antarctica (Andean Province) and that of East Antarctica represent a remnant of the Gondwana Province.

Collembola: This is one of the dominant groups on subantarctic islands, and undoubtedly additional species and island records remain to be discovered. It is difficult to say much of a precise nature regarding the affinities of the subantarctic springtails because most of the genera represented are of broad distribution on southern continents in general or even of wider occurrence. Some of the genera are known largely from New Zealand and Australia, particularly for some found on Macquarie, but, in general, distribution is wide. Only a very few species, other than those newly described in this volume, are known from a single island, and most of these are from South Georgia or Kerguelen. A new species is in press from Marion. Most of the species are known from 2 or 3, or more, subantarctic islands, and more than one-third are also known from true antarctic areas or from Tierra del Fuego, the Falklands, Campbell, the Aucklands or New Zealand. Largest numbers of species are known from South Georgia, Kerguelen and Macquarie. Still more remain to be described from Macquarie. Probably Marion, Crozet and Heard have been insufficiently sampled. (See Fig. 13).

Psocoptera: Zoogeographic patterns are as yet not very well understood for this order (Smithers, pers. comm.). *Antarctopsocus* (Elipsocidae) is known to be represented only by *jeanneli* Badonnel, on Marion and Crozet. Known members of the same subfamily (Propsocinae) are *Pentacladus* in Australia, *Propsocus* in Australia, Chile and Africa, and *Spilopsocus* of Campbell I., New Zealand and Australia. *Austropsocus* (Philotarsidae) is known only with the single species *insularis* Smithers of Macquarie and Campbell (See Fig. 12). The family is represented by genera in several regions, but predominantly in New Zealand and Australia. *Rhyopsocus* (Psoquillidae) is not endemic, and besides *eclipticus* Hagen of Kerguelen there are species known from Africa and from North and South America. Other members of the family are likewise known from Africa and America, as well as from the Seychelles and Java. Thus no distinct pattern emerges for the subantarctic Psocoptera, except that none are known from South Georgia or Heard, and that the majority of

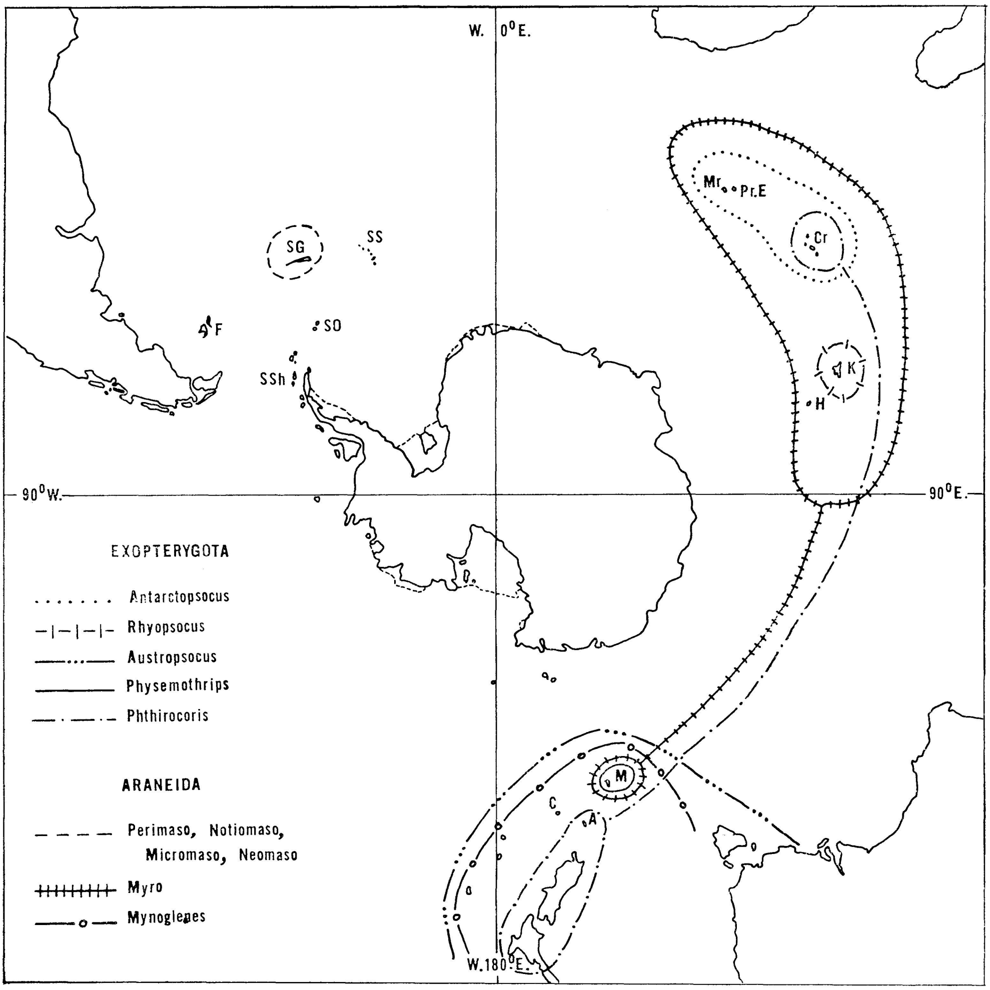

Fig. 12. Map showing distribution of certain genera of spiders (Araneida), Psocoptera, Thysanoptera (*Physemothrips*) and Hemiptera-Heteroptera (*Phthirocoris*). See Fig. 11 for identification of islands.

known relatives of the 3 endemic species (2 endemic genera) of the other 4 islands are in New Zealand and Australia, with some also in Africa or elsewhere. No relatives seem to be known from southern South America.

Thysanoptera: Only 2 species of thrips are known from subantarctic islands, and 1 of these, *Anaphothrips secticornis* (Trybom) is undoubtedly introduced. *Physemothrips chrysodermus* Stannard represents a genus known only from Macquarie. (Fig. 12). According to Stannard (1962) no clear relationships are known for this genus.

Hemiptera-Homoptera: The same 2 species of aphids have been recorded from South Georgia and Macquarie. Some additional species are shortly to be reported from Marion by Ph. Dreux. None of these species are endemic, and probably all were accidentally introduced by man, although some might have come by natural air transport.

Hemiptera-Heteroptera: The single species known from true subantarctic islands, *Phthirocoris antarticus* Enderlein is apparently endemic to the Crozet Is. This enicocephalid bug belongs to a very primitive tribe of the subfamily Enicocephalinae. Jeannel (1947, 1965) related *Phthirocoris* to African groups, in stressing its uniqueness and high degree of aptery, neoteny and other specializations. It differs from other enicocephalids in being much more slender in body, less sclerotized and in developing only a single large ovum at a time in the ovary of the female. In his later paper, however, Jeannel overlooked the fact that Gourlay (1952) had described a species of *Phthirocoris* from New Zealand and Woodward (1956) had described another from the Auckland Islands and the South Island of New Zealand. Thus we have a case of a primitive relict group known from the Crozet Is., Auckland Is. and New Zealand (Fig. 12, 19). This raises the question of whether there might still be other closer relatives in southern South America, Australia, New Caledonia or

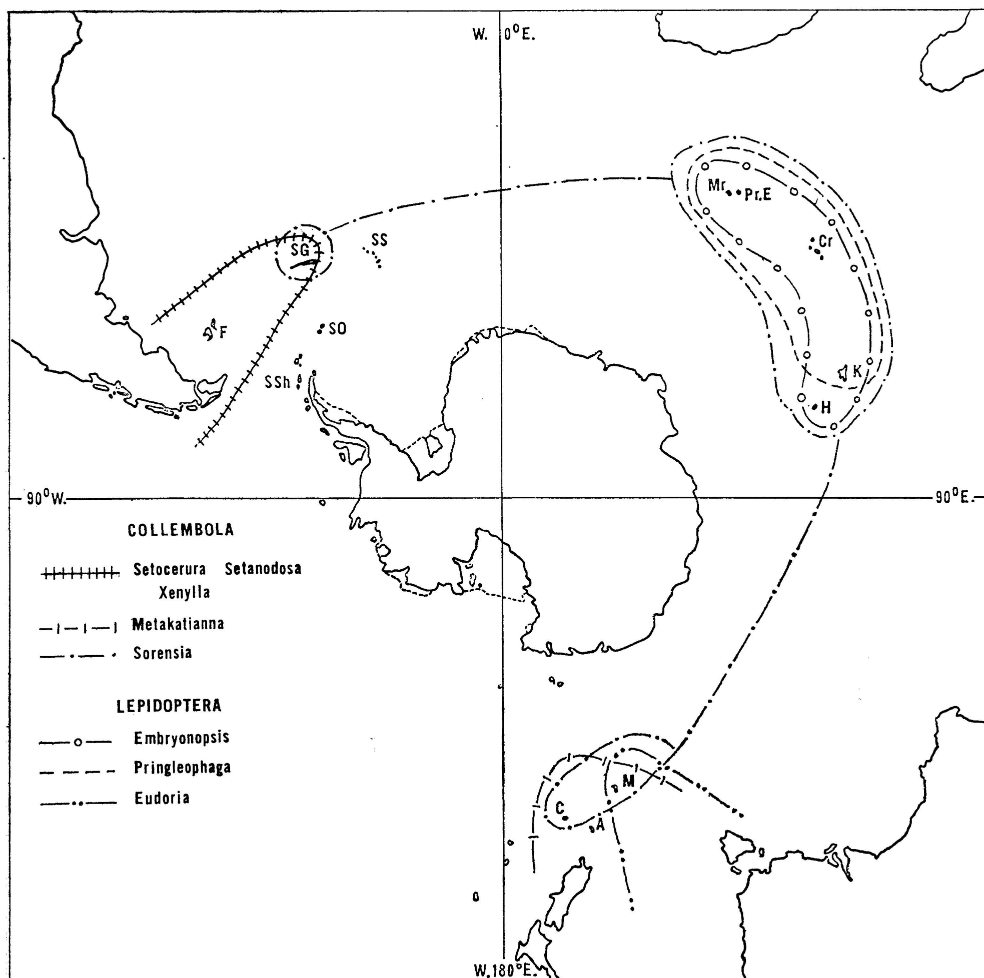

Fig. 13. Map showing distribution of certain genera of Collembola and all the native Lepidoptera. See Fig. 11 for identification of islands.

elsewhere. Even without such, the distribution of *Phthirocoris* may discount slightly Jeannel's emphasis on the close African affinities of the Crozet fauna. Woodward is inclined to follow Jeannel in placing *Phthirocoris* in a tribe by itself.

Lepidoptera: This large order is very poorly represented on subantarctic islands. Only 3 or 4 species are known from the 6 island groups. These represent 3 families. Two of the genera are endemic and have only flightless species, and the other is non-endemic and its representative is a flying species. *Pringleophaga kerguelensis* Enderlein (Tineidae: Tineinae) (fig. 20) is the larger of the 2 flightless species and is recorded from Marion, Crozet and Kerguelen. It has been suggested that the Marion population may be different from the typical form from Crozet and Kerguelen. The flightless moth on Heard was described by Brown (1964) as a new species of *Pringleophaga*, but actually is shown above by Common (p. 231) to be the same as the other flightless species, *Embryonopsis halticella* Eaton (Yponomeutidae), now known from Marion, Crozet, Kerguelen and Heard. The latter species is smaller, but is very similar to *Pringleophaga* in wing shape and general appearance.

The third species is *Eudoria mawsoni* (Womersley & Tindale) (Pyralidae), a common species on Macquarie frequently seen in flight. The genus is widespread. (Fig. 13).

Apparently nothing is known regarding close relatives or ancestors of the 2 flightless moths. Viette (1948) has discussed the subject, but primarily refers to differences of opinion regarding their family placement. It is interesting that no flightless moths are known from Macquarie, although there are these 2 on Kerguelen and 1 of them also on Heard, and several each on Campbell and the Auckland Is. In my paper above on Coleoptera, I mention some young lepidopterous larvae collected on South Georgia, but it appears that this may represent an unsuccessful introduction accidentally made by man.

In contrast to the situation on the true subantarctic islands, there are 6 endemic genera of flightless moths on Campbell I. alone, besides a dozen other moths. Thus, even though Campbell is farther south than Marion, Crozet and Kerguelen, and much smaller than the latter, its fauna is very much larger, relating to its more continental nature and greater proximity to the Auckland Is. and New Zealand.

Coleoptera: This large order is rather haphazardly and unevenly represented on subantarctic islands, even though it is the best represented insect order. Beetles are not very readily carried about by air currents, though they are rather hardy. Some are capable of being transported by floating trees. The buffetting to which these are subjected in this zone is certainly a strong deterrant, even though wood from southern South America is frequently found on subantarctic islands as far as Macquarie, the farthest by sea-current/wind route from South America (Barber et al. 1959). If the respective island faunas had developed from a common origin then there should be more uniformity in present faunal representation, after the screening of maximum ice cover of the Pleistocene. However, the present contrasts are rather great, suggesting multiple chance introductions and some relicts.

Carabidae are represented by 3 species or races in the Crozets, 1 in South Georgia, but none on the other islands except 1 thought to be introduced on Kerguelen. The Migadopini, a much discussed austral group is not found on these islands, but occurs in the Auckland Is. and in southern Australia. Dytiscidae are found only on South Georgia. Staphylinidae are represented by 5 species on Macquarie, none on Heard, 2 each on South Georgia and Crozet and 1 each on Marion and Kerguelen. Pselaphidae, Hydraenidae and weevils are found only on South Indian Ocean Islands, and are totally lacking on South Georgia and Macquarie. The South Georgia and Macquarie surveys have been rather thorough, and I went to Macquarie particularly with the objective of finding weevils, as well as other beetles other than Staphylinidae, with negative results.

The hydraenid, *Meropathus chuni*, is shown in fig. 21. Lathridiidae and Perimylopidae are known only from South Georgia. Thus there are great contrasts, with apparently no beetle families except Staphylinidae in common between South Georgia and Marion, and none in common between Heard and Macquarie. Hydraenidae is represented by a species on Campbell, but the weevils on South Indian Ocean islands and those on Campbell and the Aucklands are of mutually exclusive subfamilies. Campbell has nearly as many species of Coleoptera as do all 6 of the true subantarcric island groups combined.

Weevils are dominant insects in continental areas as well as on most islands, but are lacking on the two southernmost subantarctic islands—South Georgia and Macquarie. However, Marion, Crozet, Kerguelen and Heard jointly possess a remarkable endemic tribe of weevils represented by

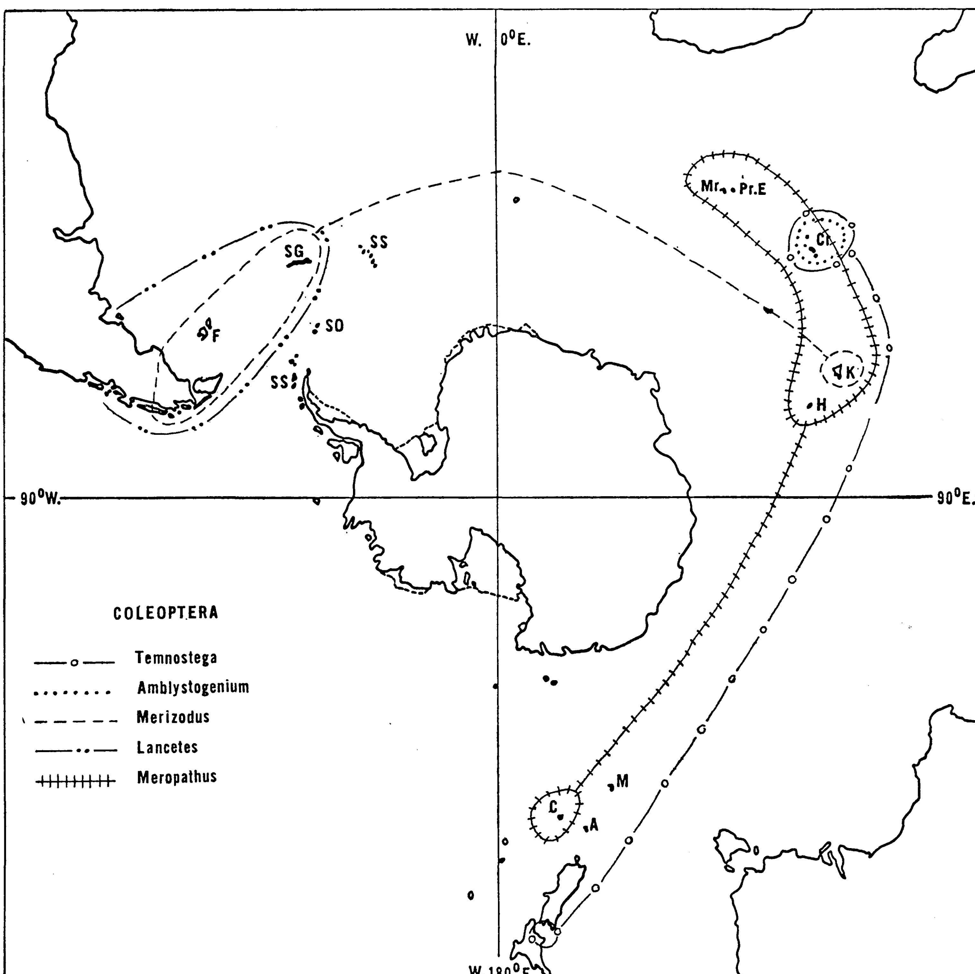

Fig. 14. Map showing distribution of certain genera of beetles: Carabidae (*Temnostega, Amblystogenium, Merizodus*), Dytiscidae (*Lancetes*) and Hydraenidae (*Meropathus*). See Fig. 11 for identification of islands. For northward extention of range of *Meropathus*, see Ordish, in press.

7 genera[1].

Although more than 30 species have been named from this complex, with the synonymy indicated in Dr Kuschel's paper in this volume, and in the footnote herewith, the number is reduced to 23 species, and might be further reduced by synonymy of some of Jeannel's Kerguelen species, unless the recent South African investigation of Marion I. has brought to light additional species. As presented in the list in this chapter, 4 species are known from Marion, 14 from the Crozets, 11 from Kerguelen and 4 from Heard. Marion has 3 endemic species, the Crozets have 10 endemics (of which 4 are found only on Ile des Cochons and 4 only on Ile de la Possession). Kerguelen has 5 endemics and Heard only 1. No single species is known from all 4 of the island groups, but 3 species are known from 3 islands each (Crozet-Kerguelen-Heard, 2 cases; Marion-Crozet-Kerguelen, 1 case). The largest genus, *Ectemnorhinus*, with 9 species, is divided into 2 subgenera, 1 restricted to Marion and Crozet, the other to Kerguelen and Heard. The generic ranges are shown in fig. 16.

Diptera: The flies and midges constitute the second-best-represented order of true insects in the subantarctic, numbering 43 species. When they are more thoroughly studied they may equal the beetles (49) in numbers of species. This order includes the southernmost free-living holometabolic insects, with 2 midges in the Antarctic Peninsula—South Shetland Is. area. Also, Diptera are better represented on South Georgia and Macquarie than are Coleoptera. Deviating from this trend there are only 3 flies known from Heard as against 4 weevils. However, there might still be a midge or other fly discovered on Heard in the future.

It may not be safe to say that Diptera are the most cold-tolerant holometabolic insects, because they are so much more readily transported by air currents than are Coleoptera, and because a higher proportion of them have less specific larval food requirements. Diptera are much more numerous in species in the Arctic than are Coleoptera, but here again vagility may be an important factor because of the recent loss of ice-cover, and also the larval requirements are important.

South Georgia has 13 species of Diptera, Macquarie 12, Crozet 11, Kerguelen 11, Marion 5 and Heard 3. This ratio is different than for most other groups, where in most cases Crozet, Kerguelen or Macquarie have more species than South Georgia. The relative representation of different families is quite unequal. Trichoceridae and Sciaridae are known from South Georgia and Kerguelen, but not from the other islands. Simuliidae is known only from Crozet and Tipulidae only from Macquarie. Several other families are known only from a single island (see Table 6). Coelopidae is not known from South Georgia. (Fig. 17, 18, 22–26).

Brundin (1966: 444) indicated uncertainty as to whether *Parochlus steineni* (Gercke) (of South Shetlands, South Georgia and southern Andes) might be a preglacial relict or not.

Hymenoptera: Only 3 species of this order are recorded. There are probably a few additional minute parasitic wasps. A single specimen was taken on Macquarie but could not be identified. The 3 known species probably parasitize coelopids and other flies breeding in kelp or other rotting vegetation and carrion. Their relationships are rather obscure. Two of the genera are endemic to the subantarctic (*Notomymar*), or to this zone together with southern cool temperate (*Antarctopria*). The other is widespread.

DISPERSAL TO SUBANTARCTIC ISLANDS

Isolation

All of the true subantarctic islands, as treated here (South Georgia, Marion, Crozets, Kerguelen,

1. I believe that *Neocanonopsis* Hoffmann, 1964 of the Crozets is a synonym of *Christensenia* Brinck, 1945, and that *N. dreuxi* Hoffmann, 1964, type of *Neocanonopsis*, is a synonym of *C. antarctica* Brinck, 1945. Both were described from Possession Island. **New Synonymy.**

Heard, Macquarie) are quite isolated from continents and in most cases quite distant from other islands, both Antarctic and south temperate. In some senses Macquarie is the least isolated, being about 1450 km (900 miles) from Antarctica, 1000 km (600 miles) from New Zealand and 1300 km (800 miles) from Tasmania, with Campbell and the Aucklands much closer but to leeward. Marion is about 1600 km (1000 miles) from South Africa. South Georgia is about 1750 km (1100 miles) from Tierra del Fuego, 1400 km (860 miles) from the Falkland Is. and about 1400 km from the Antarctic Peninsula. South Georgia is only about 480 km (300 miles) from the South Sandwich Is., but the latter cannot be considered a productive source area for fauna, and they are to leeward of South Georgia. In another sense, South Georgia is the least isolated of the subantarctic islands, since it is more or less to leeward from the Antarctic Peninsula, Tierra del Fuego and the Falkland Islands. However, these are not very rich source areas. Tierra del Fuego, the richest, is the farthest away, and the windward portions of South Georgia are rather forbidding, being largely of glaciers or bare rock. In this sense, Macquarie is one of the most isolated of all, as to windward of it is a tremendous expanse of ocean without any land for about 3000 km (2000 miles) to Heard, which is both small and the poorest of the subantarctic islands.

Faunal Origins

As with Antarctica, it is difficult to prove whether many of the present indigenous species of the subantarctic islands are relics of former larger land masses or have been air-dispersed since the maximum glaciation of the Pleistocene. Most likely, again, both relics and waifs are involved. The tendency would be to ascribe endemic genera or complexes to the relict category, and local endemic species of temperate continental genera to the waif origin category. However, many of the groups represented are still too poorly known for southern continents in general to permit sound deductions on the question of origin and history. With the mounting evidence for antarctic land connections of the past, the role of relics resulting from transantarctic migration or antarctic evolution seems possible. On the other hand, the many close affinities with temperate continental species suggest the role of recent air dispersal. The paucity of insect fossils detected to date in the antarctic region does not contribute much data of pertinence.

Air Dispersal across Southern Seas

In general the present air circulation of the Antarctic region is not particularly favorable to immigration of insects from the cool-temperate southern tips of the southern continents. Air movements to the south are mostly at high altitudes, converging over the South Pole and dropping down to the surface, then radiating outward over the ice to the fringes of Antarctica, where they are gradually deflected into a clock-wise circulation around the Antarctic continent. Thus, essentially, the winds which almost constantly blow at high velocity against a subantarctic island are traversing only open sea, and the other subantarctic isles, after having come from the Antarctic continent. To a lesser degree, some of the winds may have travelled past the southern tips of South America, Africa, Tasmania or New Zealand. If winds had been more favorable in recent periods, possibly more groups might have become established on certain islands. However, with the limited ecological opportunity and generally strong winds, colonizations are naturally limited. That more could have established is indicated by some successful establishments of species introduced by Man, and also by empty microhabitats. For instance, there are no carabid beetles on Heard or Macquarie, although these are present on most oceanic isles and some small winged species are said to have blown across the Atlantic Ocean.

Transport by Sea Birds

Several of the large sea birds which nest on subantarctic islands are very wide-ranging in their flying habits. The Wandering albatross (*Diomedea exulans*), the Royal albatross (*D. epomophora*), the Black-browed albatross (*D. melanophris*), the Gray-headed albatross (*D. chrysostoma*) and the Giant petrel (*Macronectes giganteus*) are very strong flyers and regularly go from one side of Antarctica to another. Individuals of most of these species have been banded in South Georgia and retrieved on the coasts of Tasmania, New Zealand or elsewhere, having flown with the west wind via the South Indian Ocean (Tickell 1968; Sladen et al. 1968). Thus opportunities exist for long-distance transport of insects by these birds (Falla 1960). In the Auckland Is. I found seeds and beetles among inner feathers of petrels, though they were probably picked up by the birds floundering among bushes when confused by a lantern at night (Gressitt 1964b).

Trapping Experiments

Some data have been accumulated from work over a number of seasons on the seas in southern

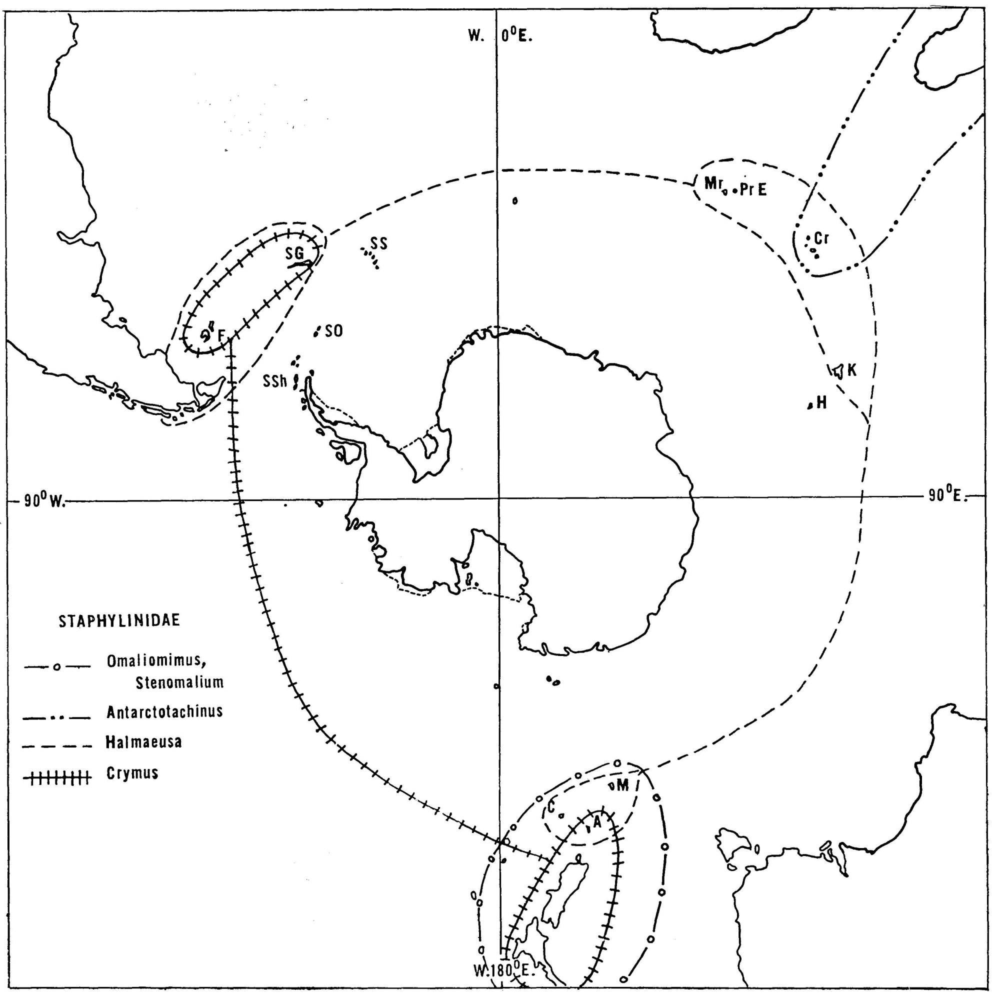

Fig. 15. Map showing distribution of certain genera of Staphylinidae. See Fig. 11 for identification of islands.

Table 9. Groups of insects trapped south of 50° South Latitude, away from land or in Antarctica.

	No. of specimens	Range of degrees Lat., S	Range of degrees Long.	Distance from probable source (km)	Group occurs on Subantarctic isles
Araneida	5	53–74	174–175E	400–1300	×
?Lycosidae	1	52	175W	900	
Salticidae	1	52	175W	900	
Micryphantidae	2	75–77	163–164E	3000–3200	×
Acarina	7	50–62	159–172E, 50W	10–1600	×
Meso: *Cyrtolaelaps*	3	65	65W	1–2	×
Crypto: *Alaskozetes*	4	60–68	54–65W	1–70	×
Collembola					
Hypogastruridae	5	62–77	164–171E, 62W	1–400	×
Isotomidae	2	64	56W	200	×
Tomoceridae	1	70	85W	1200	?
Thysanoptera	3	59–68	174–175E	800–2000	?
Thripidae	4	50–58	174–175E	290–1200	×
Aeolothripidae	1	49	174E	280	
Psocoptera	2	59–77	166–175E	800–3000	?
Liposcelidae	3	58	175E	1200	×
Homoptera					
Aphididae	35	50–79	166–175E, 175W, 57–68W	3–3100	×
Coccidae	1	58	175E	1200	
Jassidae	1	53	175W	1000	
Heteroptera					
Lygaeidae	1	60	171E	1400	
Ephemeroptera	1	55	68W	10	
Lepidoptera					
Gelechiidae	4	55–68	59–80W	150–1400	
Microlepidoptera	5	52–54	165–175E, 68–71W	3–800	
Geometridae	1	53	66W	45	
Nymphalidae	1	71	97W	3500	
Diptera					
Tipulidae	3	53	61–73W	3	×
Psychodidae	1	53	60W	10	×
Chironomidae	122	52–65	61–72W	3–370	×
Ceratopogonidae	4	54	68–72W	3–8	
Mycetophilidae	16	52–58	169E, 60–70W	3–800	
Sciaridae	5	53–59	175E, 68–71W	8–800	×
Bibionidae	2	53	61W	10	
Dolichopodidae	1	50	174E	300	×
Coelopidae	2	50–55	166–169E	3–10	×
Sphaeroceridae	4	51–53	170–174E, 61–67W	3–600	×
Agromyzidae	1	53	68W	3	
Ephydridae	21	51–62	174–175E, 57–72W	3–1320	×
Helomyzidae	1	54	70W	10	×
Drosophilidae	2	53	61W	10	
Tachinidae	2	54	68W	8	
Calliphoridae	1	55	64W	12	
Muscidae	2	54	68–70W	3–8	
Coleoptera					
Staphylinidae	1	53	61W	10	×
Lathridiidae	3	77	166E	3200?	×
Scarabaeidae	1	53	67W	20	
Aglycideridae	1	60	175E	1200	
Hymenoptera					
Ichneumonidae	2	53	175W	1000	
Braconidae	13	54	61–72W	3–10	
Eulophidae	2	53	175W, 66W	80–1000	
Encyrtidae	2	53–55	68–71W	5–10	

regions. This work has been aimed at sampling the air to determine what arthropods are being commonly transported in the air circulating in the far southern areas.

The data presented here (Table 9) have been augmented from a table previously published (Gressitt 1967) by the addition of more recent records (Holzapfel et al. 1970).

On South Georgia Clagg attempted some trapping experiments, although equipment suffered heavily from strong winds. The data on specimens trapped are presented in Table 10. Only Diptera have species in South Georgia capable of flight. Chironomidae are most conspicuous and widespread, and adults are abundant from October to April, May or early June. Flight is usually low, below the tops of the tussock grass or other vegetation, and occurs only during calm weather, as a rule. Helomyzidae were found flying only along beaches or other coastline. The Trichoceridae were taken mostly in hand-net sweepings through tussock and other vegetation. Mycetophilidae (*Mycomya*) and Psychodidae (*P. parthenogenetica*) were taken in sweeping grass, but not in trap nets.

Discussion of Dispersal

The overruling fact of great obstacles to successful dispersal and establishment of insects on subantarctic islands renders many theories less applicable here than in more favorable climates. To begin with far fewer naturally dispersed organisms reach these islands in a viable state. Those which arrived, particularly earlier following post-Pleistocene ice recession, would have found fewer favorable environments, including fewer species of established plants. Thus many of those few which arrived in a viable state would not have found appropriate plant or animal food. Those species associated with bird and seal rookeries were probably the earlier ones to establish, as well as those inhabiting the littoral zone and depending on algae or other marine shore life for food. Even with establishment, the probability that birth rate would exceed death rate (MacArthur & Wilson 1967: Chap. 4) might be poor. Since arthropods inhabiting bird rookeries would be more likely to be transported by birds, this has probably been the more likely method of transfer of such associates from island to island, or from the southern tips of the continental areas to subantarctic islands. This would apply to various non-parasitic mites, collembolans, and perhaps even certain fly puparia, psocopterans or others, as well as parasitic and normally nest-inhabiting forms.

In general, the small size of most arthropods on these islands suggests that many of them could have come by air and bird transport. Some of the larger species, such as the perimylopid beetles of South Georgia and the weevils of the South Indian Ocean isles might have been dispersed by floating in logs. On the other hand, the latter, being an endemic group, might date back to early connections, or at least to conditions of closer proximity to continents. Furthermore, they do not now inhabit logs, as there are no trees on these islands, and some must have been dispersed between these islands after the islands were separate. The fact that many dominant orders and families are absent from the fauna must be related both to unfavorable environment and obstacles to successful dispersal. Certainly the latter loom large, and there is considerable analogy to the situation with greatly isolated islands in warmer climates (Gressitt & Yoshimoto 1964).

It is suggested that new introductions take place so infrequently on these isles that many of the processes described by MacArthur & Wilson (1967: Chap. 5), such as competitive displacement, occur more rarely. Also, populations, after establishment, may not increase sufficiently before unfavorable events cause extinction. On the other hand, pressure of new invaders is low, and since competitors are few, theoretically there is greater chance of existing species persisting. One might expect that certain groups, better adapted to success in this environment, would be somewhat uniformly established on these islands subject to the same circulating winds and sea currents. This is to a certain extent true in a general way, since certain genera of prostigmatic mites, oribatid mites

Table 10. South Georgia trap-net collections (numbers of specimens trapped)

Date	Chironomidae (3? spp.)	Helomyzidae	Sciaridae (*Bradysia*)	Trichoceridae	Sample No.	Locality
31.XII.'62	46				1	Bird I.: Wanderer Val.
2.I.'63	30				2	〃
3.I.'63	6				4	〃
5.I.'63	9				5	〃
6.I.'63	3				6	〃
8.I.'63	2				7	〃
15.I.'63	4				8	〃
17.I.'63		1			9	〃
18.I.'63	2	1			10	〃
12.II.'63	1				11	Bird I.: Freshwater Bay
13.II.'63	1				12	〃
14.II.'63	1	1			13	〃
15.II.'63	3	1			14	〃
16.II.'63		1			15	〃
28.I.'64			12		IV.1	Jorobihaan
29.I.'64			4		IV.2	〃
3.III.'64	5	2		2	V. 2	Moltke Hrbr
4.III.'64	9			1	V. 3	〃
Totals	102	7	16	3		

and collembolans are found on all of the islands. However, among the higher insects there is less uniformity, and certain orders and families present on some islands are absent from others.

Because of the small size of the islands and great distances between them and from other source areas, the stepping stone theorems (MacArthur & Wilson 1967: Chap. 6) are difficult to apply here. Exponential distribution (l.c., p. 125) would apply in this case, but quantifying it would be difficult. Although the islands are small and widely separated, they are more or less in line with fairly unidirectional wind.

Brundin (1965, 1966) has attempted to discredit the role of air-borne transport of insects across seas, in demonstrating for 3 subfamilies of Chironomidae that trans-antarctic land migration and evolution in the antarctic area was a reality. He states that Hooker's ideas of plant geography, and some of Skottsberg's ideas, were sound, but that many of those of Darwin, Wallace, Matthew (1939), Simpson and Darlington (1965) were wrong in regard to far southern biogeography. However, there are many groups of insects which do not show the patterns and relationships brought to light in Brundin's studies.

Brundin appears to throw out all air dispersal over water. However, most isolated Pacific islands are of purely volcanic origin, or of coralline origin, or of a combination of both. Although the permanency of the oceans is no longer a secure theory, still many islands have evolved since the Pacific was very large and have always been distant from continents. This and much other evidence (Zimmerman 1948; Gressitt 1956; Gressitt & Yoshimoto 1964; Carlquist 1967) indicates that much of the biota on mid-Pacific islands and others has arrived by long distance trans-oceanic dispersal, possibly much of it by air, over long periods of time. Brundin's midges are rather fragile and short-lived insects, but we have trapped them alive at varying distances from shores. Many other insects are more hardy and are well represented on oceanic islands. The subantarctic area is not such a fertile field for documenting this, because of the harsh climatic obstacles. This should help

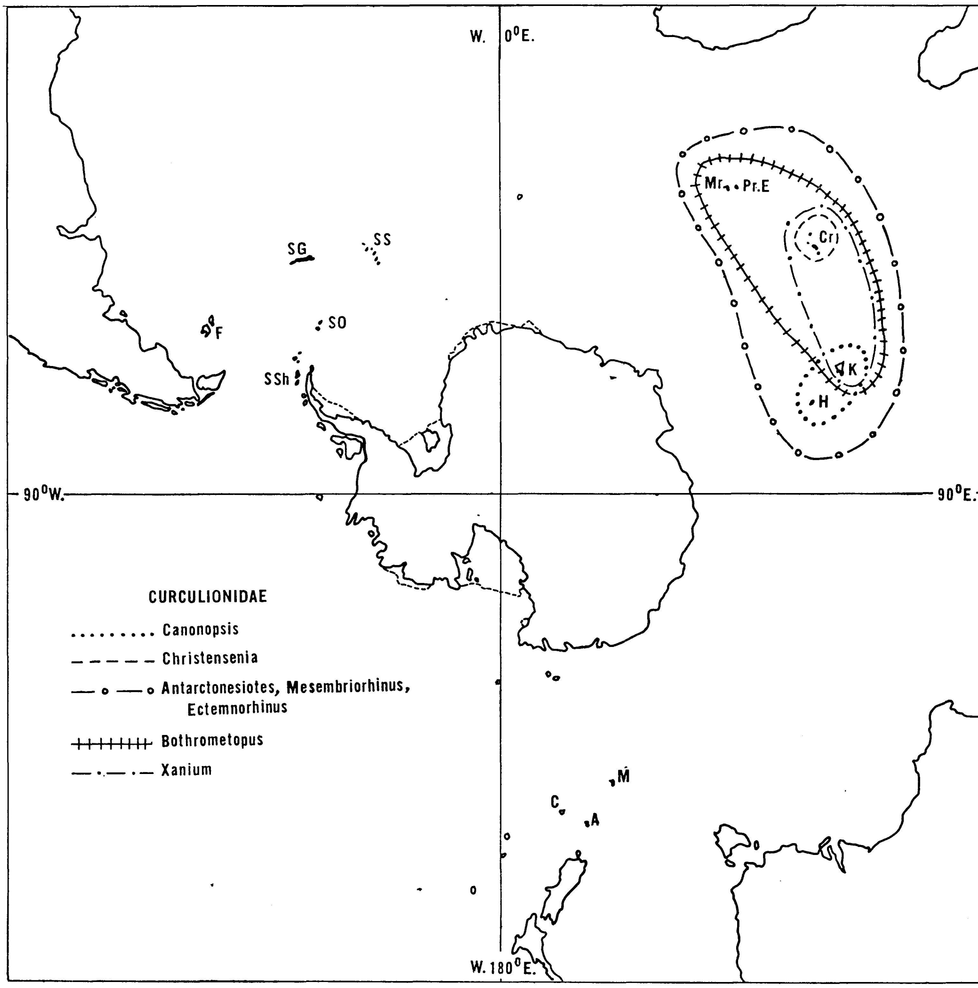

Fig. 16. Map showing distribution of genera of subantarctic weevils. See Fig. 11 for identification of islands.

explain why more insects have not populated these cold and windy islands since the Pleistocene.

Wilson & Simberloff (1969; Simberloff & Wilson 1969; Simberloff 1969) have carried out a highly significant study of arthropod propagule invasion to islets of the Florda Keys. The islets studied were first censused in detail and then had their faunas exterminated by tent fumigation. The high rate of propagule invasion following defaunation was very impressive. Recognizing that those islets were near source areas, the extrapolation to more distant isles is consistent with other facts and data.

Some very pertinent data on the populating of a new island has been documented by Lindroth et al. (1967) for Surtsey, off the south coast of Iceland. The evidence is very meaningful to me because I have seen Surtsey (and its lost sister volcano) at various stages of development, including a close circling in a small plane in 1968. Other extensive data on long or short-distance dispersal

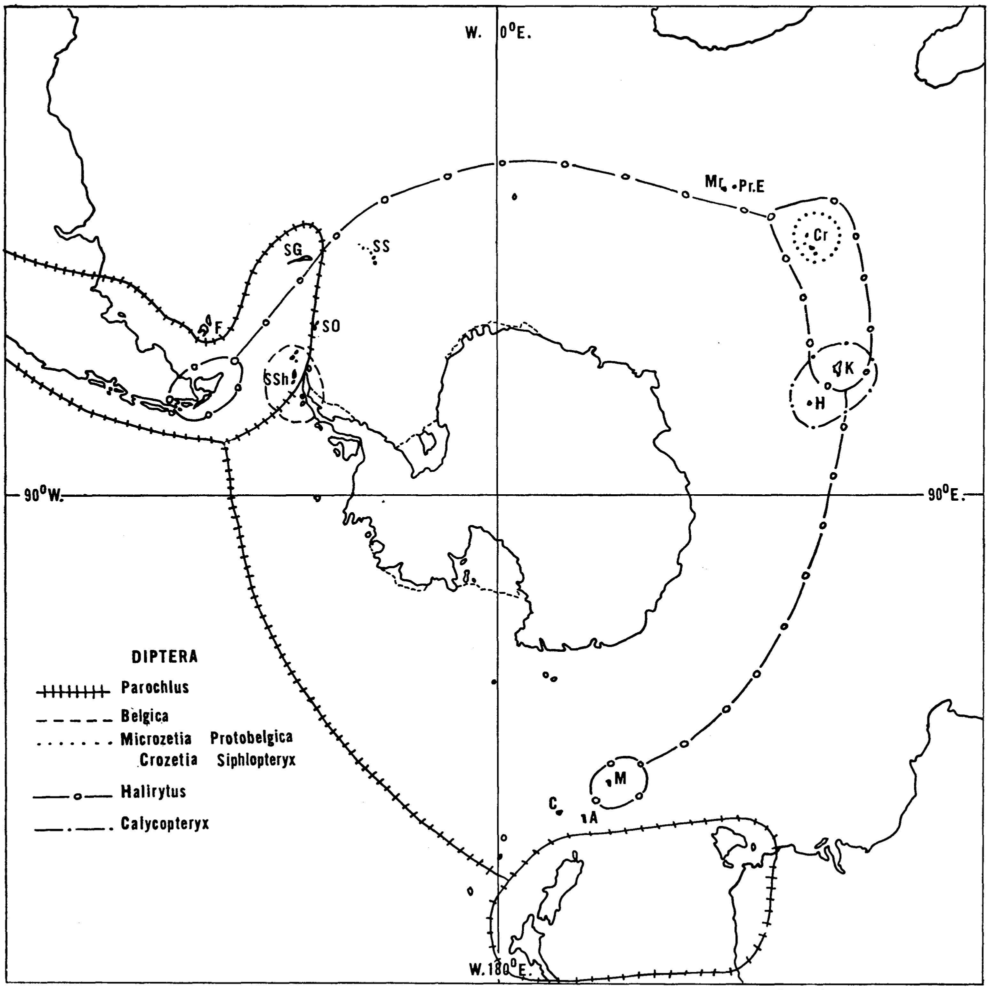

Fig. 17. Map showing distribution of certain genera of Diptera. See Fig. 11 for identification of islands. Brundin (1966: 115) states that *Parochlus* occurs on Campbell I.

have been presented by Wolfenbarger (1959), Johnson (1969) and others.

Matthews & Matthews (1970) reported on an Association for Tropical Biology symposium which indicated general agreement with the fact of over-sea dispersal, including air dispersal, for various organisms, on the part of most participants. Several stressed the natural high dispersal rates.

ZOOGEOGRAPHIC PATTERNS

Affinities of the Subantarctic Fauna

The true subantarctic islands do not form a well-defined zoogeographic unit, and demonstrate some diverse affinities in their respective elements. It is difficult to draw succinct deductions or expound theories regarding an assemblage of faunules like those which are involved here. The island groups — South Georgia, Marion—Prince Edward, Crozet, Kerguelen, Heard and Macquarie — are on 3 sides of Antarctica in different oceans and facing 4 other continents. Their points in common consist of extreme climate, location close to the Antarctic Convergence in the strong circum-antarctic west winds and currents, relative isolation and relatively small size. The environment is so unfavorable that many faunal elements which might be expected are totally lacking. On the other hand, that more could exist if established is shown by the persistence of some species introduced by Man.

These islands, possessing fragmentary and highly disharmonic faunas, lack most of the groups of plants and animals thought of as characteristically 'far southern.' These are southern-distributed groups found in the southern portions of the various southern land masses, or at least in southern South America and New Zealand and/or Tasmania.

Several of these groups of plants or animals, often called 'antarctic' in distribution because of their occurrence on both sides of the Antarctic continent, are frequently cited (Darlington 1965). One of these groups is *Nothofagus*, the southern beech tree. This genus is the dominant tree in southernmost South America and in southern New Zealand, and also occurs in Tasmania, a few areas of southeastern Australia, in New Caledonia and New Guinea. There is fossil pollen of *Nothofagus* in Kerguelen, but this can be blown a long distance. The pollen is also to be found in Antarctica, as well as fossil leaves. Of course the antarctic continent supported many temperate plants in late Tertiary. Although there are a few species of trees in the Auckland Is., *Nothofagus* does not occur there or on Stewart I. Another prominent 'antarctic' tree is *Araucaria*, with a number of species in temperate South America and in New Caledonia, and scattered species in New Guinea, E. Australia and Norfolk I. It is also known as fossils in New Zealand, Kerguelen and Antarctica. Among insects, a prominent example of this distribution, and an unique and isolated group is the hemipterous family Peloridiidae. This group of small inhabitants of wet moss is known from Chile, New Zealand, eastern Australia and Lord Howe I. Various groups of chironomid midges (Brundin 1966) are shown to have close sister-grouping in the 2 respective areas across Antarctica. Certain groups of carabid beetles such as Migadopini (Jeannel 1965, Darlington 1965) also demonstrate similar relationships, as do various other groups. A bee genus, *Leioproctus*, is known only from temperate South America, New Zealand, Australia, Lord Howe I., New Caledonia and New Guinea (Michener, pers. comm.). On the other hand, many dominantly tropical groups show no close kinship in the respective areas. Though it is quite possible that Antarctica was both a migration route and an area of evolutionary development in the Tertiary, very little entomological evidence of it exists in fossil records. The fact that these groups are largely lacking from subantarctic islands does not constitute convincing evidence for or against transantarctic migration or continental drift. Although there is now abundant evidence for continental drift and more extensive and more temperate land area in far southern regions, the drifting was probably well advanced at an earlier stage in evolution than the spread of many present day groups. How much it affected the distribution of ancestors of these groups is difficult to say.

The fact that mammals and fresh water fishes of South America and Australia-New Zealand show little or no relationships, whereas a number of groups of plants and insects do show close relationships suggests that there was a stepping stone situation between the respective continents during late evolutionary periods. Thus, those organisms which were more adept at crossing water barriers show southern distribution patterns to greater degrees. Of course the successful spread of many groups between the southern continents required greater proximity than at present and a more favorable climate. The fact of the purely far southern distribution of the Peloridiidae has been used as an argument for continuous land connections. However, this need not necessarily be so,

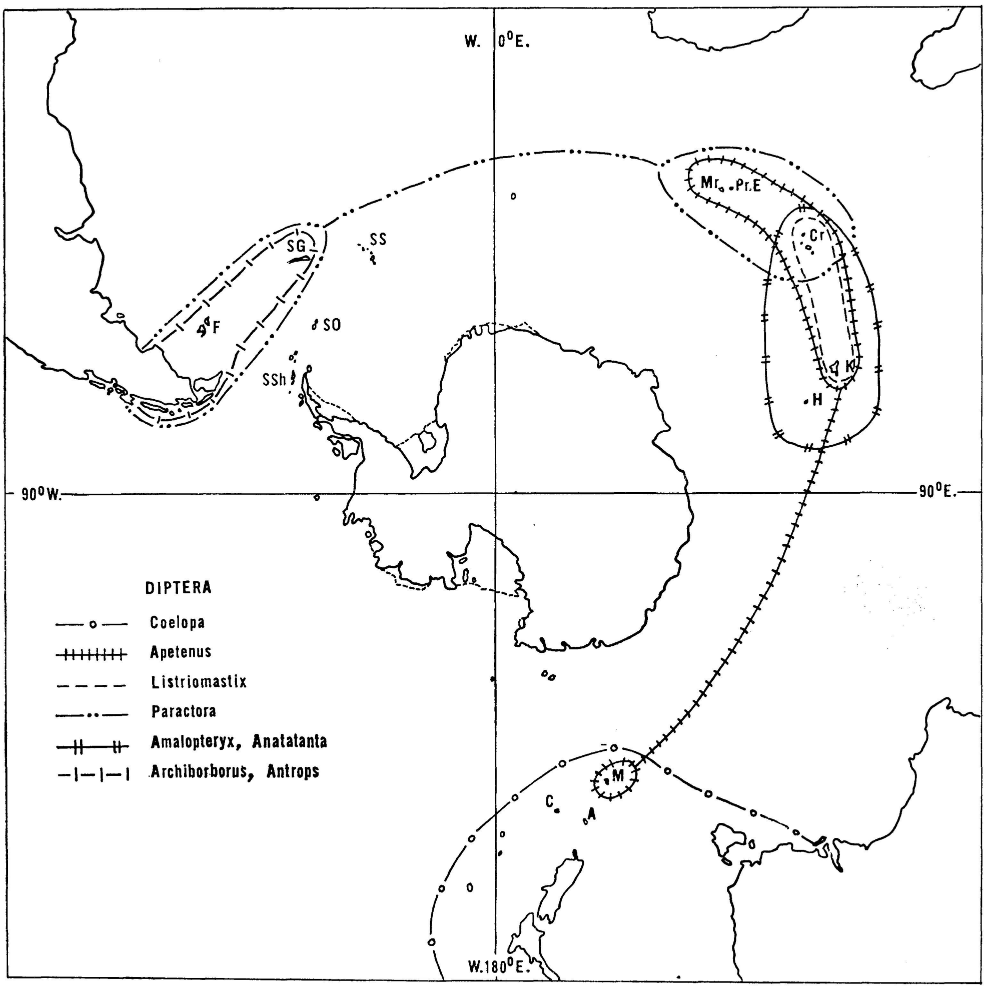

Fig. 18. Map showing distribution of additional genera of Diptera. See Fig. 11 for identification of islands.

as given sufficient time, almost any kind of insect, particularly small ones, may become air-borne. Though most peloridiids are flightless, flying individuals appear in a South American species, as with many kinds of normally flightless ground beetles (Darlington 1965).

In some respects, South Georgia's fauna is related to that of southern South America, the Falklands and the Antarctic isles and Antarctic Peninsula, whereas the South Indian Ocean isles (Marion, Crozet, Kerguelen & Heard) have some affinities with Africa (more particularly certain African mountain-tops), and Macquarie has elements in common with Campbell, the Aucklands or other New Zealand areas. On the other hand, a number of circum-antarctic relationships are indicated. These involve genera with species represented on a series of islands, generally in succession. These may be said to be distributed in a clock-wise direction and related to "west wind drift," since both the air and sea currents revolve around Antarctica from west to east at high rates,

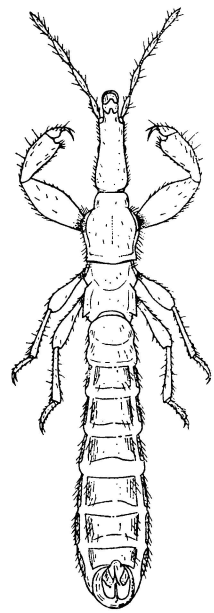

Fig. 19. *Phthirocoris antarcticus* Enderlein (Heteroptera: Enicocephalidae), Crozet (Possession I.), adult male (partly after Jeannel 1947).

providing means of transport, even though under greatly adverse conditions of climate.

The maps (Fig. 12–18) show several examples of this type of distribution. In these cases, the elements so indicated are believed to occur only on these islands. It is of course possible that some occur on southern continental extremities and have not yet been recognized there.

The highly disharmonic nature of the entomofauna of these islands is to be expected considering the dominating harsh climatic factors, the small size and isolation of the islands and the many obstacles to successful colonization. The relative numbers of species are more or less consistent with declining patterns of representation between the southern tips of the major far southern land masses, such as southern South America, New Zealand and Tasmania, and the cool temperate islands such as Falklands, Campbell and Aucklands on the north, and Antarctica to the south. Several of the individual subantarctic islands have faunules roughly similar in makeup to that of Antarctica, though with a few additional groups represented.

Trans-Antarctic Relationships

Jeannel (1965) reviewed an historical biogeographical area he established earlier called 'Sudamadie.' This included South Africa, Madagascar and the Mascarene Is. as the principal portion or continental part, with an extension to the Crozet Is. as the southern part. Sudamadie was partly to account for the elements common to South Africa and Madagascar, which are not found elsewhere but with a few occurring in the Mascarene Is. or Crozet Is.

One of the cases Jeannel used as an argument for including the Crozets in Sudamadie was the staphylinid genus *Antarctotachinus* which he stated had its closest relative (*Omaliopsis*)[1] in South Africa and Madgascar. Steel (1964: 345), and also Jeannel, showed that *Antarctotachinus* is very closely related to *Omaliomimus* Jeannel[2] of Macquarie, Campbell, Aucklands and New Zealand.

Jeannel also pointed out probable close relationship between *Omaliopsis*, *Antarctotachinus* and *Arpediomimus* (Falklands, Aucklands, New Zealand). The last is synonymized with *Crymus* in this volume.

Another of Jeannel's 3 cases used to place the Crozets in Sudamadie was the carabid genus *Amblystogenium* which is related to 4 other genera of Plocamotrechini in southern Africa (1 of them in Madagascar). *Amblystogenium* is considerably changed by modifications related to long-standing aptery.

Jeannel (1965) has stressed the carabid tribe Migadopini as one which evolved in the Antarctic when it was temperate. Darlington (1965: 36) suggests that its evolution has been complex and that it has close relatives (Elaphrini) in the north temperate zone, that it is not entirely flightless, and that it presently occurs in some warm areas (E. Australia, Uruguay), as well as in far southern South America, Falklands, Aucklands, New Zealand and Tasmania.

The carabid tribe Broscini is more widespread in the northern hemisphere and in the far southern areas, but comes closer to the tropics in the north and is more widespread and a little less southern than the Migadopini (Darlington 1965: 39). The Trechini is also far northern and far southern, but also spans the tropics. *Bembidion* has a distribution similar to that of the Trechini. Darlington suggested that many of these groups with conspicuous far southern distribution (not including S. Africa) may have originated in the northern hemisphere, and spread across the tropics and then disappeared there. Brundin (1966: 64 etc.) takes strong exception to Darlington's views, and presents extensive evidence for close trans-antarctic relationships in chironomid midges.

Jeannel's (1953b) third case was the pselaphid *Pseudeuplectus* of Crozet, which is related to forms in Madagascar, but not to that on Campbell I. (see Park 1964).

Jeannel (1965) felt that the southern Indian Ocean islands were formerly much larger in area and that the old land mass largely sank, with the present remnants of the fauna being carried on the younger lava flows. In this case the islands would not have been built up from deep ocean bottom as is the case with many of the Pacific insular groups, but from the sunken subcontinent. Jeannel indicated that most of the major changes in land configuration took place in the Tertiary. Thus "Sudamadie" was a fragment of Gondwanaland. Of these islands, only Kerguelen is known to have fossils other than post-Pleistocene peat deposits. There is much lignite there, containing mosses, grasses, angiosperms (*Nothofagus* and others), and the conifer *Araucarioxylon* (apparently a good *Araucaria*). This flora was attributed to the Eocene or Oligocene. Jeannel stated that the submarine plateau was part of Antarctica in the Mesozoic and that bridges still remained through part of the Tertiary. He referred to the paleantarctic lines, with much transfer in the Jurassic, with connections from Africa to New Zealand in lower Cretaceous and with Australia but not Africa in upper Cretaceous, and to Australia, but not New Zealand, in the Eocene. Jeannel stated that *Nothofagus* was paleantarctic from Cretaceous to Oligocene, but extended only to Kerguelen, and did not occur on Sudamadie.

Although Jeannel placed much weight on continental drift, he still felt that after the movements separated the southern continents, these small southern Indian Ocean islands received much of their

1. Actually synonymous with it, though Jeannel would not use the older *Antarctotachinus* of Enderlein because of the name having incorrect connotation of relationship.
2. Jeannel (1965: 358) referred to *Omaliomimus* as authored by Steel, though he himself named it (Jeannel 1940: 117), and as having only 2 species (Macquarie, Campbell, Aucklands), whereas several are known from New Zealand, 1 of which latter Jeannel had used as the type of the genus.

Jeannel (1965: Fig. 4, Fig. 9, Fig. 45) shows "Dougherty I." (near 48° S, 135° W) on his 3 maps of the Antarctic area, whereas there is no evidence that such an island ever existed. Unfortunately Hennig's (1960) maps show it also, but without name.

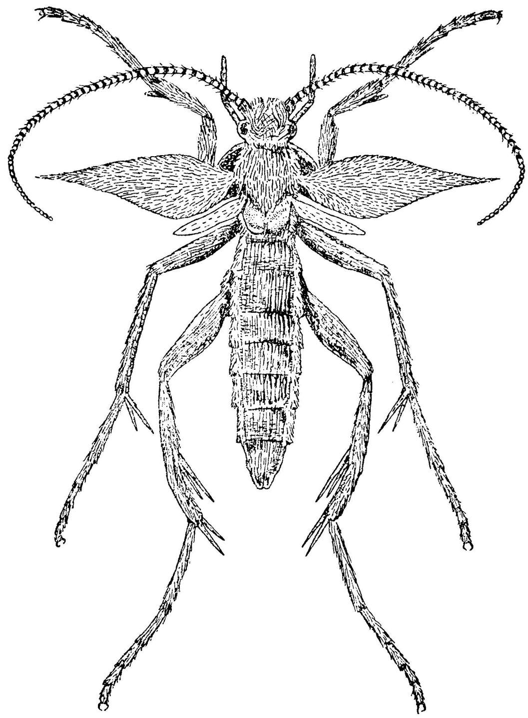

Fig. 20. *Pringleophaga kerguelensis* Enderlein (Lepidoptera: Tineidae), Kerguelen (after Viette 1948: pl. 1, but antennal segments are mostly too long and thus too few).

biota by passive transport by winds and sea currents. Among plants he felt that only *Pringlea* was really endemic, and that the other conspicuous floral elements, such as *Acaena*, *Azorella*, *Ranunculus*, *Cotula*, and *Galium* were all brought by the west wind drift over some thousands or millions of years. With them came many of the genera of insects and other arthropods distributed on these islands around Antarctica, and relying on *Acaena* and the other plants characteristic of the region. With the cooling of the Miocene, *Araucaria* and *Nothofagus* disappeared, and with the further cooling and glaciation of the Pleistocene, much of the previous fauna was pushed northward or exterminated. In connection with the west wind drift, the importance of the inter-tidal zone can be stressed. Such insect elements as *Temnostega*, *Meropathus*, *Mesembriorrhinus*, *Halirytus* and others live in that zone, and *Listriomastax*, *Apetenus* and others breed in the washed up kelp.

Jeannel (1965), in treating the Crozet fauna, pointed out that the flora of Crozet was typically subantarctic, whereas the fauna included 11 relics of Eocene immigration from S. Africa or elsewhere. He felt that *Antarctoniscus* (trichoniscid), *Euplanaria* (polyclad), *Hahnia*, *Crozetulus*, *Amblystogenium*, *Antarctotachinus*, *Pseudeuplectus*, *Phthirocoris* and *Siphlopteryx* came from Sudamadie, *Nuncia* from Australia, and that *Temnostega* was paleantarctic (like *Kenodactylus* on Campbell I.). To explain the presence of a small colony of *Temnostega* in the Cook Straits of New Zealand, he attributed it either to natural west wind drift, or to the transport in a storm from the Crozets to Cook Straits of the ship carrying the discoverer of Marion and the Crozets (Marion-Dufrèsne) and 28 of his men (who were eaten by the Maoris). The reason that the Crozets have had no influence on the fauna of Marion is because they are down wind from Marion. Thus the marine spread of South American

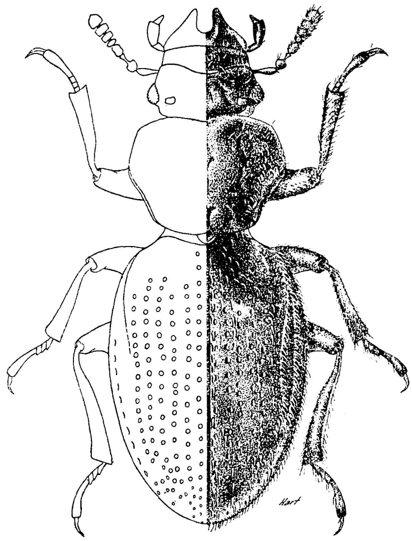

Fig. 21. *Meropathus chuni* Enderlein (Coleoptera: Hydraenidae), male, from Heard I.

elements from Marion, Crozets and the others was after the subantarctic plateau and the peninsula from Africa to the Crozets had sunken, before the end of the Oligocene.

The fact that the Crozets have a few elements distinctly related to Africa which are lacking in other subantarctic islands suggests at least two different possibilities. One is that the Crozets were part of a southern African land mass as postulated by Jeannel, or some variation of this in the form of closer stepping stones. Another might be that in the northward recession of biota in the Pleistocene and in the pushing southward again following, some elements reached or remained on the Crozets but failed to attain Kerguelen, Marion or Heard. Jeannel indicated a Tertiary connection between the Crozets and Africa.

Like Macquarie, Marion is on a fork of the Indian Ocean submarine ridge, but the Crozets, Kerguelen and Heard are not on the ridge, but on a plateau. Jeannel considered Marion to be part of a bridge between South America and Africa.

Hennig (1960/1966: 26) has reviewed the relationships of the known Diptera of the South Indian Ocean islands, in terms of possible connecting links between old and new world fauna, or for evidence of A-S (Australian-New Zealand—South American) sister-species or sister-group relationships. He immediately eliminated quite a few as introductions or derivatives from northern or widespread forms. In addition, *Paleopetaurista* is synonymized with a European form by Dahl in the present volume. For the remaining cases, Hennig found no clear evidence of links or A-S relationships, and he challenged Jeannel's conclusions regarding the fauna of these S. Indian Ocean islands as giving evidence of trans-antarctic connections. Hennig questioned Seguy's statement of relationship between *Siphlopteryx* and *Paraptilotus* of Africa. Since Hennig's review, Seguy has described 2 more endemic genera from the Crozets, *Microzetia* and *Protobelgica*. Brundin (1966: 56, fig. 12) does not make very clear the fact that Hennig's diagram is purely hypothetical, and is not based on any insect species. No Diptera are known from Bouvet I., for instance.

1. Steffan (pers. comm.) considers Seguy's *Sciara auberti* to be a *Lycoriella*. Hennig (1937) placed *Actoceles asymmetrica* End. of Macquarie in *Coelopella*, whereas Harrison (1959) put it in *Paractora* and Hardy (1962) and Watson (1967) did not mention it.

Fig. 22. *Halirytus macquariensis* Brundin (Diptera: Chironomidae), female, Macquarie (after **Brundin** 1962: 946).

Hennig (1960/1966: 58) stated that no groups of Diptera, as then known, had been proven for certain to have had trans-antarctic migration through direct land connection between southern South America and the New Zealand—Tasmania area. He felt that there might have been the equivalent of 'island hopping' when the climate was warmer. On the other hand (p. 75) he indicated that in the Nematocera and some non-cyclorraphous Brachycera (almost none among Cyclorrapha) there were indications of A-S groups. He indicated that to prove A-S relationships the groups on opposite sides of Antarctica must be monophyletic. Hennig felt that the last date for transantarctic migrations was Eocene/Oligocene or Oligocene/Miocene, and more likely the former.

A number of the indicators of close relationships between the southern continents appear to be fresh-water forms. The chironomid midges (Brundin 1966), the Plecoptera (Illies 1965a,b), and Ephemeroptera (Peters & Edmunds 1970) are examples which are conspicuous and include many species. Another is in the harpacticoid Copepoda. Delamare-Deboutteville & Rouch (1962) reported on 3 species of *Antarctobiotus* in the Patagonian Andes, while a species each is known from South Georgia, the Crozet Is. and Tasmania. In the mayflies the Leptophlebiidae of Australia and New Zealand are closely related to those of southern South America, but the New Guinea representatives, as with so many other groups, are Oriental. In many phytophagous groups, close relationships between southern South America and New Zealand—Australia are very scarce (Gressitt 1961, 1964a,b). Many groups rich in the tropics barely reach to the southern continental areas exclusive of Antarctica, and quite a few of these are lacking in New Zealand or even in southernmost South America or Tasmania. In general the groups mentioned above are dominant in cooler climates, and many of them are distinctly cold-adapted forms found only in the far south and in the Andes, or both in the far south and the far north with the tropics forming gaps in their occurrence. Illies felt that the Plecoptera arose in the southern hemisphere with later parallel development in both south and north. He also discounted air-borne dispersal for stone-flies. Ross (1956), who studied the cool-adapted Trichoptera, did not invoke southern continental connections or migrations to explain present distribution, and was criticized by Brundin.

Brundin (1966) has documented numerous A-S relationships (sister-groups between Australia and/or New Zealand on one hand and southern South America on the other) in the cool-adapted chironomid midges. This and much other accumulating evidence, such as the fossil amphibian and reptile in Antarctica (Sandved 1970), indicate transantarctic land connections at least through the Mesozoic. Brundin considered his evidence to indicate Antarctica as an evolutionary center. He indicated separate connections, a) from South America via East Antarctica to Tasmania and Australia (latter all apomorph, or derived, indicating one-way traffic from South America); and b) from South America via West Antarctica to New Zealand, both sides with plesiomorphs, indicating 2-way transfer. The latter connection was of greater evolutionary importance. The dating was back to the mid-Mesozoic for chironomids. An African connection was broken off in the upper Jurassic. Skottsberg (1940) who invoked land bridges rather than continental drift was not certain that there had been a connection to Africa. Brundin indicated that Gondwanaland broke up between upper Jurassic and upper Cretaceous, New Zealand separating in lower Cretaceous, Australia in mid Cretaceous, and the continents reaching their present positions at the end of the Cretaceous. Brundin felt that many of the bipolar groups originated in austral areas, with their plesiomorphs there and apomorphs north-temperate. He felt that most evolution was southern or northern, with most tropical proliferation consisting of apomorphs. He believed this applied to Mecoptera, some Hemiptera and possibly the Lepidoptera, besides Plecoptera and much of the Diptera. He stressed that the north-south continuity of South America permitted the persistence of many groups, whereas there was much extinction because of subsidence south of New Zealand and aridity for long periods in Australia.

The transantarctic distribution of several conspicuous groups of plants has long been cited as evidence of southern continent connections or drift. Two of these, *Nothofagus* and *Araucaria* are involved with subantarctic islands, as they are known as fossils from Kerguelen. Podocarps were also heavily involved with transantarctic connections. Much has been written on the significance of the distribution of these groups (Florin 1963; Couper 1960; Cranwell 1964; Fleming 1963a,b, 1964; Darlington 1965; Hair 1964; Preest 1964), as well as on the geology and related problems (Adie 1964a,b; Allan 1964; Knox 1964; Brundin 1964, 1965, 1966). Cockayne (1958) commented on the extensive extinction south of New Zealand and stated that the subantarctic flora is just a small fraction of what once existed in the region; Florin and Couper considered Antarctica a migration route. Cranwell pointed out that though there were fossil podocarps in S. Africa, Madagascar and Kerguelen, *Nothofagus* was not represented in those places (except possibly by fossil pollen in Kerguelen). *Nothofagus* occurs from South America to New Guinea, via New Zealand, Tasmania, Australia and New Caledonia. The *brassi* group, of which there are a number of species in New

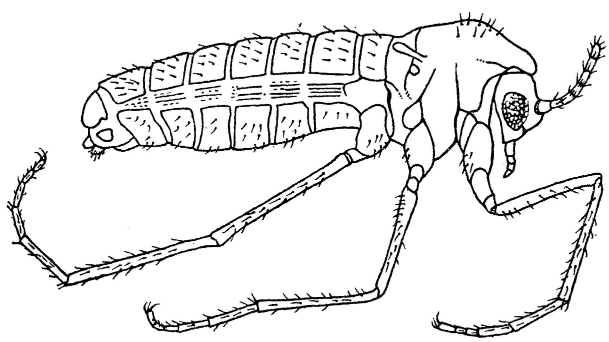

Fig. 23. *Protobelgica albipes* Séguy (Diptera: Chironomidae), female, Possession I., Crozet (after Séguy 1965: 287).

Guinea, occurs also in New Caledonia, and as fossils in New Zealand, Australia, Antarctica and South America. *Nothofagus* pollen has been found in peat deposits in South Georgia, Campbell and the Aucklands. Hair (1964) stressed that fossils of these and podocarps occur in Antarctica, but not in the tropics. Hair favored continental drift rather than land bridges. Fleming favored a stepping-stone theory to help account for the absence of many elements, but Cranwell insisted on direct land connections for spread of *Nothofagus*. Kuschel (1964) proposed an Austral Region to include the areas from southern South America across Antarctica to New Guinea, based on the distribution of *Nothofagus*, *Araucaria* and certain other biota. In actual fact New Guinea is dominantly Oriental in its makeup of flora and insect fauna, although it has certain relationships with South America through New Caledonia and New Zealand, or through Australia, or by both routes, as well as independent relationships with more strictly Australian elements.

Fleming (1963a, 1964) described as Paleoaustral or Paleonotian the older land-dispersed elements which spread during Mesozoic land connections, and Neoaustral or Neonotian those later dispersed southern elements, which spread across water gaps in the Tertiary or Quaternary. Fleming did not require land connections to account for distribution of New Zealand area shallow water forms, and felt that there were no land bridges in the Tertiary. Fleming (1962) and others have stressed the long-standing isolation of Australia and New Zealand, with for instance the New Zealand Triassic very different from that of Australia, but related to New Caledonia. Fleming felt that the Auckland Is. might have been populated by air dispersal from New Zealand during the past 10,000 years. However, a number of insect genera possibly endemic to Campbell and the Aucklands may have evolved in isolation from New Zealand. Fleming (1963b) considered that New Zealand was still subject to aerial invasion by 3 elements: a) Austral, meaning southern or 'antarctic,' characterized by elements of Kuschel's Austral Region; b) Malayo-Pacific, from the north; and c) Australian. Fleming feels (pers. comm.) after the new evidence of land vertebrates in Antarctica and data on sea-floor spreading, that cicadas populated New Zealand, Chathams, Kermadecs and Norfolk I. by over-sea dispersal during or since the Pleistocene.

Dell (1964) indicated that the subantarctic land snails must have retreated north with the Pleistocene ice ages and then re-invaded southward.

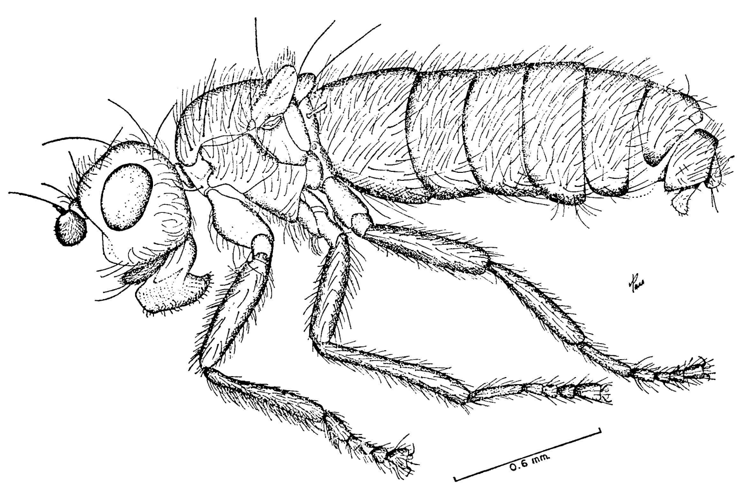

Fig. 24. *Apetenus watsoni* Hardy (Diptera: Coelopidae), male, Macquarie (after Hardy 1962: 965).

Paramonov (1955) demonstrated that the New Zealand fauna of cyrtid flies is related to that of southern South America, but not to that of Australia. Masner (1968) established a genus of scelionid wasps with species known only from New Zealand and southern South America. Allan (1964) contends that there have been no land connections since the Miocene, except possibly between South America and the Antarctic Peninsula. If the break-up was in mid-Cretaceous, then *Nothofagus* was still able to disperse across some sea barriers in Upper Cretaceous and it still grew around McMurdo Sound in the Eocene (Fleming, pers. comm.).

Fossil Record

The recent discoveries of an ancient fossil amphibian and the reptile *Lystrosaurus* (Sandved 1970) in Antarctica provide further conclusive evidence that Antarctica supported extensive biota in the Mesozoic, as well as the Tertiary. The nature of some of these fossil animals suggests much more conclusively than with the far more numerous fossil plants, that land was continuous at least with one other continent, if not with more. This may have terminated in lower or middle Cretaceous if not earlier. Thus currently disjunct 'southern elements' might have moved over land to several of the areas where they now occur. This and other evidence suggests that continental drift took place after evolution of vertebrates. The almost total lack of insect fossils from antarctic and subantarctic areas gives insufficient evidence for drawing conclusions on the history of spread of insects in southern areas. Opinions expressed by Jeannel, Darlington, Brundin or others are discussed above.

Record of fossil plants: Although the history of subantarctic islands is not well documented by fossils, there are some very significant ones known from Kerguelen. Two of the conspicuous plant genera of southern distribution are *Araucaria* and *Nothofagus* (Cranwell, 1964; Wace 1965; Darlington, 1965). *Araucaria* fossils are known from Kerguelen, but *Nothofagus* is known to be represented there only by wind-blown pollen and driftwood. The latter applies also to South Georgia, Tristan da Cunha and Campbell and Auckland Is. Other plants known from Kerguelen as fossils are mosses and ferns, podocarps and certain angiosperms (?*Ranunculus*, ?*Azorella*) other than *Nothofagus.*

EVOLUTION ON SUBANTARCTIC ISLANDS

With the meagre evidence at hand, it is difficult to make many positive statements regarding evolution on subantarctic islands. A principal difficulty is that many of the groups represented are poorly known in general, and particularly so in the far southern areas. Also, in many cases close relatives are not known, or genera represented may be of more or less general distribution.

Some evidence has suggested (Gressitt 1964b) that evolution may proceed at a fairly rapid rate on small islands subjected to strong winds and other unfavorable factors. As a general rule, wings are reduced in size or lacking. Some of the flightless species are closely related to fully winged flying species at warmer latitudes.

If it is true that these subantarctic islands have been continuously above water and have been populated for a very long period of geological history, then the rate of evolution would not have to be high to produce the endemic species present. If, on the other hand, there was much extinction in the Pleistocene and air dispersal has repopulated the islands to a considerable extent, then the rate of evolution could be moderate. However, many feel that evolution is rapid in the tropics and slower in cold areas. For equivalent groups, the number of generations per year may be much greater in the tropics, theoretically permitting more rapid change. Also, many more factors and competing species are involved in warm areas, which again have different selective pressures. The primary factor of the harsh climate is not low temperature, as free-living insects persist in Antarctica

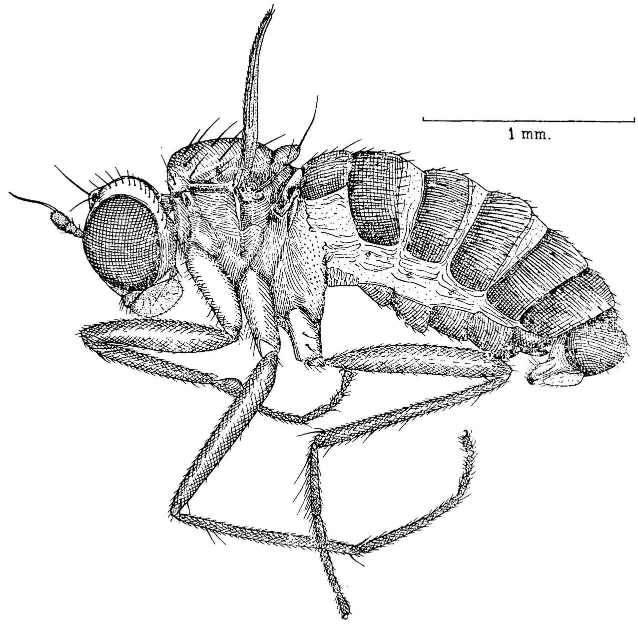

Fig. 25. *Schoenophilus pedestris* Lamb (Diptera: Dolichopodidae), male, Macquarie (after Kohn 1962: 960).

and in the arctic under far colder conditions. Major limiting factors are more likely scarcity of warmth (which permits no more than a few generations per year) and sunshine, and the powerful influence of the strong winds. With the fairly uniform environment on these islands, genetic drift from comparable gene pools may not result in rapid genetic divergence, particularly with slow reproduction. If temperature or number of generations per year is the significant factor, then evolution must be more rapid in the subantarctic than in the antarctic.

There is some evidence of active evolution, and of morphological as well as ecological plasticity of species on these islands. Among examples are wide range of intraspecific variation in most groups. The 2 South Georgia species of perimylopid beetles are highly variable in size, color and form, and this has given rise to naming of both generic and specific synonyms. Some of the wingless flies vary widely in size, setation and other characters. The same may be said for other groups. This plasticity may be related to low pressure of inter-species competition, with empty and poorly exploited habitats, and with occupation of different ones by a single species. On the other hand, Darlington (1965: 12) suggests that evolution in cold areas is generally slow, with present distinct species dating from the Tertiary.

Because of the small number of species per island and the presence of empty microhabitats, it is unlikely that the fauna is saturated in any sense. Thus some aspects of competition may be reduced, although competition between members of different families may be important in attaining equilibrium. Since immigrants are few, the turnover rate (MacArthur & Wilson 1967: 121) may be negligible and the environment is not closed to invaders.

The number of species per genus, and per family, is very low (Gressitt 1964b; MacArthur & Wilson 1967: 120). Many families are represented by a single species on one island, and some families are only found on a single island, or on only a few islands.

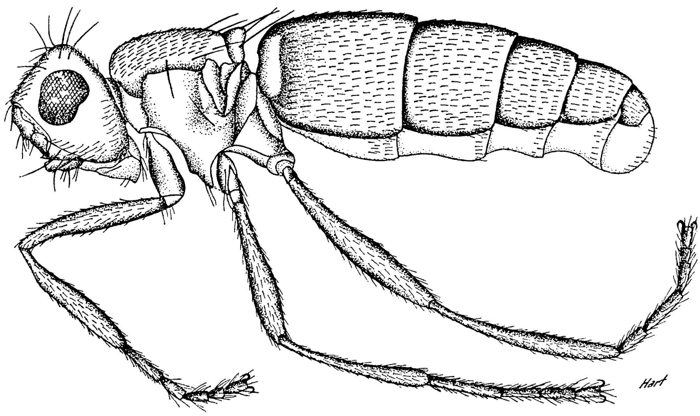

Fig. 26. *Anatalanta aptera* Eaton (Diptera: Sphaeroceridae), female, Heard I.

Because of the small numbers of species and reduced inter-specific competition, number of individuals of a species may be very high. Furthermore, except on islands where glaciers reach the coasts in many places (South Georgia and Heard), there is probably little tendency for populations of a species to be subdivided. Thus many of the situations described by MacArthur & Wilson (1967: Chap. 7) do not appear to closely apply to the subantarctic situation. However, 'character release,' with greater variability as in small bird populations on small islands, would appear to apply here. As to gigantism on small islands (as the dodo and Komodo dragon), this does not clearly occur here, although there is some suggestion of it on Campbell and the Aucklands. In regard to speciation and radiation within an island or island group, perhaps the only striking example is that of the weevils of the South Indian Ocean islands. These must have evolved in part on a larger Tertiary insular area. If they had evolved on the present islands with small island size, there would have to have been quite a bit of transfer between islands as some of the genera occur on several islands. Also in some cases a single species occurs on more than one island, and this applies also with

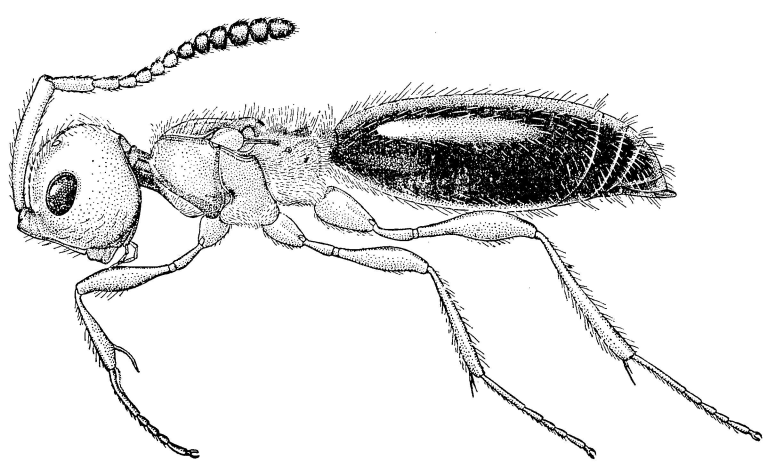

Fig. 27. *Antarctopria latigaster* Brues (Hymenoptera: Diapriidae), female, Macquarie and Campbell I. (after Yoshimoto, 1964, Pacif. Ins. Monogr. 7: 508, Campbell I.).

the flightless moths on these same islands. A difficult problem is that though some species are common to Marion and the Crozets, as well as to the Crozets and Kerguelen, the Crozets also possess several families (particularly African elements) lacking on the other islands. Possibly all of the Heard species came by oversea post-Pleistocene transport from Kerguelen as the direction is approximately correct and Heard seems to almost lack endemics.

Brundin (1966: 12) intimates that Mayr's Founder Principle (1942, see 1963) is invalid, and this goes with Brundin's refutation of air dispersal as a factor in zoogeography. However, in islands like Hawaii the evidence in favor of this principle is extensive. In subantarctic islands the evidence is less conclusive because of the severe obstacles to colonization, as well as probable slow evolution.

Wing Reduction

Loss of flight capability in groups of insects whose members normally fly is a conspicuous feature of subantarctic life. The percentage of non-flying species of normally flying groups appears to increase directly as the environment becomes less favorable in general. Thus, in Antarctica proper there is only one flying insect known (a chironomid midge, *Parochlus steineni*, found in the South Shetlands, but also in South Georgia and southern South America). On Heard Island, with the most severe subantarctic climate, no flying insects are known, and on other islands there are gradually increasing percentages of flying species. The degree of increase of flying species, however, seems to be more correlated with reduced isolation than with reduced severity of climate. It is only partly correlated with size of island.

Wind appears to be the critical factor in this aspect of evolution, or at least wind combined with temperature, size of island and/or other factors. It has been disputed whether or not the theory is correct that on small windy islands insects tend to lose the power of flight because those individuals which do continue to fly tend to be blown out to sea (or away from favorable habitats) and those which avoid flight tend to be more successful in reproduction. However, various sorts of evidence, such as results of trapping experiments, tend to substantiate the theory based on reduction in use of wings (Gressitt 1964b). Séguy (1940) demonstrated tendency towards muscle-reduction among winged Diptera on Kerguelen. Several genera of Diptera which have flightless species on subantarctic islands (see fig. 22–26) have close relatives elsewhere which are winged and capable of flight. Other factors might be interference with normal activity by wind influence (even when not blown away); or heat loss through wings at low wind temperatures.

Since these are quite small islands with a high rate of aptery, and as most of the flightless species occur near the coasts, some of the conclusions of Darlington (1943) and MacArthur & Wilson (1967: p. 158) do not apply here. On these islands some of the more stable habitats are closer to the coasts and in the higher areas appropriate habitats are fewer.

On South Georgia the small number of winged species include only a few weak-flying midges and other flies. On Macquarie both moths (1 is occasionally self-introduced and not breeding locally), the crane-fly and a few of the kelp flies and others are capable of flight. It represents a somewhat higher flying ratio than would be expected. Several of the conspicuous flightless types of Campbell and the Aucklands (moths, flies and others) are lacking on Macquarie.

Most of the subantarctic Diptera which have lost the power of flight have evolved facilities or running, jumping and hiding. Often halteres, antennae and eyes are reduced as well as wings. The possibility of genetic isolation is probably increased by loss of flight capacity. These factors are also more or less true for the brachypterous moths. Details of wing reduction in certain subantarctic species have been discussed by Seguy (1940, 1965a,b), Brauns (1951) and Hennig (1935). A summary of non-flying and flying insects is presented in Table 11.

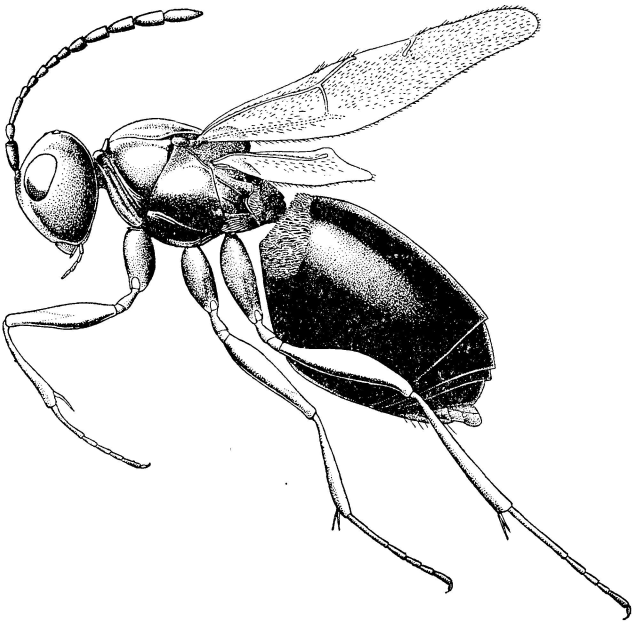

Fig. 28. *Kleidotoma* (*Pentakleidota*) *subantarcticana* Yoshimoto (Hymenoptera: Eucoilidae), female. This is from Campbell I., but another species of same genus is known from Crozet. (After Yoshimoto, 1964, Pacif. Ins. Monogr. 7: 510). The wings are 'useless.'

Of the nearly 700 specimens of the 2 kinds of aphids (introduced) taken in the subantarctic, only 4 were alates.

Possibly a number of the subantarctic species with reduced wings have close relatives, as yet undiscovered, on the far southern continental extentions. It is possible that these relatives may be

Table 11. Flight loss in groups of normally flying insects

	Islands arranged in order of decreasing severity of climate												Summary		
	Heard		S. Georgia		Kerguelen		Macquarie		Marion		Crozet				
	A-B	F	A-B	F	A-B	F	A-B	F	A-B	F	A-B	F	Species	% endemic	% flightless
Psocoptera					1M		1M		1M		1M		3	100	100
Thysanoptera							1A						1	100	100
Heteroptera											1A		1	100	100
Lepidoptera	1B				2B			1	2B		2B		3	100	67*
Coleoptera	5A		7		14		5		9		22		45	82	100
Diptera	3		4	4	5	4	3	8	3	2	6	4	38	87	42
Hymenoptera			1A				1M		1B		1B		3	100	100
Subtotals	9	—	12	4	22	4	11	9	16	2	32	4			
Total													94	86	75

A-B—Apterous (A), Micropterous (M) or Brachypterous (B).
F—Capable of flight.
*May be increased as a result of a possible additional species.
Note: Obviously introduced species are excluded from this table.

less dominant on the continents. The modifications of insular forms might represent convergence to more rugged, adaptable forms, more like their more generalized ancestors.

Tests on Campbell I. (Gressitt 1964b) showed that winged insects flew less during windy periods, but that in strong and sudden winds insects were caught up and carried with winds going off over the water. Thus large numbers of insects were trapped in nets at the edge of the shore.

SUMMARY AND CONCLUSIONS

The true subantarctic islands are close to the Antarctic Convergence, varying north and south of 50° south latitude. They include only 6 groups: South Georgia, Marion—Prince Edward, Crozet Is., Kerguelen, Heard and Macquarie. They have no mean monthly temperatures above 9°C. Strong west winds prevail. Though on 3 sides of Antarctica, and of different geological histories, they have various features, and some faunal elements, in common. South Georgia and Kerguelen, much larger than the others, are old and continental, with extensive glaciers. Heard, much smaller, is almost entirely ice-capped, is still active volcanically and poor biologically. Perhaps its entire fauna is post-Pleistocene and resultant from over-sea transport from Kerguelen. Marion, Crozets, Kerguelen and Heard have a number of elements in common which do not occur elsewhere. These may have evolved on a larger insular area and may be partly relict from an old Gondwanaland fragment. If so, there must have been considerable extinction on that land mass, with some later re-invasion from Africa after the Crozets were separated. Alternatively the African elements may have been pushed north in the Pleistocene and lost on the more southern Marion, Kerguelen and Heard. Marion and the Crozets, like Heard, are covered with partly young volcanic outpourings and cones. Macquarie is old and eroded, having been heavily glaciated like the older parts of the other isles, but may consist of part of the mid-oceanic ridge. It may be more likely that faunal transfer occurred mostly by air dispersal after the islands evolved, and particularly after the Pleistocene. This is probably particularly true of South Georgia, Marion, Heard and Macquarie.

The faunules of these islands consist of about 50 to 150 species of land arthropods on each. There is a high ratio of number of families to species, and some families are found only on a single island, or on a few. Air, sea and bird dispersal would appear to be important. As species are few and some microhabitats empty, there is probably reduced inter-species competition. However, there may be considerable competition between representatives of higher categories because predators are scarce. Equilibration is therefore more likely to occur through competition. Possibly the faunas are not yet in equilibrium.

Obstacles to dispersal and establishment are severe. Species radiation has been limited except for a few groups on the South Indian Ocean islands. These appear to represent endemic genera and must be older elements, having survived the Pleistocene.

Aptery is common, and no species on Heard I. can fly. Some of the flightless species appear to have fairly close relatives elsewhere which are capable of flight. There is no relation of numbers of species to island size or altitude range. Most insects live near the coasts, where the vascular plants and most rookeries occur.

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