

## INSECTS OF CAMPBELL ISLAND. SUMMARY<sup>1</sup>

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*Abstract:* The 300 described species of land arthropods on Campbell I. are 47% endemic. Nineteen genera (7%) appear to be endemic, but some of these undoubtedly occur also in the Auckland Is. The dominant relationships of the Campbell I. fauna appear to be with New Zealand. The Campbell fauna is much more similar to that of the Auckland Is. than to that of Macquarie I. There are not many indications of close relationship with the fauna of southern South America. There appear to be a number of subcontinental elements in the Campbell fauna, and perhaps a minority came by oversea dispersal. The severe windy climate has a great influence on evolution on the island. There is a strong tendency toward wing loss. A number of the winged species use their wings very little. Many Campbell species appear to be very plastic, both ecologically and morphologically.

*Composition of the Campbell I. fauna:* There appear to be more than 381 species of land arthropods on Campbell I. These belong to 27 distinct groups (classes, subclasses or orders). About 138 families and 280 genera are represented on the island (see table 1 and fig. 10). Of these, 300 species are reported upon in this volume, besides about 60 from nearby areas such as Macquarie I., the Auckland Is., the Snares and the Antipodes.

### SYSTEMATIC LIST

Before discussing the zoogeography of the Campbell I. fauna, the following list of the Campbell species is presented, to give a concisepicture of the fauna. This list is an attempt to enumerate the species in systematic order, and not always in the order followed in the main text, which represents the division of the collection among collaborators. The list includes some groups not treated in the text. I am grateful to several collaborators (B. Ainscough, L. Brundin, L. Eldridge, Danielle B. Fellows, J. A. Wallwork, N. Wilson) for supplying tentative information on representation in groups not yet studied. The list is limited to Campbell I. and omits species recorded or described in this volume from the Auckland Is., Snares, Antipodes or Macquarie I.

The last column indicates additional distribution records, such as areas not indicated in the main columns, or more specific records, such as for the southern part of New Zealand only (South Island, or Stewart I.). Also, for normally winged groups, an "X" on right side of last column indicates that the species has the wings absent, brachypterous or slightly reduced, and thus is flightless or practically flightless.

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Table 1. Systematic list of Campbell I. species indicating distribution.

	Endemic	Antarctica	Aucklands	Snares or Antipodes	Macquarie	Heard	Kerguelen	New Zealand	Tasmania	Australia	S. America	Other areas
<b>AMPHIPODA</b>												
Talitroidea												
Hyalidae												
<i>Allorchestes compressus</i> Dana			×						×	×		
Hyaellidae												
<i>Chiltonia minuta</i> * Bousf.	×											
Talitridae												
<i>Parorchestia campbelliana</i> * Bousf.	×											
? <i>P. insularis</i> Chilt.			×									
<i>Orchestia aucklandiae</i> Bate			×					×				Stewart, South I.
<i>O. bollonsi</i> Chilt.			×	×				×				South, Bounty Is.
<b>ISOPODA</b>												
Oniscoidea												
Armadillidiidae												
6 species	?											
Oniscidae												
<i>Spherillo rugulosus</i> (Miers)			×					×				South I.
Porcellionidae												
2 species	?											
Trichoniscidae												
9 species	?											
Styloniscidae												
<i>Styloniscus magellanicus</i> Dana			×								×	
<i>Notoniscus australis</i> (Chilt.)	×											
Scyphacidae												
<i>Scyphoniscus magnus</i> Chilt.			×									
<b>ARANEAE</b>												
Dictynidae												
<i>Oramia* hoggi*</i> Forst.	×											
<i>O. charybdis</i> (Hogg)								×				
<i>Pounamua gressitti*</i> Forst.	×											
Agelenidae												
<i>Gohia clarki*</i> Forst.								×				
<i>G. wenhami</i> (Forst.)			×									
<i>Hina* delli</i> (Forst.)			×									
Toxopidae												
<i>Laestrygones albiceres</i> Urq.			×					×				Chatham Is.

\* New taxa

	End.	Ant.	Auck.	Sn- Ant.	Macq.	H'rd	Kerg.	N. Z.	Tasm.	Aust.	S. Am.	Other areas
Amaurobioididae												
<i>Amaurobioides maritima</i> Cambr.			×						×	×		
Theridiidae												
<i>Icona alba</i> Forst.			×									
<i>Pholcomma hickmani</i> * Forst.	×											
Symphytognathidae												
<i>Textricella wisei</i> * Forst.	×											
Argiopidae												
<i>Araneus pustulosus</i> Walck			×					×				
Linyphiidae												
<i>Mynoglenes insolens</i> Simon			×	×	×							Chatham Is.
<i>M. marrineri</i> Hogg			×	×	×							
<i>Linyphia setosa</i> * Forst.	×											
Attidae												
<i>Clynotis barresi</i> Hogg			×									
OPILIONES												
Phalangiidae												
<i>Pantopsalis renelli</i> * Forst.	×											
Triaenonychidae												
<i>Neonuncia campbelli</i> Forst.	×											
PSEUDOSCORPIONIDA												
Chernetidae												
<i>Apatochernes antarcticus</i> * Beier	×											
<i>Systellochernes* zonatus*</i> Beier	×											
ACARINA												
MESOSTIGMATA												
Laelaptidae												
<i>Ayersacarus* plumapilus*</i> Hunt.	×		×		×							
<i>A. gressitti*</i> Hunt.	×											
<i>Leptolaelaps reticulatus campbellensis*</i> Hunt.	×		×									
<i>Androlaelaps pachyptilae</i> (Zumpt & Till)						×						
Haemogamasidae												
<i>Eulaelaps stabularis</i> (Koch)								×				Africa, Asia, Europe, N. America
Trachytina												
? genn. spp.	?											
Uropodina												
Thinozerconidae												
n. gen.: n. sp.	×											
Polyaspididae												
<i>Calotrachytes sclerophyllus</i> (Michael)								×				









	Endemic	Antarctica	Aucklands	Snares or Antipodes	Macquarie	Heard	Kerguelen	New Zealand	Tasmania	Australia	S. America	Other areas	Flightless
<b>Symphyleona</b>													
<b>Sminthuridae</b>													
<i>Sminthurinus discordipes</i> Salm.	×												
<i>Pseudokatianna campbellensis</i> Salm.	×												
<i>P. triclavata</i> Salm.	×												
<i>Longkingia salmoni</i> * Wise	×												
<b>PLECOPTERA</b>													
<b>Grypopterygidae</b>													
<i>Aucklandobius complementarius</i> End.			×										
<i>Apteryoperla campbelli</i> Ill.	×												×
<i>A. longicauda</i> Ill.	×												×
<b>ORTHOPTERA</b>													
<b>Rhaphidophoridae</b>													
<i>Notoplectron* campbellensis*</i> Richards	×												×
<b>PHTHIRAPTERA</b>													
<b>Mallophaga</b>													
<b>Menoponidae</b>													
<i>Austromenopon affine</i> (Piaget)													
<i>A. ossifragae</i> Eichler													
<i>A. ellioti</i> Timm.													
<b>Philopteridae</b>													
<i>Austrogoniodes concii</i> (Keler)													
<i>A. cristati</i> Keler													
<i>Harrisoniella hopkinsi</i> Eichler													
<i>H. grandis</i> (Piaget)													
<i>Perineus</i> sp.													
<i>P. diomedae</i> (F.)													
<i>P. obscurus</i> (Rudow)													
<i>P.</i> sp.													
<i>Halipeurus</i> sp.													
<i>Philoceanus garrodiae</i> (Clay)													
<i>Pelmatocerandra setosa</i> (Giebel)													
<i>Trabeculus hexacon</i> (Waterston)													
<i>Docophoroides brevis</i> (Dufour)													

## HOSTS

*Diomedea e. epomophora* Lesson*Macronectes giganteus* (Gmelin)*Pelecanoides urinatrix exsul* Salvin*Eudyptes pachyrhynchus sclateri* Buller*E. crestatus crestatus* Miller*Diomedea e. epomophora* Lesson*Catharacta skua lonnbergi* Mathews*Diomedea e. epomophora* Lesson; *D. chrysostoma* Forste*Diomedea melanophris impavida* (Mathews); *Phoebetria palpebrata* (Forster)*Phoebetria palpebrata* (Forster); *Macronectes giganteus* (Gmel.)*Diomedea chrysotoma* Forster*Puffinus griseus* (Gmelin)*Garrodia nereis* (Gould)*Pelecanoides urinatrix exsul* Salvin*Puffinus griseus* (Gmelin)*Diomedea ep. epomophora* Lesson



<i>D. murphyi</i> (Kellogg)	<i>Macronectes giganteus</i> (Gmelin)												
<i>D. sp.</i>	<i>Diomedea ex. exulans</i> L.												
<i>Pectinopygus</i> spp.	<i>Phalacrocorax c. campbelli</i> (Filhol)												
<i>Saemundssonina stresemanni</i> Timm.	<i>Catharacta skua lonnbergi</i> Mathews												
<i>S. lari</i> (O. Fabr.)	<i>Larus dominicanus</i> Licht.; <i>L. novaehollandiae scopulinus</i> Forster												
<i>S. sp.</i>	<i>Sterna vittata bethunei</i> Buller												
<i>Quadriceps fuscolaminulatus</i> (End.)	<i>Larus dominicanus</i> Licht.												
<i>Q. lingulatus</i> (Waterston)	<i>L. novaehollandiae scopulinus</i> Forster												
Trichodectidae													
<i>Damalinea ovis</i> (Schrank)	<i>Ovis aries</i> L.												
Anoplura													
Hoplopleuridae													
<i>Polyplax spinulosa</i> (Burm.)	<i>Rattus norvegicus</i> Berkenhout												
Echinophthiridae													
<i>Antarctophthirus microchir</i> (Trou. & Neum.)	<i>Otaria hookeri</i> Gray												
<i>Lepidophthirus macrorhini</i> End.	<i>Mirounga leonina</i> (L.)												
	End.	Ant.	Auck.	Sp.- Ant.	Macq.	H'rd	Kerg.	N. Z.	Tasm.	Aust.	S. Am.	Other areas	F'less
<b>PSOCOPTERA</b>													
Elipsocidae													
<i>Spilopsocus avius*</i> Smithers	×												×
Philotarsidae													
<i>Austropsocus insularis</i> Smithers					×								×
Trogiidae													
<i>Trogium pulsatorium</i> (L.)								×	×	?	?	Subcosmopolitan, Crozet Is.	×
<b>THYSANOPTERA</b>													
Thripidae													
<i>Taeniothrips hawaiiensis</i> (Morg.)												Hawaii, E. Asia	
<b>HOMOPTERA</b>													
Aphididae													
<i>Aulacorthum circumflexum</i> (Buckt.)								×				Widespread	
<i>A. malvae</i> (Mosley)								×				"	
<i>A. solani</i> (Kalt.)								×				"	
<i>Brachycaudus helichrysi</i> (Kalt.)								×				"	
<i>Jacksonia papillata</i> Theo.					×			×				"	
<i>Myzus ascalonicus</i> Doncaster								×				Scotland, Iceland, Norway, U.S.A.	
<i>Rhopalosiphoninus staphy- leae</i> (Koch.)								×				Widespread	

	Endemic	Antarctica	Auckland	Snares or Antipodes	Macquarie	Heard	Kerguelen	New Zealand	Tasmania	Australia	S. America	Other areas	Flightless
<b>Pseudococcidae</b>													
<i>Phenacoleachia australis*</i> Beardsley			×										♂ ×
<i>Nipacoccus campbellensis*</i> Beard.	×												
<i>N. longispinus*</i> Beard.			×										♂ ×
<i>Trionymus danthoniae</i> Morrison			×									Stewart I.	♂ ×
<b>TRICHOPTERA</b>													
<b>Hydroptilidae</b>													
<i>Oxyethira albiceps</i> (McLach.)			×					×				Chatham Is.	
<b>LEPIDOPTERA</b>													
<b>Tineidae</b>													
<i>Proterodesma byrsopola</i> Meyr.			×					×					
<b>Hyponomeutidae</b>													
<i>Tinearupa sorenseni</i> Salm. & Bradley	×												×
<i>Campbellana attenuata</i> Salm. & Bradley	×												×
<b>Elachistidae</b>													
<i>Euproteodes galathea</i> Viette	×												×
<b>Oecophoridae</b>													
<i>Endrosis lactella</i> Denis & Schiff.			×					×	×	×		Cosmopolitan	
<b>Cosmopterygidae</b>													
<i>Reductoderces fuscoflava</i> Salm. & Bradley	×												×
<b>Tortricidae</b>													
<i>Capua plagiatana</i> Walker			×					×					
<i>Tortrix melanosperma</i> Meyr.								×					
<i>Sorensenata agilitata</i> Salm. & Bradl.	×												×
<b>Pyraloidea</b>													
<b>Pterophoridae</b>													
<i>Platyptilia aeolodes</i> Meyr.			×					×				Chatham Is.	
<i>P. falcatalis</i> (Walk.)								×					
<b>Pyralidae</b>													
<b>Crambinae</b>													
<i>Exsilirarcha graminea</i> Salm. & Brad.	×												×
<b>Scopariinae</b>													
<i>Scoparia rotuella</i> (Feld. & Rogen.)								×					

	End.	Ant.	Auck.	Sn.- Ant.	Macq.	H'rd	Kerg.	N. Z.	Tasm.	Aust.	S. Am.	Other areas	F'less
<i>S. halopsis</i> Meyr.			×										
<i>S. triscelis</i> Meyr.			×					×					
<i>S. parnifera</i> Meyr.			×					×				(South I.)	
<i>S. ? albafascicula</i> Salm.	×												
<i>Antiscopa epicomia</i> (Meyr.)			×					×				Kermadec Is.	
<i>Witlesia pachyerga</i> (Meyr.)								×				(North I.)	
<i>W. psammitis campbellensis</i> * Munr.	×												
<i>W. gressitti</i> * Munr.	×												
Nymphulinae													
<i>Musotima nitidalis</i> (Walk.)			×					×		×		Chatham Is.	
Geometridae													
<i>Hydriomena similata</i> Walk.			×					×				(North, S. & Stewart)	
<i>Epiphryne charidema</i> (Meyr.)			×					×				(North & S. Is.)	
<i>Xanthorrhoe orophylloides</i> Huds.			×										
<i>X. campbellensis</i> * Dugd.	×												
<i>Chloroclystis impudicus</i> * Dugd.	×												
<i>C. suffusa</i> Huds. group								×				(North & S. Is.)	
Noctuidae													
<i>Agrotis ypsilon</i> (Hufn.)			×					×				Polynesia, E. Asia, Holarctica	
DIPTERA													
Trichoceridae													
<i>Nothotrichocera antarctica</i> (Edw.)			×										
<i>Paracladura antipoda</i> (Mik)			×										
Tipulidae													
<i>Limonia (Dicranomyia)</i> <i>arthuriana</i> (Alex.)								×				(South I.)	
<i>L. (D.) kronei</i> (Mik)			×										
<i>Erioptera (Trimicra)</i> <i>brachyptera</i> Alexander	×												×
<i>E. (T.) pilipes campbell-</i> <i>icola</i> * Alex.	×												(×)
<i>Molophilus (Molophilus)</i> sp. nr. <i>jenseni</i> Alex.								×					
<i>M. (M.)</i> sp.	?												
Psychodidae													
<i>Psychoda brachyptera</i> * Quate	×												×
<i>P. pulchrima</i> Satch.								×					
<i>P. campbellica</i> * Quate	×												
<i>P. eremita</i> * Quate	×												
<i>P. spatulata</i> Satch.				×	×			×		×			×
<i>P. severini</i> Tonnoir								×		×		Holarctica	







	End.	Ant.	Auck.	Sn.- Ant.	Macq.	H'rd	Kerg.	N. Z.	Tasm.	Aust.	S. Am.	Other areas	F'less
<i>Selonomus* linearis*</i> Steel	×												×
<i>Omaliomimus albipenne</i> (Kies.)			×		×								×
<i>O. venator</i> (Broun)			×		×								×
<i>Arpediomimus kroni</i> (Kies.)			×					×				(South I.)	×
<i>Nesomallum* campbellensis*</i> Steel	×												×
<i>N. imitator*</i> Steel	×												×
<i>Allodrepa* decipiens*</i> Steel	×												×
Aleocharinae													
<i>Baeostethus chiltoni</i> Broun	×												×
<i>Halmaeusia sparsepunctata*</i> Steel	×												×
<i>H. nesiotus*</i> Steel			×										×
<i>Atheta amicula</i> (Steph.)								×				Subcosmopolitan	
<i>Colle* campbellensis*</i> Steel	×												×
Pselaphidae													
<i>Pselaphotheseus* hippolytae*</i> Park	×												×
Byrrhidae													
<i>Liochoria sorenseni</i> Brks.	×												×
Ptinidae													
<i>Ptinus tectus</i> Boiel.												Cosmopolitan	
Lathridiidae													
<i>Melanophthalma globipennis</i> (Reitt.)			×										×
Tenebrionidae													
<i>Uloma</i> sp.	?												
<i>Pseudhelops tuberculatus</i> <i>posticalis</i> Broun	×												×
Salpingidae													
<i>Antarcticodonus fallai</i> Brks			×										×
Melandryidae													
<i>Orchesia rennelli*</i> Gr. & Sam.	×												×
Orthoperidae													
<i>Holopsis oblongus*</i> Endr.-Y.	×												
Coccinellidae													
<i>Veronicobius aucklandiae</i> (Kirsch)			×										×
Curculionidae													
Cryptorhynchinae													
<i>Notacalles* planidorsis</i> (Kirsch)			×									Stewart I.	×
<i>N. piciventris</i> (Broun)			×					×					×
<i>N. kroni</i> (Kirsch)			×					×					×





	End.	Ant.	Auck.	Sn.- Ant.	Macq.	H'rd	Kerg.	N. Z.	Tasm.	Aust.	S. Am.	Other areas	F <sup>1</sup> less
<i>Antarctopria latigaster</i> Brues					×								×
<i>A. latigaster campbellana</i> * Yosh.	×												×
Cynipoidea													
Cynipidae: Eucoilinae													
<i>Kleidotoma (Pentakleidota)</i> <i>subantarctica</i> * Yosh.	×												×

### ZOOGEOGRAPHY

Campbell Island has an arthropod fauna with interesting characteristics which speak for detailed consideration. The fauna is by no means as limited as suggested by early studies of this and other isolated subantarctic islands. It appears to be much larger than those of Kerguelen, the Crozets, Marion, Heard, Macquarie or South Georgia, none of which are greatly different from Campbell in latitude. Lesser isolation than most of the others is obvious in glancing at a map. Also, Campbell's situation on a subcontinental shelf in relative proximity to New Zealand correlates with its richer fauna of more continental aspect. On the other hand, some aspects of the fauna are not particularly suggestive of continental nature. The very disharmonic nature of the fauna, with the absence of so many groups, and the high ratio of flightless species, suggest an isolated oceanic island. The disharmony is probably in part related to the extreme environment, and the loss of flight to the prevailing windy nature of the island.

The subantarctic insular environment is very much poorer than that of the southern tip of South America, at the same latitude. Thus the isolated nature of the environment must be of considerable significance, and the climate cannot be held solely responsible for the highly disharmonic fauna. If then Campbell is a subcontinental rather than oceanic island, there must have been considerable extinction of fauna since the island became isolated. This is very likely true to some degree, for the flora demonstrates a parallel situation, with a relatively small number of families and species represented as compared with a similar environment in the Tierra del Fuego area.

The relative representation of insects and plants on Macquarie, Campbell and the Auckland Islands is somewhat comparable. In each case there appear to be roughly about 3.4-3.5 times as many species of terrestrial arthropods as species of vascular plants.

The contrast between the subantarctic insular environment and that in the northern hemisphere at the same latitude is very great. The temperature maxima are very much higher at the same latitudes in the northern hemisphere and a far richer biota occurs. The subantarctic is dominated by the antarctic climate which is far colder than the arctic. The contrast with the Antarctic continent is also great, as the fauna of the latter is much smaller and is nearly one-half ectoparasitic upon vertebrates.

On Campbell there appear to be almost three times as many species as families of arthropods, whereas on Macquarie there are less than twice as many species as families. The

ratio in the Aucklands is probably close to that of Campbell. With the other evidence for the oceanic nature of the Macquarie fauna, the ratio of less than two species per family suggests youth of the fauna, with little time for proliferation of species. The small number of endemic genera on Macquarie also suggests this. This evidence also may suggest a high extinction rate, lack of proliferation, and separate colonization for each element of the fauna. These suggestions may also apply to Campbell in considerable degree. A number of the genera presently appearing to be endemic to Campbell actually occur on the Aucklands or northward. It is interesting that on Macquarie and Campbell the species: family ratio is about the same for plants and arthropods (Macquarie 2 : 1; Campbell 3 : 1). On Macquarie the ratio of species to genera is 1.16 : 1 for plants and about 1.4 : 1 for arthropods, whereas on Campbell it is about 1.7 : 1 for plants and about 1.6 : 1 for arthropods.

In the tropical oceans a strongly disharmonic fauna is indicative of an oceanic island. By being well isolated and never connected with a continent, its fauna is limited by the degrees to which insects have been successful in crossing ocean barriers. In the subantarctic seas, however, a fauna may be extremely limited and yet not necessarily be of purely oceanic origin. There are such rigorous limiting factors, not merely concerned with over-water dispersal, that many groups of arthropods cannot tolerate the environment. Thus if islands such as Campbell are actually remnants of a former larger subcontinental land mass, as their geology seems to indicate, the fauna may have become depauperized from a trend to adversity resulting from changing climate and loss of appropriate environments in the reduction in size of the island. Also, the former New Zealand subcontinent may very likely not have had direct and complete connection with Australia or Antarctica (and South America) in the Tertiary or for a much longer period, or ever. The present New Zealand fauna lacks many otherwise more or less cosmopolitan groups. This is good evidence of very long isolation. Also, the fact that many old "links" which are extinct elsewhere survive in New Zealand is evidence of long isolation from more advanced forms which have eliminated the primitive forms through competition on continental areas.

Thus the land fauna of Campbell (and of the Aucklands) might be classified as a depauperized fragment of an ancient subcontinental fauna, with over-sea recolonization. For those islands farther northeast, the Antipodes and the Bounty Is., the depauperization has proceeded further because of greatly reduced island size; or cataclysms or glaciation may have eliminated or largely eliminated the former land fauna, making the present fauna essentially oceanic in origin. (The Bounty Is. are said to be very rocky and devoid of vegetation). For the Snares, much nearer to the South Island of New Zealand, the situation is probably similar, but the proximity would presumably permit more facile over-sea colonization. Actually, these smaller islands have not been sufficiently investigated entomologically to permit adequate characterization of their faunal makeup and origin. The Chatham Is., much farther north, have a very remarkable fauna for an island group so small and likewise so suggestive of oceanic origin when merely viewed on the map. There is even better representation of fresh-water insects and other groups in the Chathams than in the Aucklands. This again suggests that the group is an old subcontinental fragment.

In the case of Macquarie I. the picture appears to be rather different. Macquarie is more isolated in terms of sea-bottom topography than Campbell and the islands to its north (although recent soundings have shown a more substantial ridge between Macquarie and New Zealand which might have been significant in the distribution of non-abysal marine

animals). Also, Macquarie is entirely of volcanic origin, contrasting geologically with Campbell. Thus, with its much poorer arthropod fauna, it appears to be a rather typical oceanic island. Its land fauna could have come by over-sea dispersal. Its lack of weevils, tenebrionids and other beetle groups (except staphylinids) represented on other subantarctic islands, appears to be strong evidence of oceanic faunal origin.

The various subantarctic islands have been quite unequally investigated entomologically. Thus the tables (2, 4) and maps (figs. 2-9) do not give a complete or balanced picture. For instance, previously South Georgia and the Falkland Is. have been insufficiently collected. This is also true of Marion I. It is difficult to judge how adequately Heard, Kerguelen and the Crozets have been covered. Currently, a survey in South Georgia is being completed by Bishop Museum (H. Clagg). Another has just been made among the islands just south of Tierra del Fuego (J. Boyd). It is hoped to do further work in the Auckland Is. during the 1964-65 season.

In addition to the question of uneven sampling of different island groups, a point to be borne in mind in this discussion is differing standards for families, genera or other categories in different groups of arthropods. Thus in one group genera may seem to have limited local distribution, whereas in another they may have much larger ranges. Although some of this may be real, it is very likely that different interpretations of genera and generic characters enter into the problem. Also, the differing geographical extent of material seen by investigators is important. These differences may profoundly affect zoogeographic conclusions. In some groups where genera have been said to be in common between the southern continents, specialists are concluding that different genera are involved. In other cases conclusions of the reverse nature are being made, suggesting closer relationships of southern areas.

*Environmental aspects:* In comparing the arthropod fauna of Campbell with those of Macquarie, the Aucklands and others, viewing in several different perspectives is necessary. Different geological origin, age, degree of isolation, extent of recent vulcanism, glaciation and erosion, as well as latitude, climate, size, ecological diversity and other factors need to be considered. Also, the history of introduced animals (including arthropods), introduced plants, populations of seals and sea birds, and activities of man, must be taken into consideration.

Campbell is intermediate in latitude, in degree of isolation, and in climate, among the three associated island groups, Macquarie, Campbell and the Aucklands, although the range is not great. Macquarie differs from the other two in being of purely volcanic origin. Campbell gives the impression of being younger with its several fairly conspicuous conical hills. However, vulcanism is by no means recent and there has probably been no activity since the late Pliocene. This may have been a little later than the last vulcanism at Macquarie and the Aucklands. In regard to glaciation, all three islands underwent severe glaciation during parts of the Pleistocene. Also, all three have undergone very extensive erosion on the westward sides from sea and wind, greatly reducing the size of the island in each case. In regard to size, Campbell is slightly smaller than Macquarie, and much smaller than the Aucklands. Because Campbell has slightly higher mountains than Macquarie, has deeply indented harbors, more species of plants, more varied geology, and less severe climate, it has greater ecological diversity. Campbell also differs from Macquarie in having more large hills and ridges, without the extensive plateau and the many tarns

or lakes possessed by Macquarie. Again, Campbell is intermediate, for the Aucklands are richer and more varied in these respects, with higher altitudes, richer flora, varied geology, as well as having several sizeable, as well as small, islands subsidiary to the main Auckland Island.

In regard to history of introduced animals, the three islands are very different. In each case the effects of these animals on the vegetation are conspicuous, and within the Aucklands several strikingly different situations prevail. It is difficult to assess the effect that the vegetational changes have had upon the arthropod faunas. On Macquarie, rabbits, cats and the introduced large New Zealand rail (weka, *Gallirallus australis*) are very abundant. The rabbits have greatly reduced the tussock as well as *Stilbocarpa* and other herbs, greatly changing the appearance of the island. The weka feeds actively on insects, and the cats have greatly reduced the petrels and other ground-nesting birds. Rats are also present on Macquarie, and a few sheep on Wireless Hill north of the isthmus. On Campbell, sheep have greatly changed the vegetation, reducing the tussock, *Stilbocarpa*, *Pleurophyllum* and other herbs, and increasing the *Bulbinella*. Rats are extremely abundant and feed on insects and tussock. Cattle and cats are present but much less abundant. The introduced land birds doubtless prey upon insects. In the Aucklands, the main island has been ravaged by pigs, which have greatly reduced tussock, herbs and birds. Cats are also numerous, affecting bird breeding, and goats are present in the north. Rats are absent but mice present. Of the smaller islands, Adams I. has no introduced mammals and apparently represents the primeval condition. It has luxurious growth of tussock and the various succulent herbs. Disappointment I. has no introduced animals, and is a great albatross colony. Enderby I. has rabbits and cattle, with tussock nearly gone and *Bulbinella* dominant above the scrub as on Campbell. Rose I. has rabbits and limited tussock. It formerly had cattle. Ocean I. had sheep for 50 years but not in recent years. It is dominated by rata and *Hebe* scrub, and petrel rookeries. Ewing I. is said to have had no introduced mammals, but on a large area the large *Olearia* trees have replaced tussock and ferns. French I. has been free of disturbance, but is too small and low for some environments.

Since Campbell does not have sizeable off-shore islands like those of the Aucklands, nor a hill separated by a long low isthmus as does Macquarie, there are no obvious general barriers to spread of arthropods, weeds or introduced mammals within the island. (The cattle, however, remain at a small population on a limited part of the island, and most weeds are limited to the camp areas).

Of course many stringent environmental factors are involved in limiting spread. The small off-shore islets around Campbell are largely bare rock. They are fairly inaccessible and remain uninvestigated. The Courrejolles Peninsula is in a sense an island, for its steepness keeps out sheep, and perhaps also cats and rats. The dense mollymawk rookeries on the terraces prevent the development of much tussock.

Many species of arthropods, such as the scutigerellid *Hanseniella campbellensis* Jub.-Jup., occur from the upper inter-tidal zone to nearly the highest altitudes. In both these situations, and on intervening slopes, analogous rocky environment may occur, with moss and mat plants.

The drastic reduction in the populations of elephant seals, sea lions, fur seals and larger penguins as a result of man's activities has had great bearing on arthropod populations and other balances. Also, these and the introduced animals and plants have had a bearing

on populations of the smaller sea birds and others, which again has affected arthropod populations adversely. Perhaps only a few arthropods introduced by man have succeeded in establishing on Campbell. Some of those common to the southern part of the South Island of New Zealand might have been brought by man, but might have come by natural dispersal. If some of these represent relics from a time when there was a common connecting land-mass, perhaps on further study they may prove to have differentiated somewhat from the New Zealand populations. The evidence from the Campbell and Auckland Lepidoptera (Pyraloidea) indicates identical or closely related species on Campbell, Aucklands, Chathams and Kermadecs, suggesting good dispersal possibilities, with same species with ap-

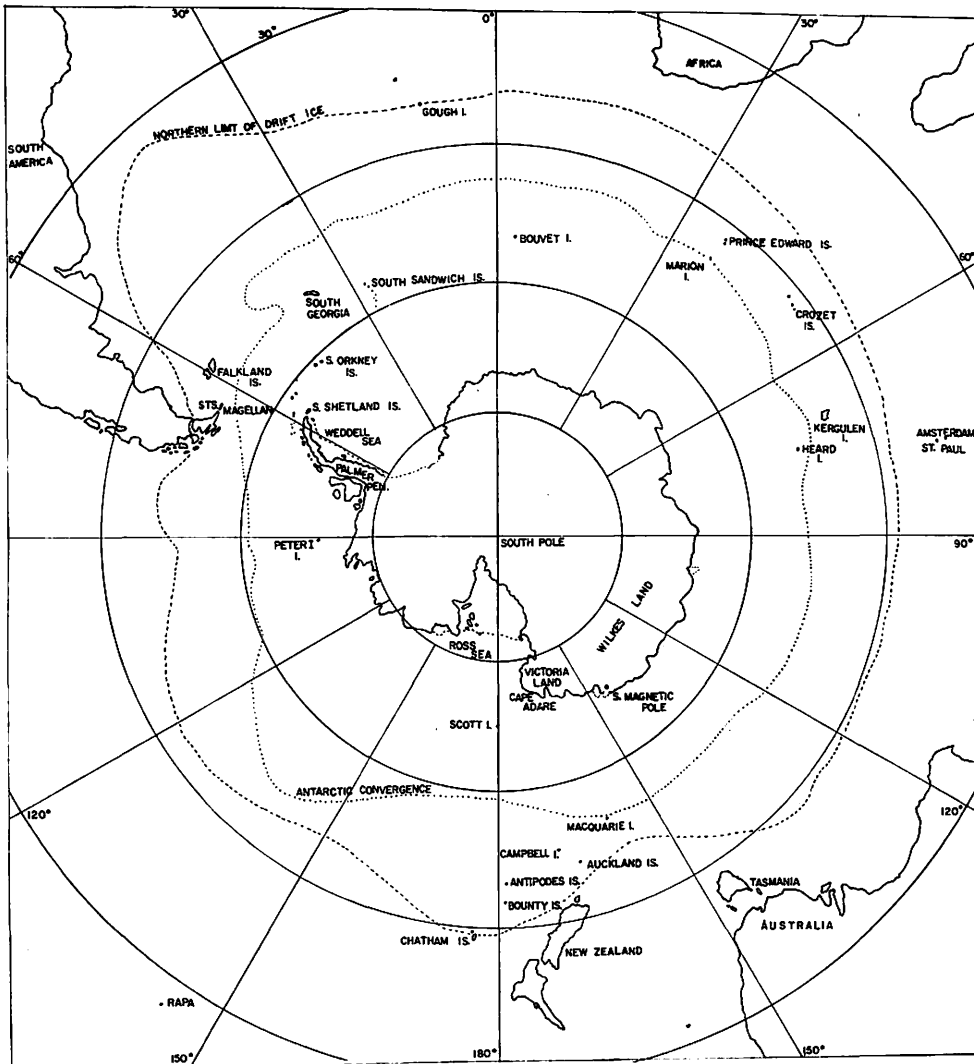


Fig. 1. Outline map of the subantarctic-antarctic area, showing subantarctic islands, and other features, for identification in connection with the following series of distribution maps.

propriate dispersal propensities reaching most of the islands, and also introductions by man (Munroe, *in litt.*).

Macquarie may have no man-introduced insects outside of the camp buildings, and even in the Aucklands there are probably few, other than possible introductions from southern New Zealand.

#### GENERAL DISTRIBUTION BY GROUPS

In the following discussion special emphasis is given to generic ranges and other interesting points, as the known distribution of the species is indicated in Table 1, above.

*Amphipoda*: Of the 6 terrestrial species recorded, 2 are endemic and the other 4 occur in the Aucklands, with 1 extending to Tasmania and Australia, 2 to New Zealand, and 1 of these to the Snares and Bounty Is.

*Isopoda*: This group has not yet been studied but only roughly sorted (by Danielle B. Fellows and Lucius Eldridge). There appear to be over 25 species, of which 21 may be terrestrial. Of the 4 terrestrial species already recorded, 1 is endemic, and the other 3 occur in the Aucklands, with 1 of these extending to the South Island of New Zealand.

*Araneae*: The 16 species of spiders on Campbell represent 10 families and 12 genera. Six of the genera are endemic to the New Zealand area. Three (*Gohia*, *Hina*, *Icona*) are limited to Campbell and the Aucklands, but there are related undescribed forms in New Zealand. Five genera are of wide southern hemisphere distribution, of which *Hahnia*, *Araneus* and *Linyphia* are subcosmopolitan. Only 5 of the species are endemic to Campbell, and 9 occur also in the Aucklands. Four occur in New Zealand and 1 of these is not yet known from the Aucklands. Two species are common to Macquarie, Campbell and the Aucklands, and one of these, *A. maritima*, occurs also in Tasmania, Australia and S. Africa. It is interesting that the genus *Myro* occurs in S. America, S. Georgia, S. Africa, Crozets, Kerguelen, Heard, Tasmania, Macquarie, the Snares and New Zealand (undescribed), and in Baltic amber, but not on Campbell or the Aucklands.

*Opiliones*: Two endemic species of harvestmen are known from Campbell I. The 2 genera occur also in New Zealand. There are no opiliones on Macquarie, 6 in the Aucklands, and many in New Zealand.

*Pseudoscorpionida*: Surprisingly, 2 genera of pseudoscorpions occur on Campbell. One of the genera is described as endemic in the main text of this volume, but Dr. Beier's paper in the Supplement demonstrates that both of the Campbell genera and species occur in the Aucklands, besides an additional species. Thus in this group Campbell and the Aucklands are closely related. The group has not been found on Macquarie.

*Acarina*: The mites are only partly studied. Also, mites are in general so poorly known that little generalization can be made on their distribution. Of the identified species, 14 appear to be endemic, 2 found on Antarctica, 4 in the Aucklands, 1 on the Snares, 3 on Macquarie, 1 on Heard, 1 on Kerguelen, 5 in New Zealand, 3 in Tasmania, 4 in Australia and 2 in S. America and elsewhere. One genus appears to be endemic, 3 are in common with Antarctica, but these and others are of wide occurrence. Of the unreported material, a majority appears to represent new species.

*Chilopoda*: The only centipede extends to Australia and New Zealand and appears to

be introduced.

*Diplopoda*: The 2 millipedes are not yet named. One appears to occur also in New Zealand.

*Symphyla*: The 2 symphylids belong to widespread genera, and 1 of the species is common to California and is probably widespread and introduced.

*Collembola*: The springtails are the second best represented order of insects on Campbell. The 46 species include 26 endemics, 5 in common with the Aucklands, 1 with Macquarie, 14 with New Zealand, 1 with Tasmania, 2 with Australia and 1 with S. America. Of the 29 genera, 3 are endemic, 1 is limited to Campbell, Aucklands and Macquarie, 3 to the New Zealand area, 3 to the New Zealand-Australia area, 1 is southern circumpolar, and 18 are of wide distribution.

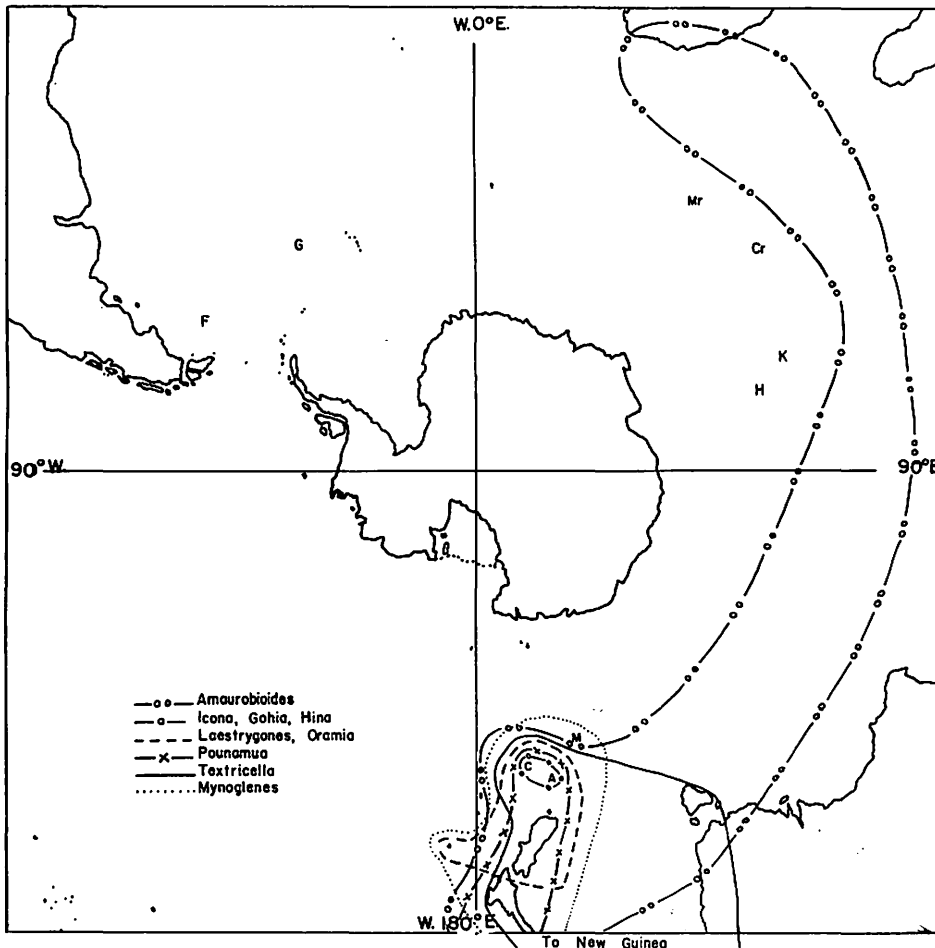


Fig. 2. Map of ranges of the spider genera known from Campbell I. *Textricella* extends as far north as New Guinea. Initials stand for islands as indicated on preceding map.

*Plecoptera*: The 3 species of Campbell stoneflies are of very great interest as they represent a family found in the southern continents. They represent 2 genera restricted to the New Zealand area. One genus is remarkable because it includes species with both terrestrial and aquatic larvae, and wingless adults. Illies, as he explains in his paper, feels that these species are not secondarily apterous, and stand as evidence that Campbell is continental and that the genus antedates the separation of Campbell and the Aucklands from New Zealand.

*Orthoptera*: The single species (a "weta") represents an apparently endemic genus of not very close affinity with others in the Aucklands, the Snares and New Zealand.

*Phthiraptera*: The distribution of the lice is controlled by that of their hosts, so the records are of greater interest in relation to their hosts than to the locality alone. The principal hosts are sea birds, partly of wide range, and seals, besides introduced animals.

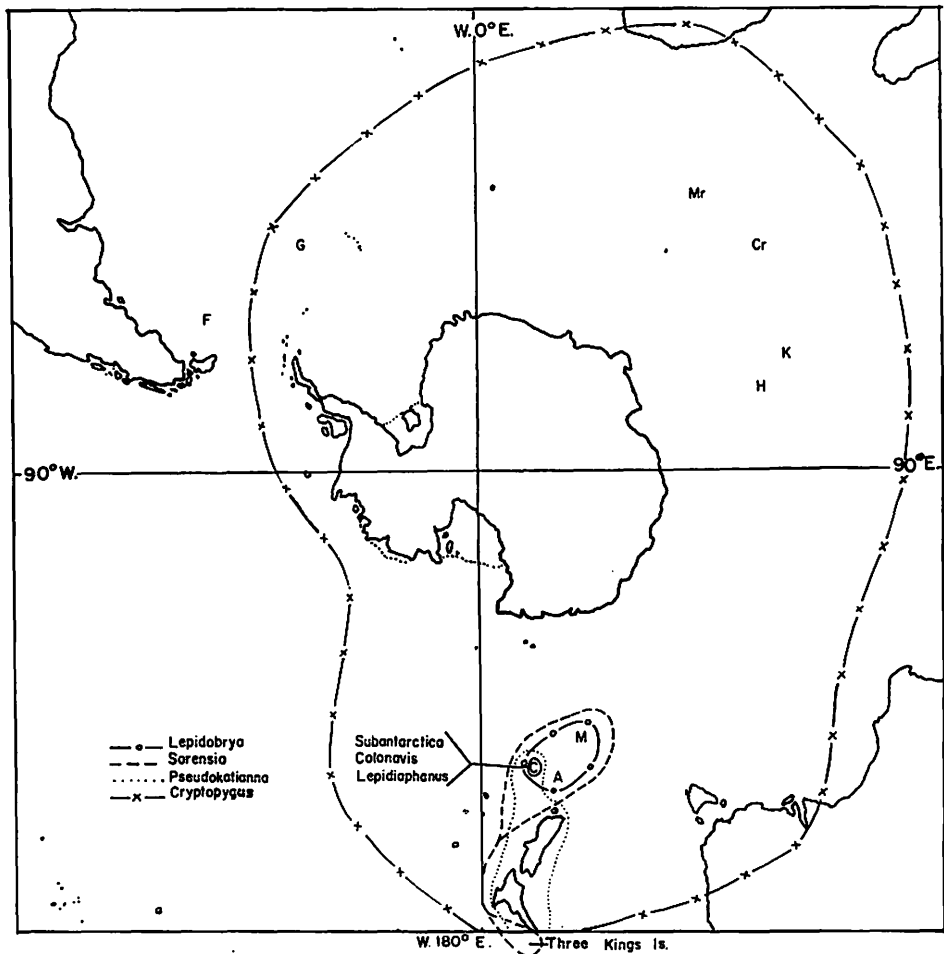


Fig. 3. Map of ranges of some of the genera of Collembola occurring on Campbell I.



*Psocoptera*: The 3 species, of 3 genera, all flightless, represent an endemic species of an Australian genus, species known only from Macquarie and Campbell, and a subcosmopolite also recorded from the Crozets.

*Thysanoptera*: The only thrips is probably a widespread species, introduced by man or by natural dispersal.

*Homoptera*: Probably all of the 7 species of aphids were introduced by man. The 4 species of mealybugs (3 genera) are of great interest. The *Phenacoleachia* is extremely interesting. The genus is known only from New Zealand, now extended to the Aucklands and Campbell. Of the other 3, 1 is endemic, 1 occurs also in the Aucklands and the third on the Aucklands and Stewart I. These belong to 2 genera of wide range. The fact that the known males (3 of the 4 species) are wingless is of great interest.

*Trichoptera*: The single species occurs also in the Aucklands, Chathams and New Zea-

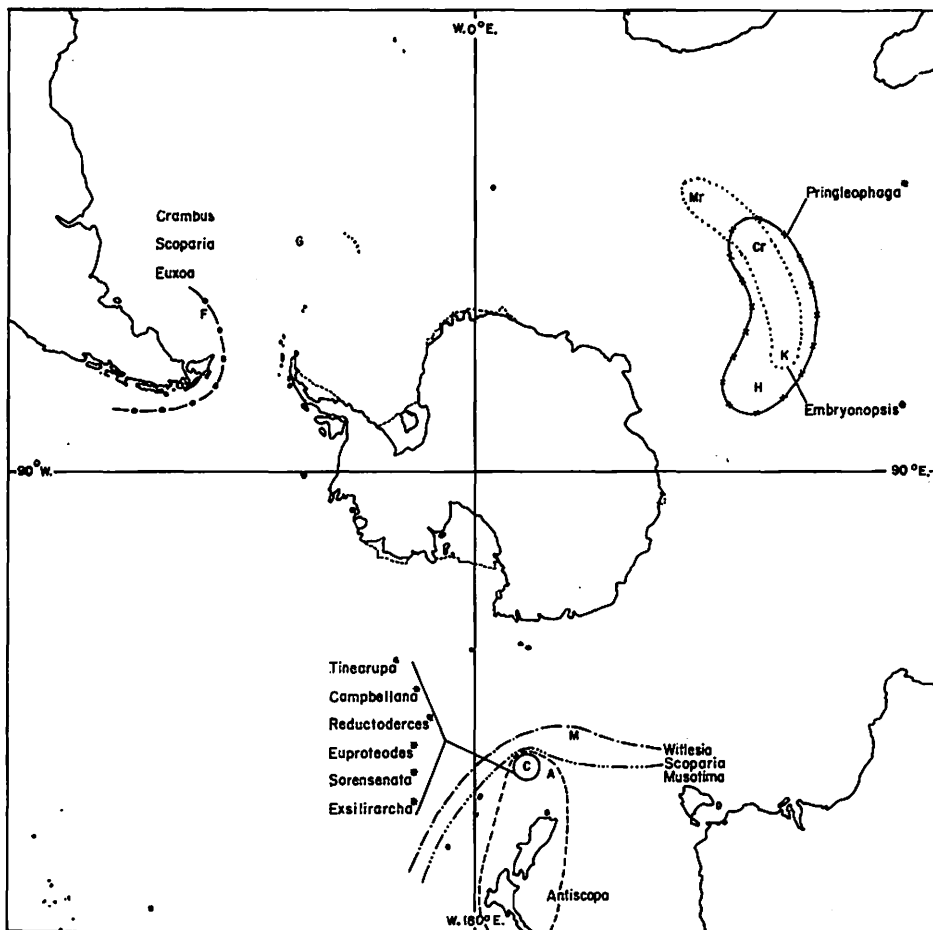


Fig. 4. Map of ranges of some of the genera of moths occurring on Campbell I., and of some other subantarctic islands.

land. The genus is cosmopolitan.

*Lepidoptera*: The Lepidoptera fauna of Campbell I. is very conspicuous with its high ratio of endemic genera, most of which include but a single flightless species each. Six genera are recorded as endemic. However, at least one of these, and perhaps more, occur in the Auckland Is., but have not yet been recorded from there. In any case, this is a high ratio for the total of 20 genera of Lepidoptera recorded from Campbell and the possible total of 27 genera from the Aucklands (including unrecorded ones in the new collections at hand). The 20 Campbell genera represent 10 families of moths. No butterflies, skippers, sphinx moths or other large types are represented. Of the 20 genera, 5 may be endemic, 1 is common to Campbell and the Aucklands, 1 occurs also in the Aucklands, Chathams and New Zealand, 1 extends to SE Asia, and 12 are cosmopolitan or subcosmopolitan. The affinities of the endemic genera are largely obscure. As far as indicated, the known relatives are in the Auckland Is. and New Zealand.

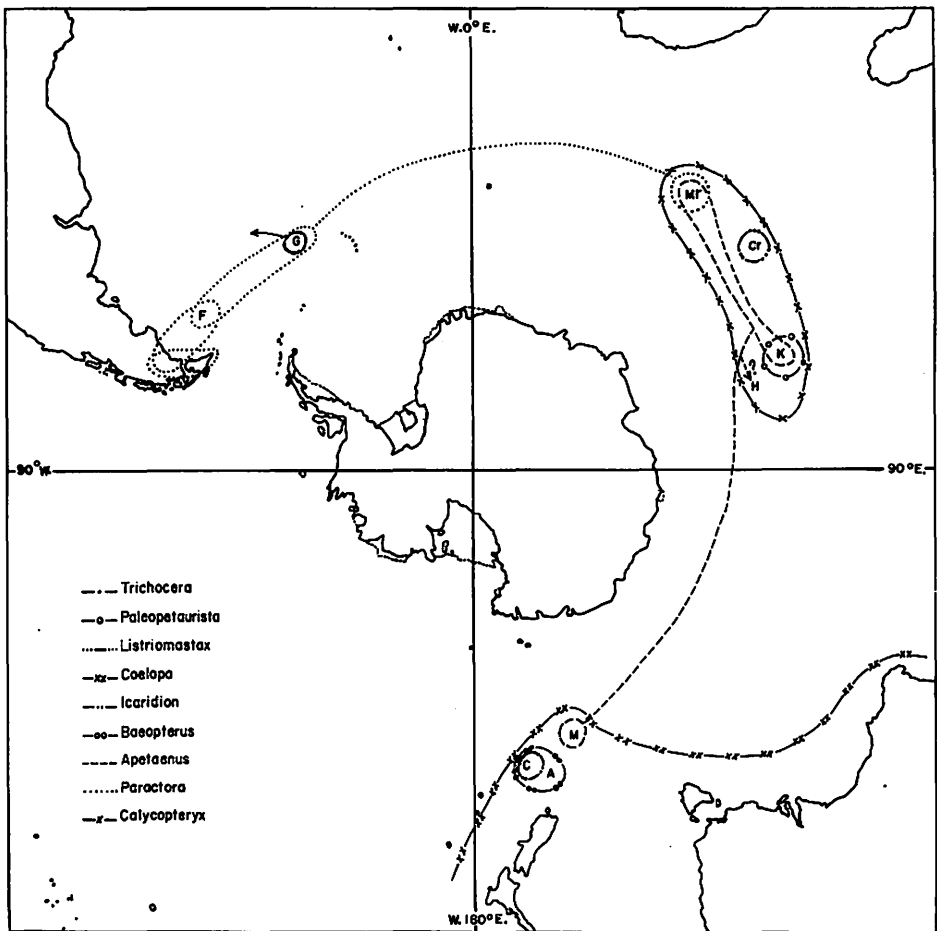


Fig. 5. Map of generic ranges of certain subantarctic Diptera.

*Diptera*: This is the order with the largest number of species (81) on Campbell I. It is represented by 23 families. The families with the largest number of species (5 or more) are Tipulidae, Psychodidae, Chironomidae, Mycetophilidae, Coelopidae, Ephydriidae and Muscidae. Large families such as Culicidae, Stratiomyiidae, Asilidae, Tabanidae, Agromyzidae, Drosophilidae, Tachinidae and Sarcophagidae are absent. Of the 81 species, 35 (possibly up to 41) appear to be endemic. Of the 49 genera, 1 is recorded as endemic, but appears to occur also in the Auckland Is. Three others appear limited to Campbell and the Aucklands (or Snares), 4 to Campbell and New Zealand, 3 extend to New Zealand and Australia, 3 to southern continents including New Zealand, Australia and South America, 3 to Europe, and 24 are cosmopolitan or subcosmopolitan. Only 4 of the genera are also known from Macquarie, and 2 of these are represented by identical species. One species has different subspecies on Macquarie and Campbell. No genera on Campbell appear to be in common with Heard, Kerguelen or South Georgia. Thus a great difference between

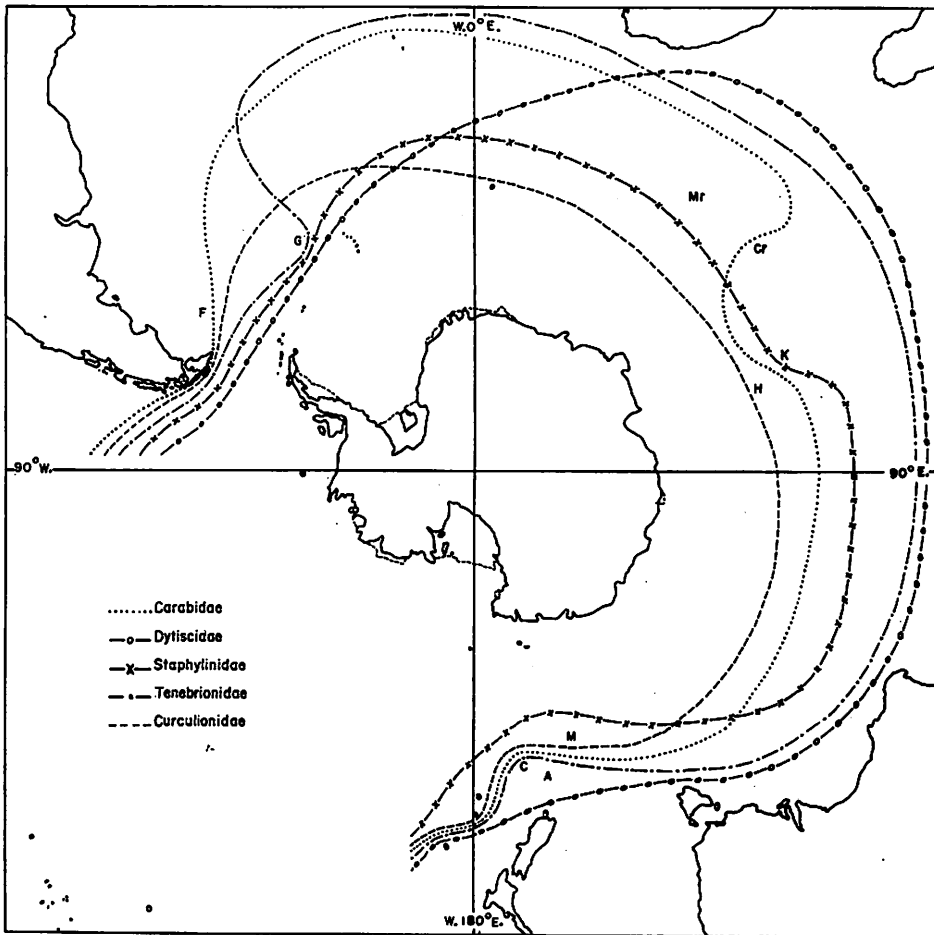


Fig. 6. Map showing southern known extremes of distribution of 5 families of beetles.

Macquarie and Campbell is the greater faunal affinity of Macquarie with the Kerguelen-Heard area. Twelve species of flies have wings reduced or lacking.

*Siphonaptera*: The 3 species represent 3 families. Each occurs on some other subantarctic islands, and 1 is cosmopolitan.

*Coleoptera*: This order is very disharmonically represented on Campbell in terms of average world representation. However, it reflects to some extent the relative representation in other very cold and extreme environments. Fifteen families occur on the island. The best represented is the Curculionidae with 15 species of the total of 43 species of beetles. This dominance is in line with that on tropical oceanic islands. Perhaps the family is the largest in the world. The second largest beetle family on Campbell is the Staphylinidae, with 12 species. This is the only family of Coleoptera known to occur on Macquarie, where it is represented by 4 species (of which 2 are in common with Campbell and the

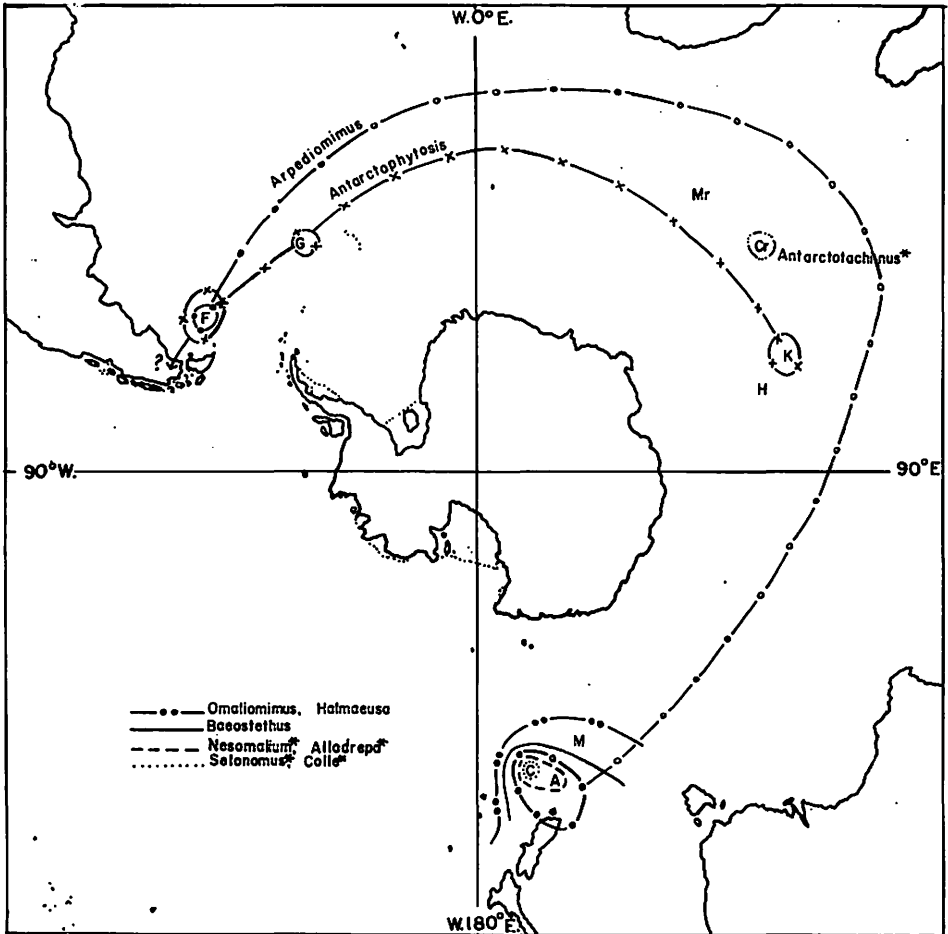


Fig. 7. Map showing generic ranges of Staphylinidae occurring on Campbell I. and other subantarctic islands.

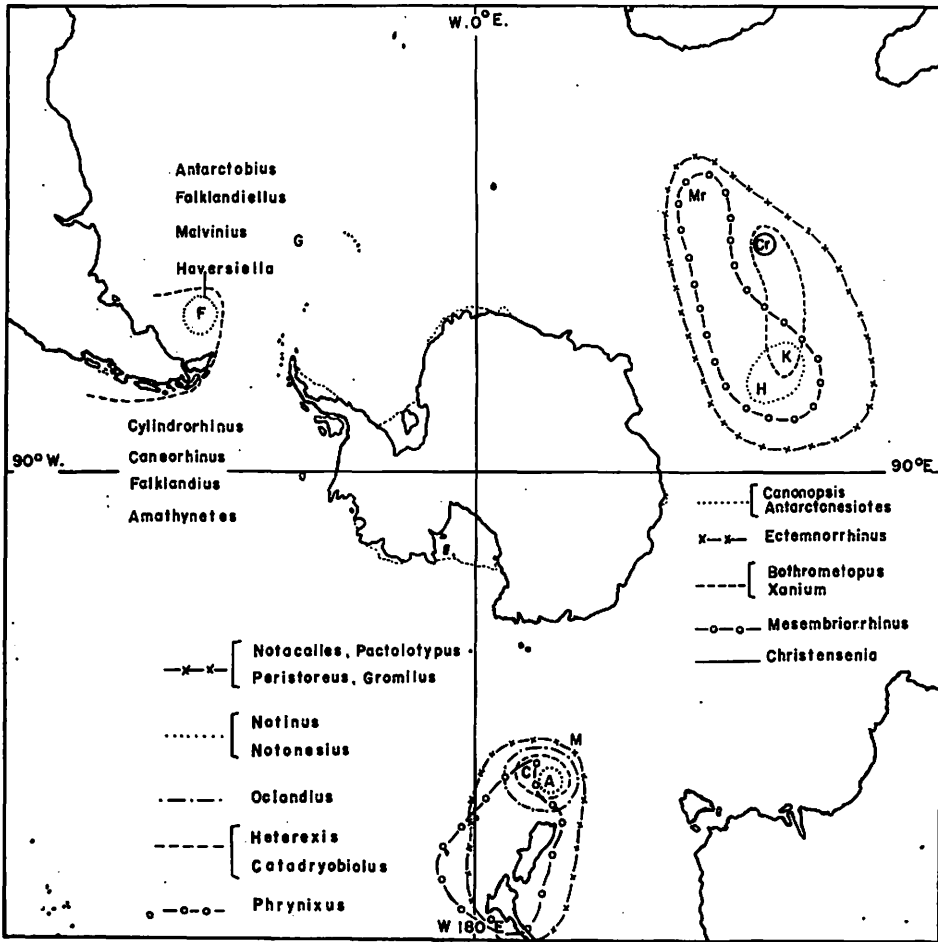


Fig. 8. Map showing ranges of most of the genera of subantarctic weevils.

Aucklands, and another with the Aucklands only). Its representation on Campbell is rather striking, with 2 apparently endemic genera (1 species each), as well as 2 so far known only from Campbell and the Aucklands (3 species). Of the other 5 Campbell species of Staphylinidae, 2 are endemic, 1 is common to the Aucklands, another to the Aucklands and New Zealand, and 1 is subcosmopolitan.

Of the 43 species of Campbell beetles, 23 are endemic, 17 occur also in the Aucklands (5 of these also in New Zealand), 2 are more or less cosmopolitan, and 1 is common to New Zealand. Apparently all but 4 of the Campbell species are flightless or generally flightless. Besides the 3 endemic genera and 4 or more common to Campbell and the Aucklands, 1 genus is common to southern South America, 2 to the Falklands and South Georgia, with 1 of these and 1 other to Indian Ocean subantarctic islands, 3 to New Zealand, and most of the rest are of wide range. When the Aucklands fauna is fully studied, no doubt more genera and species will be found in common with Campbell. One of the

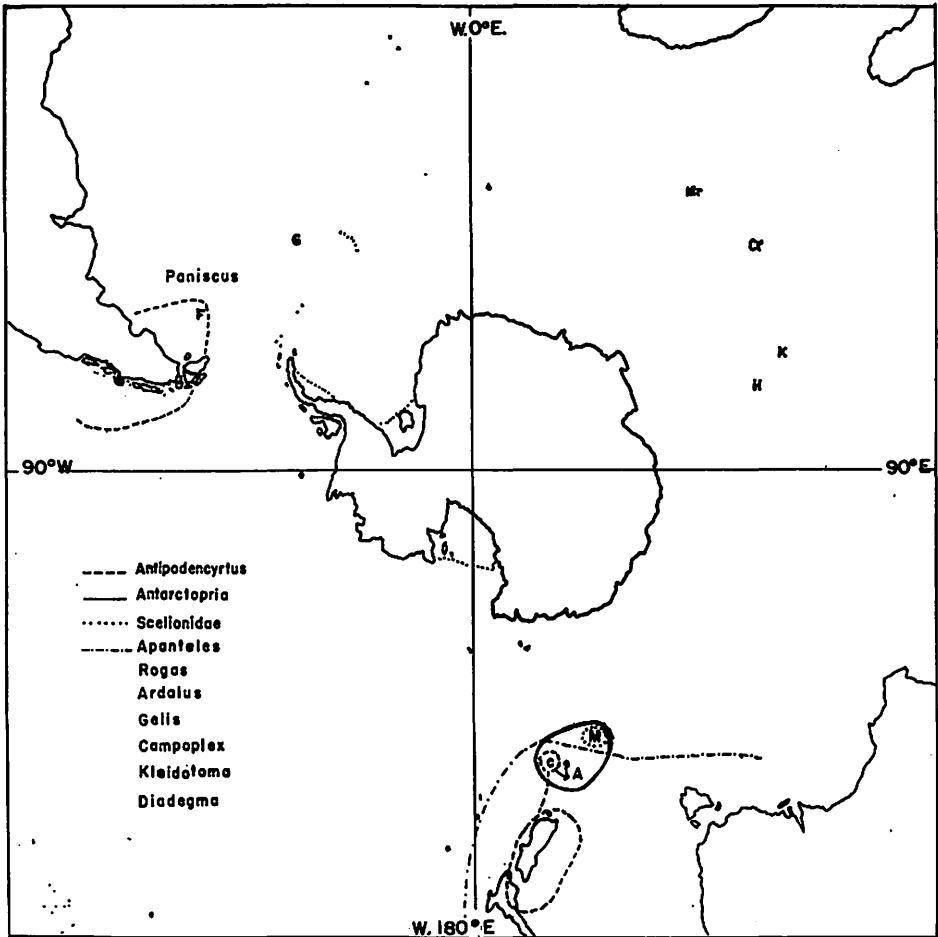


Fig. 9. Map showing ranges of most of the known genera of subantarctic Hymenoptera. The records of an ant (*Camponotus*) from Kerguelen and Crozet are omitted as they are probably erroneous.

endemic Campbell genera seems to have its closest relative in western North America and another in the northern Pacific.

**Hymenoptera:** Campbell I. is the second most southern island (apart from southern South America) with records of the occurrence of this order. The southernmost, Macquarie, has only 1 or 2 species, whereas Campbell has about 10. This is probably one of the most specialized Hymenoptera faunas that exist, with its high ratio (50%) of species with wings reduced or lacking. All the species are endemic except one in common with Macquarie (one other not identified). Of the 9 genera, 1 is known only from the nearby subantarctic islands, 1 is common to New Zealand, and the others are cosmopolitan or largely of northern distribution. The absence of ants, bees and aculeate wasps is conspicuous. All of the Campbell species are parasitic, most of them apparently in Diptera and Lepidoptera.

## SUBANTARCTIC FAUNAL REPRESENTATION

In comparing Campbell with other subantarctic islands, the richer fauna correlates also with higher minimum temperatures and more extensive flora. Macquarie is slightly cooler and has a much more limited fauna and flora. Heard I. is much colder, and has much more limited biota. Heard is of course also farther from continents than Campbell and Macquarie. Kerguelen is larger and much farther north, but is colder than Macquarie or Campbell, as well as being more isolated. It is close to the Antarctic Convergence and has an icecap somewhat less extensive than that of Heard. Jeannel (1940) considered that the biota of Kerguelen, and particularly its rich fossil flora, proved that it was long connected to Antarctica. He showed the Indian Ocean as very narrow in the Eocene, with Australia, New Zealand and South America still connected to Antarctica. This information is now partly disproved (Adie 1964).

Some of the characteristics of faunal representation on Campbell in particular are discussed in the preceding and following sections. Conspicuous general faunal differences between the insular subantarctic fauna and that of the Arctic include the absence of butterflies, scarcity of Hymenoptera and abundance of beetles in the subantarctic, as compared with the abundance of butterflies and Hymenoptera and scarcity of beetles in the Arctic. Only one butterfly was seen in the Auckland Is., a strong flying vanessine.

Table 2 indicates the number of species recorded, or known to have been collected on various subantarctic islands and Antarctica. This information is rather unbalanced, since collecting and study of the various faunas has been quite unequal. Even for the Auckland Is., the estimates are very conservative. The graph in fig. 10 probably gives a much more realistic estimate (600 species) for the Aucklands.

*Distribution patterns:* Many genera extend clock-wise (W-E) to Macquarie from long distances around Antarctica as far as from South America. Very few of these genera extend to Campbell. Thus Macquarie and Campbell really have rather little in common, considering their proximity. This appears to suggest that forms successful in oversea dispersal as far as Macquarie failed to carry a bit farther to Campbell. Possibly some of these failed to establish upon Campbell because of competition from forms already present there.

Present patterns of subantarctic distribution do not shed a great deal of light on the question of the validity of the "Austral Region" (Kuschel 1964). One problem is the absence of so many "southern" groups on the actual subantarctic islands. Further coordinated studies of groups for the whole area, covering evolutionary patterns, will help solve this question. In any case, the fact that some of the groups common to the southern continents extend into New Guinea is overbalanced by the predominance of tropical Oriental elements there.

Brundin (1964) stressed the necessity of showing that the species in one southern area represent a specialized offshoot of those found in another, to prove that Antarctica was a faunal migration route. His examples from the chironomid subfamily Podonominae appear to satisfy this requirement, and the subfamily is represented on Campbell I. (But see below, Faunal Origins). Brundin also indicated that for proof of Antarctica as an evolutionary center requires whole complexes of bicentric Austral groups closely related to one another. Penniket (1961; also see Knox 1964) presented interesting data in the Ephemeroptera which seems to satisfy Brundin's second requirement, showing that there are few

Table 2. Approximate numbers of species known from subantarctic-antarctic areas

	Antarctica	S. Georgia	Falklands	Marion	Crozet	Kerguelen	Heard	Macquarie	Campbell	Aucklands	Snares Antipodes Bounty
Araneae	-	4	?	2	6	2	1	3	16	21	6
Opiliones	-	-	1	-	1	1	-	-	2	5	1
Pseudoscorpionida	-	-	-	-	-	-	-	-	2	3	-
Acarina	20	5+	8+	2+	10+	10+	5+	35	71	80	1+
Chilopoda	-	-	-	-	-	-	-	-	1	3	-
Diplopoda	-	-	-	-	-	-	-	-	2	3	1
Symphyla	-	-	-	-	-	-	-	1	2	2	-
Collembola	11	8	10	2	4	9	5	12	46	50	?
Ephemeroptera	-	-	-	-	-	-	-	-	-	1	-
Odonata	-	-	-	-	-	-	-	-	-	1	-
Plecoptera	-	-	-	-	-	-	-	-	3	5	-
Blattaria	-	-	-	-	-	-	-	-	-	1	-
Orthoptera	-	-	1	-	-	-	-	-	1	1	2
Psocoptera	-	-	1	1	1	2	-	1	3	3	?
Thysanoptera	-	-	-	-	1	-	-	1	1	?	-
Mallophaga	16	4+	5	2	?	13	4	20	23	20	?
Anoplura	6	?	1	?	?	1	?	1	3	3	?
Homoptera	-	-	-	-	-	-	-	2	11	14	?
Heteroptera	-	-	1	-	1	-	-	-	-	1	-
Neuroptera	-	-	-	-	-	-	-	-	-	1	-
Trichoptera	-	-	1	-	-	-	-	-	1	2	-
Lepidoptera	-	1	16	1	1	4	1	1	29	40	6
Diptera	2	9	18	3	7	12	3	14	81	95	20
Siphonaptera	1	1	3	?	?	2	2	5	3	5	1
Coleoptera	-	7	52	4	11	17	10	5	43	65	10
Hymenoptera	-	-	1	-	-	-	-	2	10	19	?
Totals	56	39	119+	17	43	73	31	103	354	453+	48

genera known to be in common between southern continents, but several groups of closely related genera—the groups, or subfamilies, being entirely southern. Unfortunately, this order is absent from Campbell, though represented in the Aucklands.

Of the 300 identified species on Campbell, the following are in common with other areas (excluding ectoparasites):

Antarctica	2	St. Paul	1	Tasmania	10
Macquarie	15	Heard	2	Australia	19
Auckland Is.	74	Crozets	1	South America	5
Snares/Antipodes	8	Kerguelen	2	(4 are cosmopolitan)	
New Zealand	88	Marion	1	Other regions	28
				(incl. 16 cosmopolitan)	

In addition, there are 3 species with separate subspecies indicated for Macquarie and



Campbell. The above figures are exclusive of the ticks, lice and fleas. The number in common with the Auckland Is. is certain to be increased when the new collections are fully studied.

*Southernmost extensions:* In the case of many groups, the southernmost known records (apart from South America) are from Campbell I. Many of the families now known from Campbell have not been recorded from South Georgia, Heard or Macquarie, the isolated subantarctic islands farther south than Campbell. The following families are in this category:

Dictynidae	Ceratozetidae	Hyponomeutidae	Carabidae
Toxopidae	Schelorbataidae	Elachistidae	Ptiliidae
Amaurobioididae	Scutacaridae	Oecophoridae	Leptodiridae
Theridiidae	Stigmaeidae	Cosmopterygidae	Pselaphidae
Symphytognathidae	Tydeidae	Tortricidae	Byrrhidae
Argiopidae	Trombidiidae	Pterophoridae	Lathridiidae
Attidae	Henicopidae	Geometridae	Salpingidae
Phalangiidae	Sphaerotrichopidae	Simuliidae	Melandryidae
Trienonychidae	Metopidiotrichidae	Mycetophilidae	Orthoperidae
Chernetidae	Scolopendrellidae	Cecidomyiidae	Coccinellidae
Haemogamasidae	Scutigereidae	Syrphidae	Braconidae
Phthiracaridae	Gryopterygidae	Empididae	Ichneumonidae
Camisiidae	Rhaphidophoridae	Sapromyzidae	Eulophidae
Plateremaeidae	Elipsocidae	Canaceidae	Encyrtidae
Carabodidae	Trogiidae	Milichiidae	Cynipidae
Microzetidae	Hoplopleuridae	Calliphoridae	
Eupelopidae	Pseudococcidae	Muscidae	

Some of these families will undoubtedly later be recorded from South Georgia or Heard I. There are at least 5 families recorded from South Georgia and Macquarie which are not known from Campbell.

#### DISHARMONY

The disharmonic nature of the Campbell fauna is conspicuous, with great gaps in the fauna. In general, there is not the obvious speciation characteristic of many isolated tropical oceanic islands. This in general suggests greater youth of the fauna for subantarctic islands.

The orders present in the Auckland Is. which are absent to southward are Ephemeroptera, Blattaria, Odonata and Neuroptera, as well as the suborder Heteroptera. Some important families found in the Aucklands but not on Campbell include Culicidae, Stratiomyiidae, Asilidae, Lonchaeidae, Agromyzidae, Tachinidae, Nitidulidae, Elateridae, Cerambycidae and Anthribidae.

In fig. 10 a graph shows the relative reduction in numbers of groups, genera and species, progressing from the Auckland Is., through Campbell and Macquarie to Antarctica proper. The solid line represents numbers of groups, such as orders of mites and insects, and subclasses for other groups of arthropods. The dashed line represents numbers of species (over a factor of 15), with the actual figures or estimates indicated. The dotted line in-

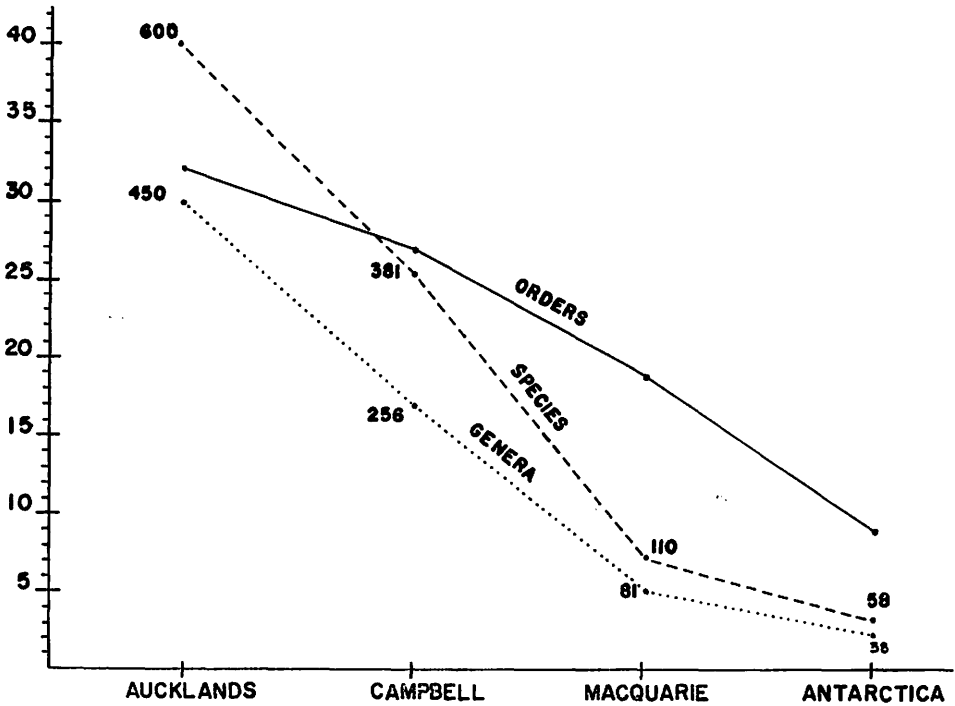


Fig. 10. Graph showing numbers of orders, genera and species of land arthropods occurring in the Auckland Is., Campbell I., Macquarie I. and Antarctica. The numbers are based on published records combined with estimates of numbers in unstudied collections at hand.

dicates numbers of genera (over a factor of 15), with the figures or estimates indicated. Again, the different faunal nature of Macquarie as compared with Campbell, is evident.

*Faunal comparison of Campbell and a tropical atoll:* The insect fauna of Campbell I. is comparable in number of species to that of a fairly rich humid tropical atoll in the mid-Pacific. A tabulation is made of the species recorded from Campbell as compared with the estimates for Arno Atoll in the Marshall Is. (Usinger & La Rivers 1953; Gressitt 1954, p. 136). The third column in Table 3 represents the number for the world over a factor of 2,500 to make the figures somewhat comparable. The contrast in some groups is rather conspicuous, *i. e.* the fairly large numbers for Orthoptera, Thysanoptera, Heteroptera and Hymenoptera on Arno, as compared with small numbers, or absence, on Campbell. On the other hand, the relative dominance of Collembola on Campbell is conspicuous. Perhaps these were inadequately sampled on Arno, as with the Mallophaga. However, the Collembola are obviously well adapted to cold areas, being the best-represented free-living group in Antarctica proper.

In regard to Table 3 it should be further remarked that the fauna of Arno Atoll is more harmonic than that of Campbell, even though Arno's fauna is extremely disharmonic. Probably in the Arno survey the Heteroptera and aquatic insects were more thoroughly covered than some other groups. Soil fauna, Lepidoptera and ectoparasites were relatively more thoroughly covered on Campbell. On the other hand, there are few insects in the

Table 3. Comparison of species representation on Campbell, Arno and the World.

Order	Campbell I.	Arno Atoll	<u>The World</u> 2500
Thysanura	0	1	0.1
Collembola	46	1	1
Protura, Zoraptera	0	0	0.001
Ephemeroptera	0	0	1-
Odonata	0	5	2+
Plecoptera	3	0	1
Embioptera	0	0	1-
Dermaptera	0	5	0.5
Orthoptera s. lat.	1	26	9
Isoptera	0	4	1-
Psocoptera	3	3	1-
Thysanoptera	1	14	1+
Mallophaga	23	3	1+
Anoplura	3	1	0.1
Homoptera	11	16	10
Heteroptera	0	24	12
Neuroptera s. lat.	0	1	2
Mecoptera	0	0	1-
Trichoptera	1	0	2
Lepidoptera	29	18	45
Diptera	81	83	34
Siphonaptera	3	0	0.6
Coleoptera	43	69	109
Hymenoptera	10	22	42
Orders	14	17	25+
Species	258	296	276-( $\times 2500$ )

salty atoll soil environment. It is very unlikely that Heteroptera occur on Campbell, and there are probably no additional aquatic insects except Chironomidae (not reported in this volume). Isoptera, Dermaptera and Orthoptera are more dominantly tropical insects and are hardly expected on subantarctic islands. Dominantly temperate aquatic insects like Plecoptera and Trichoptera are hardly to be expected on an atoll. Their representation on Campbell was somewhat unexpected, and appears, at least as regards the wingless stoneflies, to give evidence of continental nature.

An important difference between Campbell and Arno in ecology and population levels is that Campbell is weak in predators and Arno is rather rich in predators (insects and skinks, particularly). Thus populations of herbivorous insects are kept fairly low on Arno. On the other hand, herbivorous insects are less dominant on Campbell in proportion of species representation. Among other differences are the importance of cockroaches and ants on Arno, and their absence from Campbell. The question of insect pollination of plants is an interesting one, as this is important on Arno (perhaps 2/3 of the higher plants are insect pollinated). On Campbell, insect pollinators are probably very few, as there are no bees or other common pollinators other than syrphid flies. Perhaps wingless flies such as *Coenosia* play a role here.

It would be difficult to find an isolated tropical high island analogous in faunal size to Campbell, for comparative purposes. An island of similar size would be richer unless very young, or ruined from introduced biota like the Mangarevan Is. Most young islands, such as those in the Northern Mariana Is., still have volcanic activity and much disturbance. Comparison of fauna between Campbell and the Pribilof Is. should be interesting from the standpoint of more similar climate.

It is interesting to compare the Campbell fauna with that of arctic Canada and with Spitzbergen. The dominance of Diptera is common to all, but in the Queen Elizabeth Is., N. Canada (Downes 1962), Lepidoptera and Hymenoptera are relatively far more important than on Campbell, while Coleoptera are much more poorly represented in the north. Collembola are not mentioned by Downes. On Spitzbergen (Summerhayes & Elton 1923, 1928) the picture is somewhat similar to that of high Arctic Canada, but Lepidoptera are proportionately scarcer than on Campbell. Collembola, as well as spiders and mites, are well represented on Spitzbergen. For N. Canada, Downes stressed the tendency of niches to remain empty, and the randomness of representation. In Spitzbergen, some of the communities in less favorable environments support a fauna similar to that of the Antarctic Peninsula, whereas the most restricted fauna discussed for N. Canada by Downes includes one moth and one parasitic wasp. The latter fauna is suggestive of that of Macquarie I., except that Macquarie has a larger fauna, with six orders of true insects not listed by Downes. Spitzbergen was completely glaciated after separation from Europe, and the insect fauna came by oversea dispersal, through wind, flight and on birds and ships, if not also by drift wood or drift ice (Elton 1925).

#### ENDEMISM

The degree of endemism for Campbell I., as it now appears, is moderately high. Of the approximately 300 species fully identified from Campbell in this volume, 141 species, or 47 %, appear to be endemic to the island. However, when the Auckland Is. fauna is fully studied, this endemism rate may be reduced. Campbell and the Aucklands have lower endemism than might be expected considering their isolation. This is very true if they are compared with the Canaries or Juan Fernandez.

As to genera, the present picture seems to indicate 19 genera as endemic to Campbell I. This represents generic endemism of 7%. In the case of genera, the degree of endemism is likely to be reduced much more than that for species, particularly when the Aucklands fauna is fully studied. Recent field work in the Aucklands provided much material not yet recorded from those islands. A number of the forms collected appear to represent genera now considered endemic to Campbell. It is likely that a number of new genera of mites are to be described from Campbell in the as yet unreported groups. However, it would be surprizing if many of these were actually endemic to Campbell, and did not also prove to occur in the Aucklands and/or Macquarie. Probably many of these genera occur also in New Zealand or more widely, as the groups involved have not been adequately studied, or even studied at all, for this part of the world.

Data on endemism and genera and species possessed in common with Macquarie and the Auckland Is. are presented in Table 4.

In many cases there have proven to be closely related but different populations of a

Table 4. Apparent endemism of Campbell arthropods, by groups, and relationship to Macquarie and Aucklands

	No. genera	Endemic genera	No. species	Endemic species	In common with Macquarie		In common with Auckland Is.	
					genera	species	genera	species
Amphipoda	4	0	6	2	?	?	3	4
Isopoda	10?	?	21	5?	?	?	?	?
Araneae	12	0	16	5	1	1	8	9
Opiliones	2	0	2	2	-	-	2	0
Pseudoscorpionida	2	0	2	0	-	-	2	2
Acarina	50	6?	71	16	2+	3+	4+	4+
Chilopoda	1	0	1	0	-	-	0	0
Diplopoda	2	0	2	1	-	-	1	0
Symphyla	2	0	2	1	?	?	?	?
Collembola	29	3	46	26	3+	4+	4+	5+
Plecoptera	2	0	3	2	-	-	2	1
Orthoptera	1	1	1	1	-	-	0	0
Psocoptera	3	0	3	1	1	1	3?	3?
Thysanoptera	1	0	1	0	0	0	?	?
Anoplura	3	0	3	0	3?	3?	2?	2?
Mallophaga	13	0	23	0	12?	20?	12?	22?
Homoptera	10	0	11	1	2	1	8?	9?
Trichoptera	1	0	1	0	-	-	1	1
Lepidoptera	20	5	29	11	1	0	15	12+
Diptera	49	1?	81	35	4	3*	40?	16+
Siphonaptera	3	0	3	0	2	2	3?	3?
Coleoptera	33	3	43	23	1	2	4	16
Hymenoptera	9	0	10	9	1	1	8	?
Totals	262	19	381	141	33	41	122	97

- Group not represented.

\* Subspecific relationship is involved in 1 species.

group on Campbell and the Aucklands. In some of these cases there is a closely related species on Stewart I. or the southern part of the South Island of New Zealand. Often the genus may be essentially New Zealand in distribution, extending as far as Campbell, but in other cases extending as far as South America, Australia or rarely South Africa. As more groups are studied jointly from all these areas, more cases of common occurrence of genera on southern continents and subantarctic islands might come to light, or the genera actually may prove to be more restricted as concerns different continents.

#### FAUNAL ORIGINS

Among the various taxonomic chapters of this volume, diverse views are expressed on the question of the origin of the Campbell fauna. Some workers feel strongly that the island is continental and represents a fragment of a former larger New Zealand land mass, with air dispersal of no significance. Others feel that much of the fauna could have come by oversea dispersal, and that more elements would be present if the island were a continental remnant. There appears to be too much evidence for extensive glaciation in the not

far distant past to assume that conditions could have remained unchanged for long periods. Aspects such as extinction rates and introductions by man are not clear.

Fleming (1964) felt that present data argued too strongly against the derivation of all southern elements through land connections. He stressed that much spread has been recent, since present populated areas were covered with ice. He proposed a "Neoaustral" or "Neonotian" biotic element, to include the young genera, facile at dispersal, which repopulated the oceanic islands through West Wind Drift of air and sea, after maximum glaciation. The other, older, element he called "Paleoaustral" or "Paleonotian" which was widespread in the area as early as the Mesozoic. It is difficult to say whether any of this latter element exists now on Campbell I. Illies obviously feels that the two wingless Campbell Plecoptera represent the equivalent of this element and have been uninterruptedly on Campbell and have had melted water available all of this time. Fleming's position would apparently not permit this because of glaciation. Certainly much of the Campbell fauna suggests much younger age, and possible oversea dispersal. There is of course the possibility that a few elements, such as the wingless Plecoptera, certain Collembola and mites, and a few others, survived the ice-age. They might have persisted, as some arthropods do now in Antarctica, under rocks on exposed slopes or ridges where prevailing winds prevent accumulation of deep snow, so that solar radiation melts ice in contact with rocks up-slope sufficiently to provide moisture in the microenvironment to maintain a few primitive plants and animals (since the air in Antarctica is too dry for most organisms).

Holdgate (1961) and Knox (1964) have pointed out that of the three elements in southern areas (endemic, northern and southern-related), the last is often in the minority. Also, that present distribution is not necessarily a key to past history. Paleobotanical studies have much to contribute to the understanding of past history (Fleming 1964; Cranwell 1964). Cranwell pointed out that Antarctica was the center of evolution of early *Nothofagus* species which are now extinct. Knox (1946) felt that a modified land-bridge or island-archipelago theory will eventually provide the most plausible explanation of southern biogeography.

Contradicting the indications of trans-antarctic migration (Brundin 1964) and evolution on Antarctica (Penniket 1961; Knox 1946), Hennig (1960) stated that none of the Diptera groups occurring in Australia, New Zealand and South America demonstrate evidence for Antarctica as a center of evolution, or even as a migration route. However, Hennig did not rule out the possibility that future comprehensive studies might uncover such evidence of migration or evolution.

Thorne (1964) stated that though circumpolar biotic elements occur among the over-water dispersed biotas of Bounty, Antipodes, Snares, Aucklands and Campbell, these islands should not be separated in a subantarctic zone (as in Godley 1960; Skottsberg 1960; Gressitt 1961) as this obscures their closer ties with New Zealand. Only Macquarie has stronger Antarctic than New Zealand ties, and may be placed in the Kerguelen Province of the Antarctic Region, as done by Knox (1960). Thorne also pointed out that Australia was warmer and moister in the Cretaceous and Tertiary, and has few subantarctic elements, contradicting the idea of continental drift from the south having an important bearing on the Australian biota.

In regard to geological aspects relating to the origin of the fauna, Adie (1964) gives evidence that the present respective positions of the southern continents are different from



those of before the Cretaceous. At that time the other southern continents were closer to Antarctica, although their positions in regard to longitude are not yet clear. Thus the question of the function of land connections or closer stepping stones is largely a matter of whether the group evolved before or after the Cretaceous. Adie also stressed the indications of submarine ridges, such as the Scotia Arc between South America and the Antarctic Peninsula, the ridge from Macquarie towards Cape Adare through the Balleny Is., and the Gaussberg ridge between Kerguelen and East Antarctica. He also emphasized the great geological dissimilarity between West and East Antarctica (which are separated by ice lying on rock below sea level), and presented evidence that they might have once been farther apart. This suggests the possibility of separate migration routes to New Zealand and Australia, and thus closer affinities of South America and New Zealand on one hand and South Africa and Australia on the other. Certainly there is considerable evidence of closer affinity between South America and New Zealand, and this also fits with the great faunal difference between Macquarie and Campbell. That is, possibly one migration route might have been through closer connections along the route Victoria Land or Adelie Land-Balleney Is.-Macquarie-Tasmania, and the other Edward VII Land-Scott I.-Campbell I.-Auckland Is.-New Zealand.

As discussed in the following section, I feel that much of Campbell's fauna represents Recent post-glacial oversea dispersal.

#### DISPERSAL

Evidence has been accumulating that arthropods of many groups are capable of being wind dispersed for considerable distances over sea. There is fairly convincing evidence that many of the species established on oceanic islands were carried to those islands, or to stepping-stone islands or no longer existing intervening islands, by air currents (Gressitt 1961; Gressitt & Yoshimoto 1964). For instance, there is fairly high correlation between the types of arthropods currently represented on isolated oceanic Pacific islands and the types of insects trapped in air-nets on ships or planes at sea at points quite distant from probable points of origin. As continental shores are approached, more and more insects are trapped. Thus great quantities of insects are carried aloft by rising convection currents over the land, particularly on summer mornings, but at almost any time when temperatures are appropriate. At higher altitudes they are caught by horizontal currents and carried wherever the winds dictate, depending on air speed, direction, and other factors. If sunshine is not too great, and humidity not too low, they may be carried alive for great distances. The number being carried in the air is reduced geometrically with increasing distance from the continental or major insular source areas. Thus for distant isolated islands, chances of successful establishment are very small. Nevertheless, over periods of millions of years, many successful establishments could take place. As might be expected, arthropods with lower specific gravity (generally, but not always, winged) are more apt to become air-borne, and are carried greater distances.

The applicability to Campbell I. of this question of establishment on islands by air dispersal is to some extent disputed by different views expressed in articles in this volume. Some workers feel that since Campbell may be termed continental, that the matter of air dispersal is irrelevant. However, actual evidence for a local history of stable fauna dating from an hypothetical continental condition is almost non-existent. Forms such as the wing-



less stoneflies it is difficult to imagine as being air-borne for great distances. With these, and a few others, there could be some other explanation, such as survival through the ice ages, or transport on feet or feathers of birds. With such large populations of sea birds, largely the same species on neighboring islands to the north, it is conceivable that arthropods or their eggs might be carried from one piece of land to another at intervals (See below).

Fleming (1964) indicated that colonization of subantarctic islands has been by recent, and by oversea dispersal, the islands having been severely glaciated during the Pleistocene. He pointed out that plant genera such as *Sophora*, *Hebe* and *Acaena* are young, and are facile at dispersal, whereas *Nothofagus* and podocarps are old and are not facile at dispersal. The latter are absent, in general, from the subantarctic islands, although some were apparently present in Kerguelen before the period of maximum glaciation. Fleming felt that hypothetical former land connections could not explain all the present distribution in the southern areas.

Preest (1964) suggested that albatrosses and petrels probably revegetated the glaciated islands of subantarctic regions, as Macquarie, by carrying seeds on their feet and feathers. He also pointed out that much of the flora could have been wind-dispersed.

In the Auckland Is. I picked up an Antarctic prion (*Pachyptila desolata*) which had just come in from the sea after dark, battering against vegetation while blinded by artificial light. On examination it proved to have a psocid and some seeds on inner portions of its breast feathers. Also, on Ocean I. I found a weevil, *Pactolotypus depressirostris* (Kirsch) in the feathers of a giant petrel. These and similar examples suggest dispersal possibilities by wide-ranging sea birds (See Falla, 1960).

Kuschel (1964) pointed out that transport could have been by ice-berg from Antarctica to other southern continents during the time since the Cretaceous.

#### TRAPPING AT SEA

Over the past several years, Bishop Museum has been carrying on a program of trapping of air-borne organisms at sea, as well as on certain insular or far southern land areas, in order to document the theory of air dispersal to islands. The trapping at sea has been done on various military and oceanographic ships, mostly of the U. S. Navy, U. S. Military Sea Transport Service, Scripps Institute of Oceanography, and National Science Foundation, but also of the Royal New Zealand Navy, the Armada de Chile, and others. Also, trapping has been done in a Superconstellation plane of the U. S. Navy (VX-6). Work done in Antarctic and subantarctic areas, mostly in the areas south of New Zealand and Tasmania south to McMurdo Sound, has been reported in Gressitt, Leech & O'Brien 1960; Gressitt, Leech, Leech, Sedlacek & Wise 1961; Gressitt, Sedlacek, Wise & Yoshimoto 1961; Yoshimoto, Gressitt & Mitchell 1962; Yoshimoto & Gressitt 1963, and in press. Some of these data are summarized in Gressitt, in press, and Yoshimoto & Gressitt, in press. The trapping methods are described in some of the preceding references, and nets in operation on the "Magga Dan" are illustrated in Gressitt 1961: 53, fig. 20a.

Much of the data on trapping done south of 50° South Latitude are summarized in Table 5. This table shows that many of the insects trapped in the general area of Campbell I. are of groups which actually occur on Campbell and the Auckland Is. This seems to be fairly clear evidence that many of the dominant sorts of insects on these islands are likewise the dominant insects air-borne at sea in similar latitudes.



Table 5. Groups of insects trapped south of 50° South Latitude (at sea, in air, or in Antarctica)

	No. of specimens	Range of Lat. S	degrees Long.	Distance from probable source in km	Group occurs in Antarctica	Subant. Is.
Acarina	4	50-62	159-172E	1600	(*)	*
Araneae	1	59	175E	1300		
?Lycosidae	1	52	175W	900		*
Salticidae	1	52	175W	900		
Micryphantidae	1	77	162E	3200?		
Collembola						
Hypogastruridae	4	63-77	62W, 164-171E	1-400	*	*
Tomoceridae	1	70	85W	1200±	?	*
Blattaria	1	72	170E	2700?		(*)
Thysanoptera						
Thripidae	1	58	175E	1200		(*)
Psocoptera						
Liposcelidae	3	58	175E	1200		*
Homoptera						
Aphididae	7	50-54	166-175E, 66W	80-800		*
Coccidae	1	58	175±E	1200		*
Jassidae	1	53	175±W	1000		
Heteroptera						
Lygaeidae	1	60±	171E	1400		
Lepidoptera						
Gelechiidae	4	55-68	59-80W	150-1400		*
Microlepidoptera	1	54	175E	800		*
Geometridae	1	53	66W	45		*
Nymphalidae	1	71	97W	3500		*
Diptera						
Tipulidae	3	53	61-73W	3		*
Psychodidae	1	53	60W	10		*
Chironomidae	103	52-53	61-69W	3-150	*	*
Mycetophilidae	5	52-54	60-70W, 169E	3-800		*
Bibionidae	2	53	61W	10		
Piophilidae	1	55	159E	1200±		
Coelopidae	2	50-55	166-169E	3-10		*
Sphaeroceridae	2	51-53	170E, 61W	3-600		*
Ephydriidae	2	53	61-66W	10-41		*
Drosophilidae	2	53	61W	10		
Coleoptera	1	75	166E	3000		
Staphylinidae	1	53	61W	10		*
Lathridiidae	3	77	166E	3200?		*
Scarabaeidae	1	53	67W	20		
Hymenoptera						
Ichneumonidae	2	53	175W	1000		*
Braconidae	1	53	61W	10		*
Eulophidae	2	53	175W, 66W	80-1000		*

\* Group represented by forms similar to those trapped.

(\*) Group represented but not, or probably not, by forms trapped.

## CAMPBELL TRAPPING EXPERIMENT

To provide information to supplement the trappings at sea, a fairly large-scale trapping experiment was planned for land-based work on Campbell I. The main objectives were to attempt to trap, on windward shores of the island, arthropods being blown to the island from elsewhere, and on leeward shores, those being blown off the island into the sea. This would presumably prove that insects are being blown to the island currently. Also it would demonstrate that those less well adapted to life on the island are subject to constant negative selection (reproductively unsuccessful). Or in other words that non-use of wings proves beneficial and results in species which through natural selection become better adapted for survival on an island of such adverse conditions.

The prevailing winds striking Campbell I. are from the west, and would thus seem to have to bring insects from South America, southernmost Africa, Australia and subantarctic islands. However, at altitudes of 1500 meters or more there are at times northerly winds of 80-100 knots speed. These could theoretically carry insects from New Zealand to Campbell in 10 hours or less. However, there are generally no connective currents to lift insects into this windstream when northerly wind conditions are operating. When weather balloons are liberated at the weather station on Campbell, they often move eastward in the low westerly winds, but after rising to considerable heights they change to a southward course in the northerly winds. Closer to New Zealand there are frequently northerly winds at low altitudes, which accounted for many of the specimens trapped on ships. Thus it is readily conceivable that insects could be blown southward from Australia and New Zealand and then be diverted eastward in the prevailing low westerly winds. As shown in the preceding section, there is not much evidence of affinity between the faunas of Campbell and the Aucklands on one hand and of Macquarie, Tasmania and Australia on the other.

The limited land fauna of the subantarctic islands, as well as the special environmental conditions prevailing, makes them appropriate places for the study of natural dispersal. Campbell I. is theoretically a very appropriate place, for its westward (windward) coasts consist largely of cliffs. Actually, for attempts to trap insects blown to an island from elsewhere, Macquarie I. would be more appropriate than Campbell or the Aucklands, because it has a much smaller fauna of its own for possible contamination, and also because it has windward beaches or low bluffs where mechanical and aerodynamic problems could be overcome with fairly simple equipment. Campbell, on the other hand, with a more extensive fauna, and low valleys leading to coastal areas, is more appropriate to the study of wind-to-ocean destruction of active insects.

The obstacles to successful natural dispersal (which are also obstacles to successful studies of the phenomenon), are so great that concrete documentation is difficult to achieve. These obstacles center around the predominant strong winds and the associated low temperatures and excessive precipitation, with mist or sleet much of the time.

The trapping experiment on Campbell was largely a failure as regards the trapping of insects blown to the island from elsewhere. However, the trapping program for insects being blown off of the island appears to have produced some interesting documentation. Through the interest and cooperation of K. P. Rennell who continued the latter program after my departure from Campbell, the experiment was continued for over 11 months. A total of 4,309 arthropods were trapped in the main experiment on Campbell.

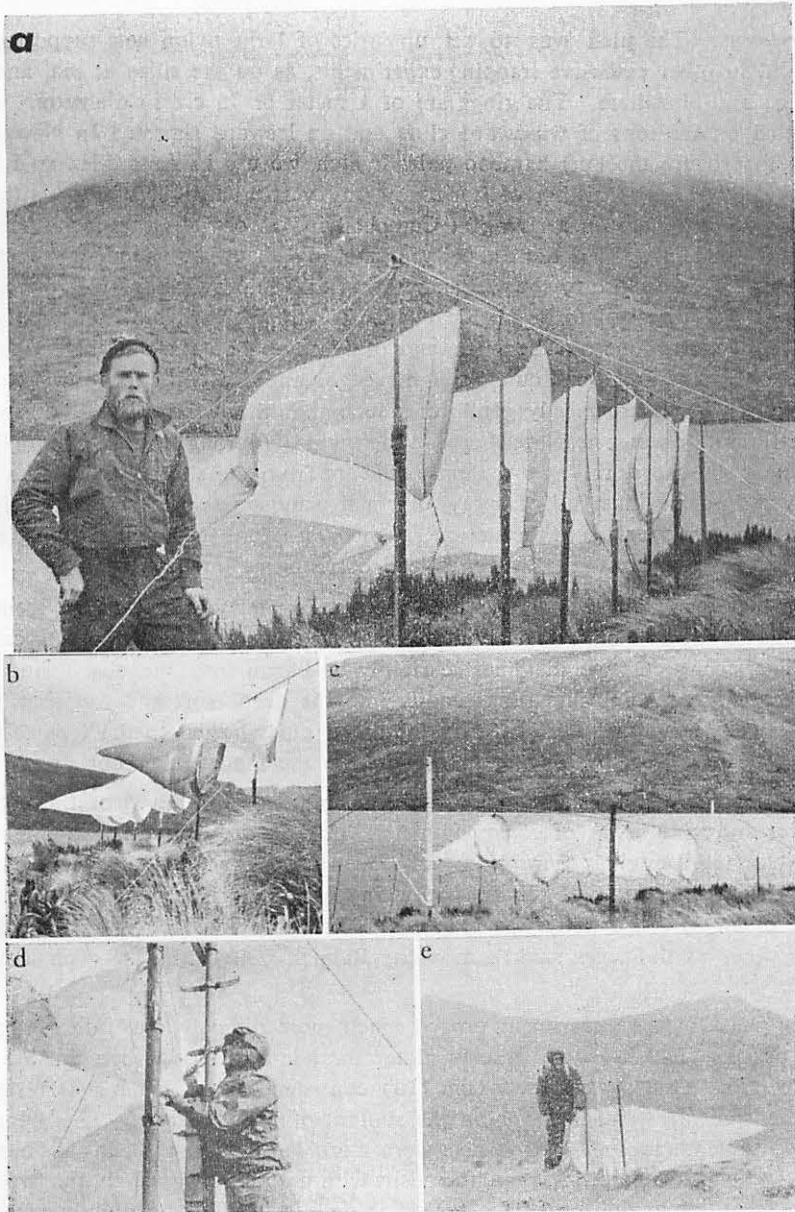


Fig. 11. Dispersal experiments on Campbell I. a, main series of nets at Bee-man Point, showing one 75 cm net and five 1 m nets, Rennell at left, 22 Dec. 1961; b, another view of same series, Nov. 1961; c, later view of nets on revised framework in 1962, with old frames at left; at this time three 75 cm and three 1 m nets are flying; d, two 75 cm nets lashed to old weather tower on summit of St. Col Peak, Gressitt held against tower by strong wind, Nov. 1961; e, one of two sets of three 75 cm nets each on ridge between St. Col Peak and Mt. Azimuth, Nov. 1961: experiment was unsatisfactory because of placement of nets.



*The experiment:* The plan was to set up series of large nylon nets supported by steel rings, as used in other extensive trapping experiments, as on the ships at sea, and on land in Antarctica and elsewhere. The rings are of 1 meter or 75 cm in diameter. Sets were to be erected on the tops of windward cliffs and on leeward shores. In New Zealand I was unable to procure the long bamboo poles which we use in Antarctica so I had fitted a series of steel rods consisting of horizontal and vertical lengths of pipe with threaded attachments. Immediately on arriving at Campbell it was obvious that from the weight of the pipes and other gear, and the difficulty of moving about the island, the metal frames would have to be used close to the weather station and improvisations elsewhere. Fortunately, Beeman Point proved to be an ideal place for the leeward location. Although it is not on the east coast, but near the inner end of Perseverance Harbor, the harbor is wide at Beeman, the point drops off quickly at the edge, and the contours leading down from the windward cliff-tops are mostly gentle and such that the wind blows downward over the point, striking the water near the shore. When wind is strong, this is strikingly obvious. Waves form at the shore, rolling turbulently outward from the shore towards the open sea, while williwaws, whirlwinds full of spray, or small waterspouts are frequent. Often, when weather balloons are liberated at the station (about 40 m from the main trapping site), they are blown downward against the water, instead of rising as intended.

The main battery of nets (fig. 11a-c; see also pp. 24, 29) was erected on Beeman Point, near the edge of the low cliff, and about 10 m above sea level. Any insects carried past this spot in a strong gust would almost certainly be blown into the sea. Since the steel uprights were only 2 m high and sank readily into the deep, soft and wet peat, tall metal fence posts were sunk into the peat and the metal pipes lashed to the tops of the posts. The frame was held erect by long cords or wires to the top of each upright.

Six nets were flown from the frame for over 11 months. Initially 5 of the nets were of 1 m diameter and the 6th was of 75 cm diameter. After a few months, as the replacements of net bags for the 1 m rings were worn out, 75 cm rings were gradually substituted, till at the end of the period, most of the nets operating were on 75 cm rings. This means that the volume of air screened daily was reduced gradually to about 65% of the initial level. After some time, as the poles sank somewhat, Rennell raised the nets on a new frame (fig. 11c).

The other phase of the experiment proved much more difficult and far less productive. Three sets of nets (2, 3, 3) were erected along the windward ridge between St. Col Peak and Mt. Azimuth. One of these sets (fig. 11d) consisted of two 75 cm nets fastened with strong wire to the old weather tower on the summit of St. Col Peak. The wind at this point was so violent (see p. 40) that nets were worn loose and had their ends blown out as a rule in less than 24 hours. After a few visits with practically no catch, the two nets were rigged on a stout line to the top of the tower, as on a ship. At the slightly greater height the still stronger wind (probably averaging 50 knots) blew the nets out at the ends from whipping because of variation in speed. One net was blown away. This location was finally given up because of the great amount of effort expended with practically no result. Also within a few days after my arrival on Campbell, I set up two additional sets of three 75 cm nets each on the ridge, towards Mt. Azimuth (fig. 11e). These were erected on the crest of the ridge, above the cliff tops. These nets were often still functioning when visited (every 2-3 days). However, as they were not erected sufficiently high on frames, too much



debris entered the nets. Because of the obstacles, poor returns and destruction of nets, this part of the program was abandoned after a few weeks. Most of the insects trapped were obviously local in origin, and probably all were, though many of them were blown up from the bottoms of the cliffs.

A Malaise trap was also operated for brief periods in Tucker Cove, not far from the Beeman Pt. nets (see below under Results).

*Results:* In the main trapping experiment at Beeman Pt., a total of 4,309 arthropods were taken over the period of just over 11 months. Data from this experiment are presented in Table 6 and in the graphs (figs. 14-20), as explained below, with additional weather data in figs. 12 and 13.

In Table 6 the species trapped in the main experiment are listed systematically with the numbers trapped for each month. The totals indicate the numbers trapped per month and also the total number trapped of each species. This table demonstrates the great numbers trapped of certain weaker fliers, Aphididae, Psychodidae and Chironomidae in general, and certain Sciaridae and Coelopidae. The absence or scarcity of some of the common Lepidoptera and Ichneumonidae is conspicuous. Many individuals of these were seen flying in calm weather upwind from the nets.

Many species were trapped through the entire year, but Aphididae, Tipulidae, *Platyura*, *Tetragoneura*, Syrphidae, *Poecilohetaerella*, *Scatella*, *Macrocanace*, *Leptocera*, *Calliphora*, Muscidae and Hymenoptera were essentially lacking in the winter trappings.

In noting the months with higher catches, it is seen that March, April and October (part) produced more than January or February. December was the richest and August the poorest. Some groups (Psychodidae, Chironomidae, *Exechia* and *Sciara*) had their maxima in early autumn (March, April) whereas many species were maximal in summer. *Coelopa*, however, had its maximum in spring (October).

In studying the table it must be borne in mind that the average net size was reduced in the later months of the experiment, reducing the volume of air screened. Thus the figures for the last few months are lower than they should be in comparison with the earlier months.

In addition to the main air-netting experiment and the smaller unprofitable ones on the high ridges, a modified Malaise trap (Gressitt & Gressitt 1962) was operated on Campbell for two periods in November and December (p. 16, fig. 6f). The catch for the first of these two periods is shown in fig. 14. The catches are given over a factor of 5 ( $\times 0.2$ ), to put them on the same scale. Since the trap was checked only every 2-4 days, the line in the graph indicates averages for these periods. For this reason the data cannot be closely correlated with weather conditions. However, there is some obvious correlation with the trapping experiment.

In the cliff-top trapping, the following specimens were taken (late November to mid December):

Amphipoda	1	Coelopidae	2
Araneae	1	Acalypratae	8
Tipulidae	10	fly fragments	7
Sciaridae	6	Staphylinidae	1
		Total	36

Table 6. Numbers of specimens taken in Beeman Pt. nets, by species and month, 1961-62,

	Nov. (21-30)	Dec.	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct. (1-26)	Totals
Amphipoda	-	-	-	-	-	-	-	-	1	-	-	-	1
Acarina (Cryptostigmata)	-	8	-	-	-	-	-	-	-	-	-	-	8
Araneae	-	-	-	1	-	-	-	-	-	-	-	-	1
Homoptera: Aphididae	12	611	137	39	7	4	-	-	-	-	-	-	810
Lepidoptera													
<i>Proterodesma byrsopola</i>	1	5	4	-	-	-	-	-	1	-	-	-	11
Diptera													
<i>Nothotrichocera antarctica</i>	15	27	6	-	1	-	1	1	-	-	-	3	54
Tipulidae	3	58	12	3	6	-	-	-	-	-	-	10	92
<i>Psychoda pulchrima</i>	19	26	14	9	3	20	26	13	10	10	14	12	176
<i>campbellica</i>	1	5	-	7	2	11	8	2	-	1	-	3	40
<i>eremita</i>	-	-	-	-	-	-	-	-	1	-	-	-	1
<i>spatulata</i>	-	-	1	10	71	112	39	2	2	-	8	-	245
Chironomidae	2	35	24	102	136	113	94	102	5	10	3	12	638
<i>Austrosimulium vexans</i>	-	1	-	2	1	1	-	-	3	4	1	3	16
<i>Bradysia rubra</i>	3	1	9	11	9	4	8	-	-	-	1	5	51
<i>Exechia hiemalis</i>	20	28	34	67	247	263	130	35	54	34	22	36	970
<i>Zygomyia submarginata</i>	1	1	-	1	8	8	9	4	12	8	-	6	58
<i>Platyura brevis</i>	-	37	28	5	-	-	-	-	-	-	-	-	70
<i>Tetragoneura minima</i>	3	19	16	1	-	-	-	-	-	-	-	-	39
<i>Helophilus antipodus</i>	-	13	2	-	-	-	-	-	-	-	-	-	15
<i>campbellicus</i>	-	5	1	-	-	-	-	-	-	-	-	-	6
<i>Syrphus novaezealandiae</i>	1	10	7	5	3	-	-	-	-	-	-	1	27
<i>Coelopa debilis</i>	8	40	15	36	39	19	52	34	16	32	86	359	736
<i>Poecilohetaerella bilineata</i>	-	2	2	-	-	-	-	-	-	-	-	-	4
<i>Scatella nelsoni</i>	2	4	4	-	-	-	-	-	-	-	-	-	10
<i>Macrocanace australis</i>	-	1	-	-	1	-	-	-	-	-	-	-	2
<i>Leptocera thomasi</i>	1	9	3	2	2	1	-	-	-	-	2	3	23
<i>Australimyza anisotomae</i>	7	9	9	4	1	3	8	3	-	-	1	4	49
<i>Calliphora quadrimaculata</i>	-	-	2	4	-	-	-	-	-	-	-	-	6
<i>viridiventris</i>	-	26	7	10	3	-	-	-	-	-	-	2	48
<i>Limnophora brunneivittata</i>	-	-	-	-	-	-	-	-	1	-	1	-	2
<i>Paralimnophora depressa</i>	6	13	8	3	2	-	-	-	-	-	-	-	32
<i>antipoda</i>	1	3	5	2	-	-	-	-	-	-	-	-	11
Coleoptera													
<i>Ptinus tectus</i>	-	-	-	-	-	-	-	-	-	-	-	6	6
<i>Veronicobius aucklandiae</i>	-	-	-	-	-	-	-	1	-	-	-	-	1
Hymenoptera													
<i>Rogas gressitti</i>	4	14	16	2	-	-	-	-	-	-	-	1	37
<i>Apanteles</i> sp.	-	-	1	-	-	-	-	-	-	-	-	-	1
<i>Campoplex disjunctus</i>	-	2	3	-	-	-	-	-	-	-	-	-	5
<i>Ardalus campbellensis</i>	-	-	-	1	-	6	-	-	-	-	-	-	7
Totals	110	1013	370	327	542	565	375	197	106	99	139	466	4309

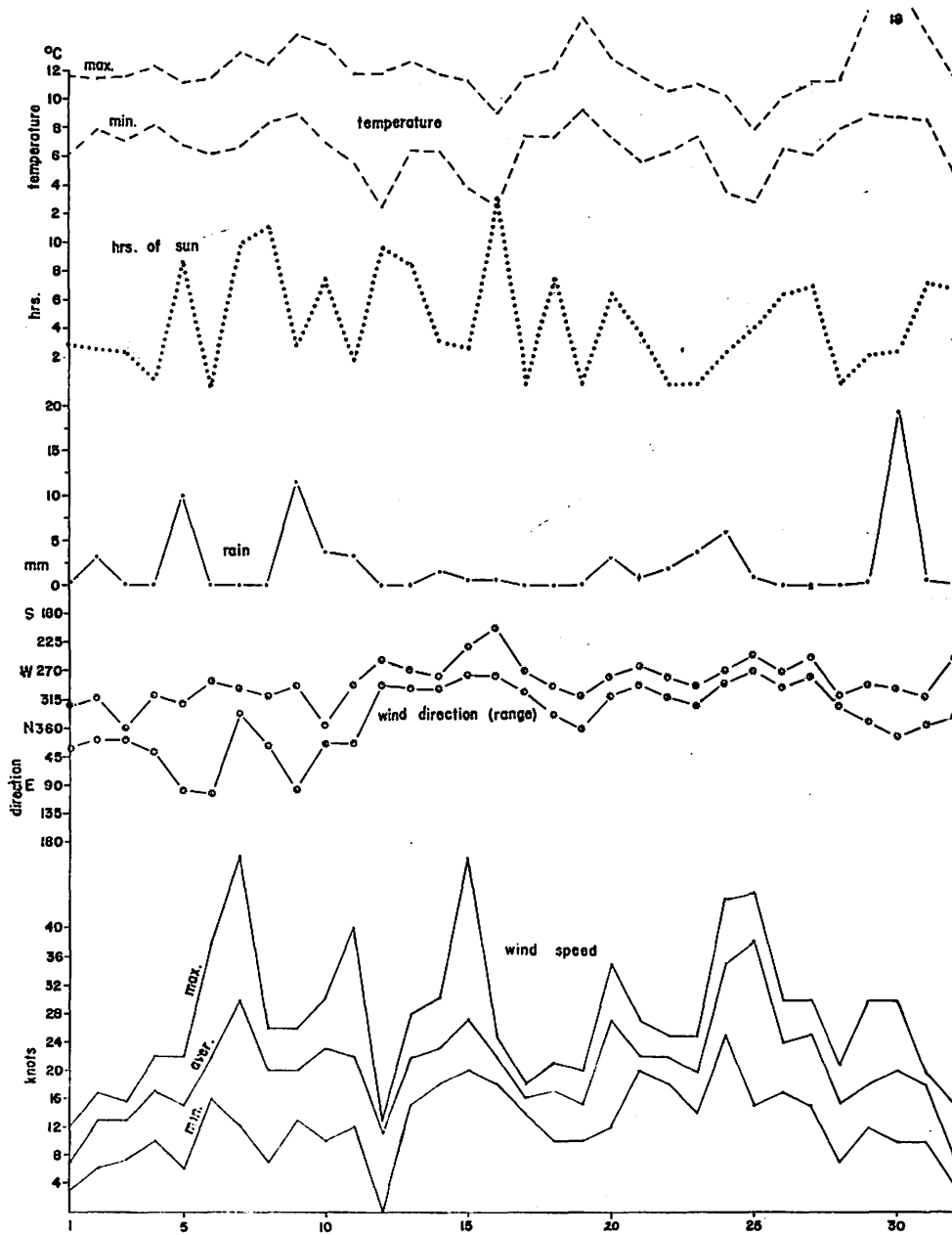


Fig. 12. Graph of general weather conditions for month of December 1961 at Beaman Point, Campbell I.: temperature maxima and minima, centigrade; hours of sunshine; mm of precipitation; wind direction range in degrees of the compass; and wind speed maxima, averages and minima.

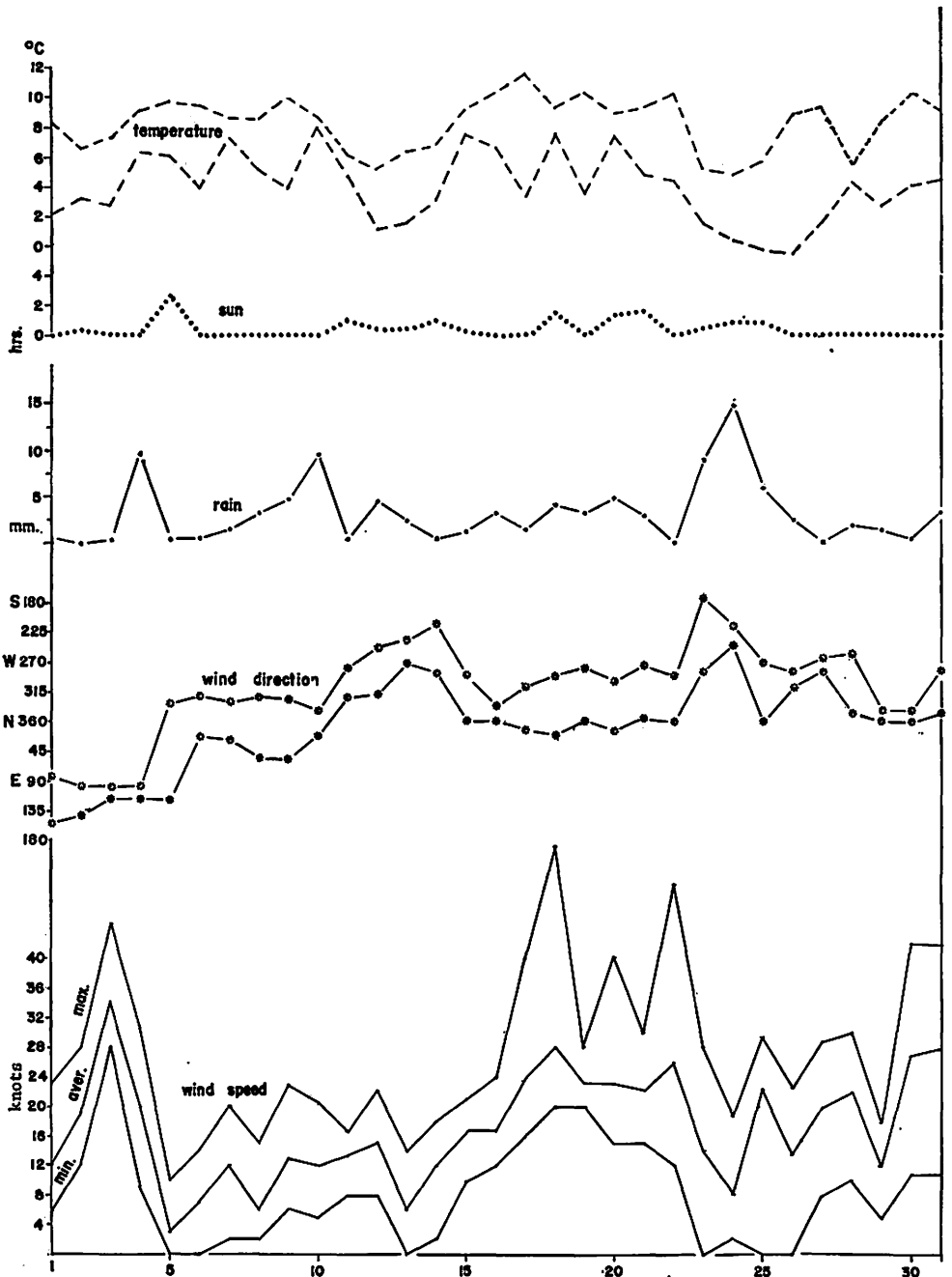


Fig. 13. Graph of general weather conditions for month of June 1962 at Beeman Point, as for fig. 12.



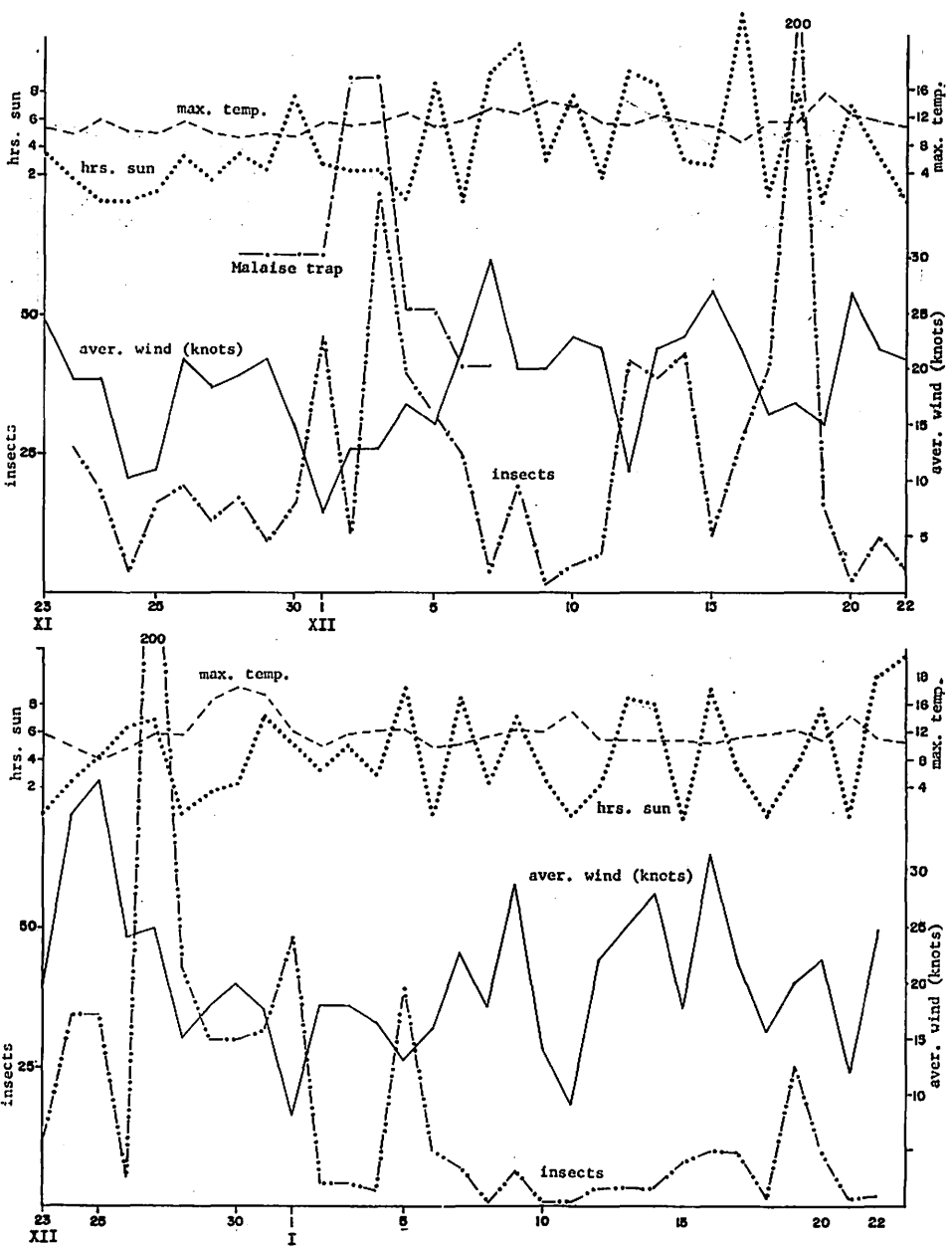


Fig. 14. Graphs of insect trappings at Beeman Point, Campbell I., November 1961 to January 1962, plotted against average wind speed in knots (scale at right), as well as maximum temperature (C) and hours of sunshine. Near center of upper graph is shown numbers of insects taken in Malaise trap in Tucker Cove (over factor of 5). In general, results show more insects trapped when wind was low and temperature and sunshine high.

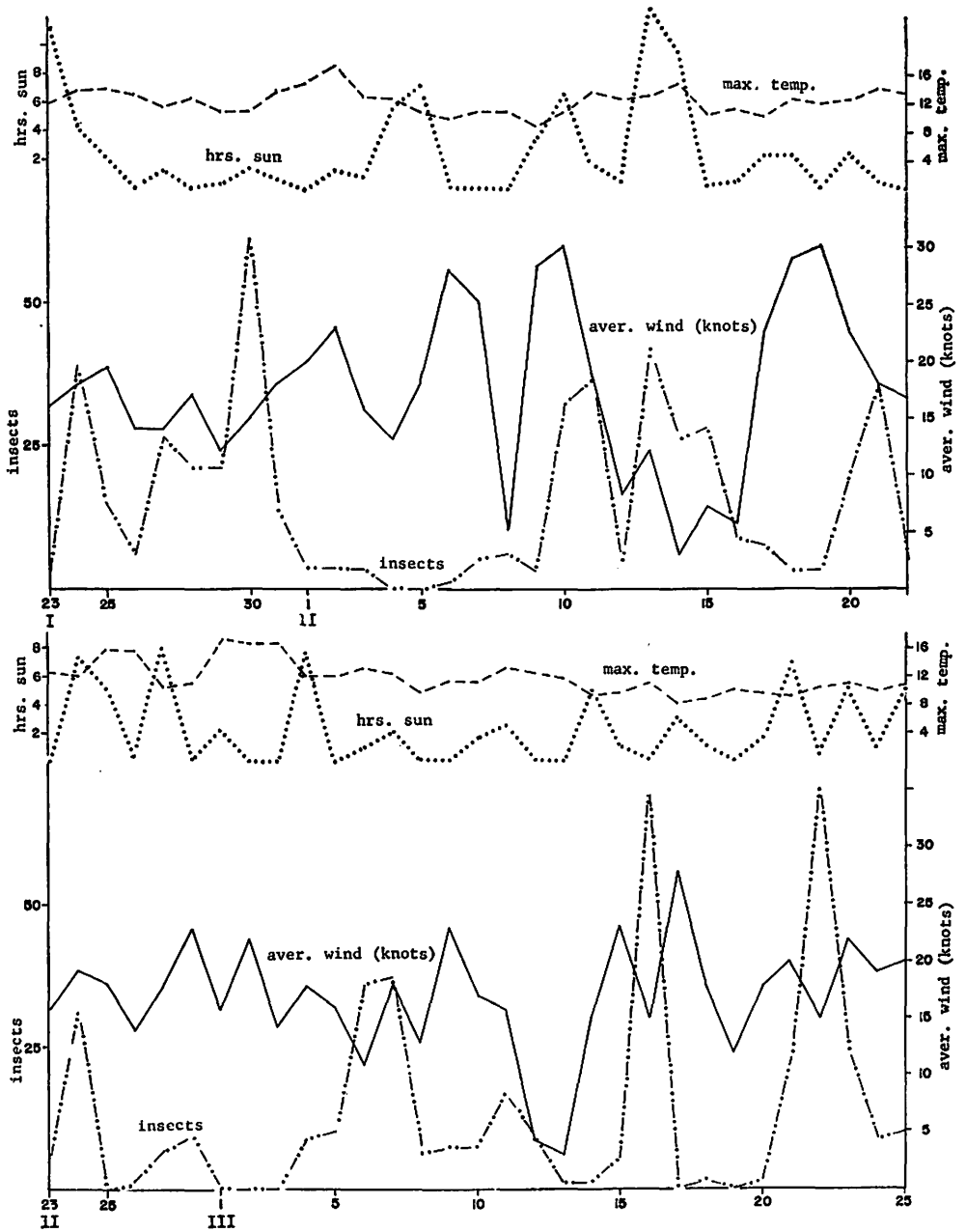


Fig. 15. Graphs of trapping at Beeman Pt., January to March 1962, as in fig. 14.

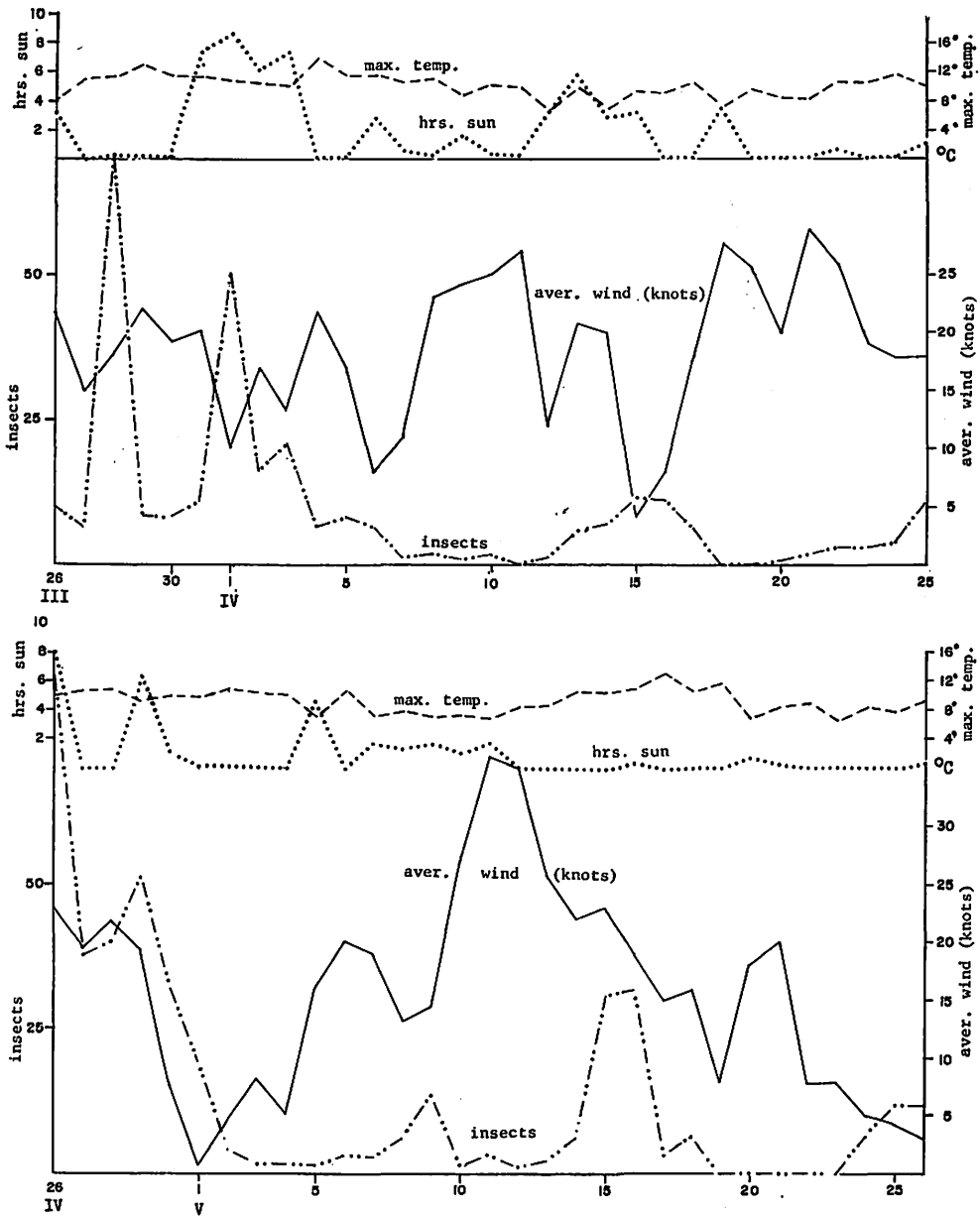


Fig. 16. Graphs of trappings at Beeman Pt., March to May 1962, as in fig. 14.

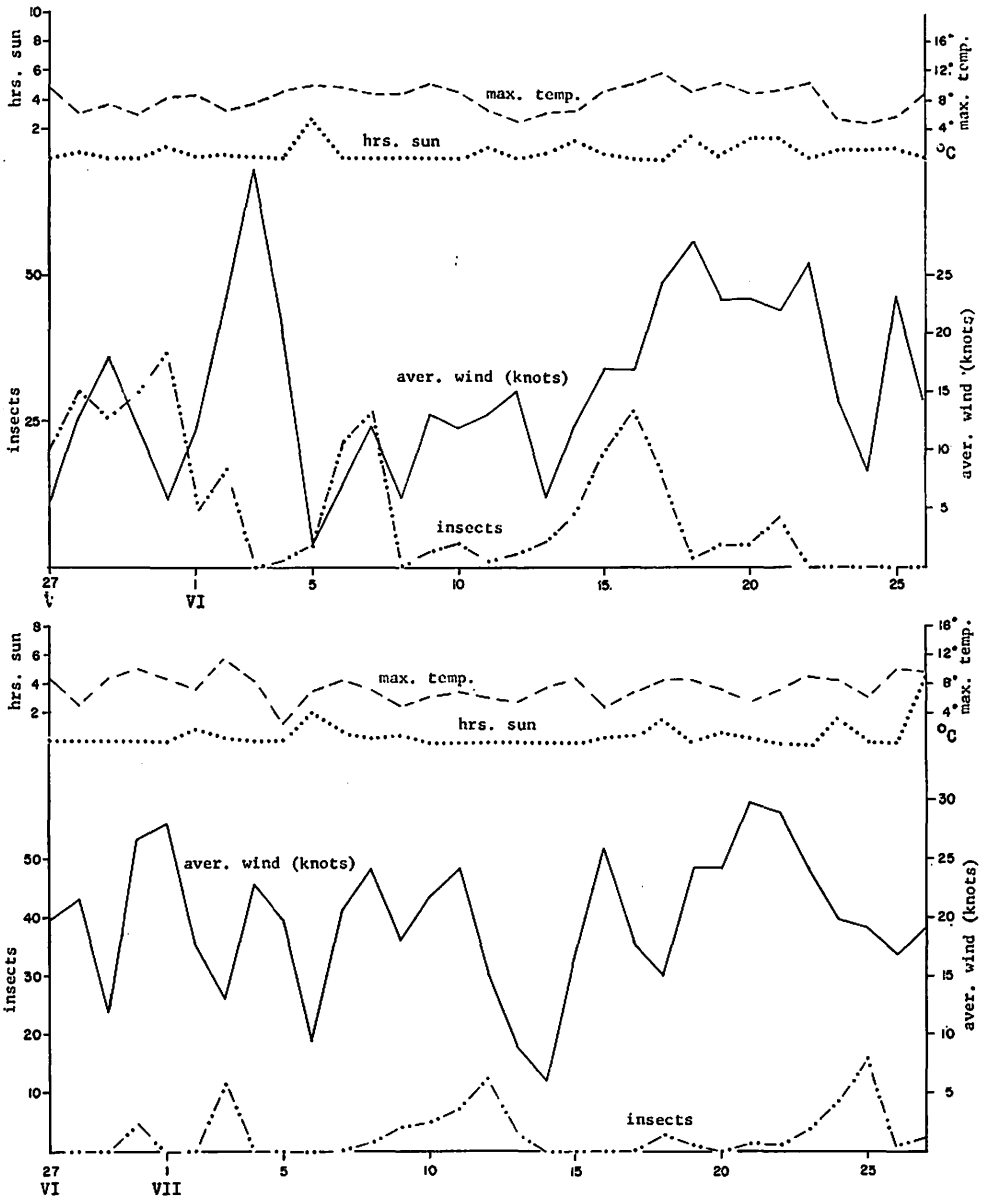


Fig. 17. Graphs of trappings at Beeman Pt., May to July 1962, as in fig. 14.

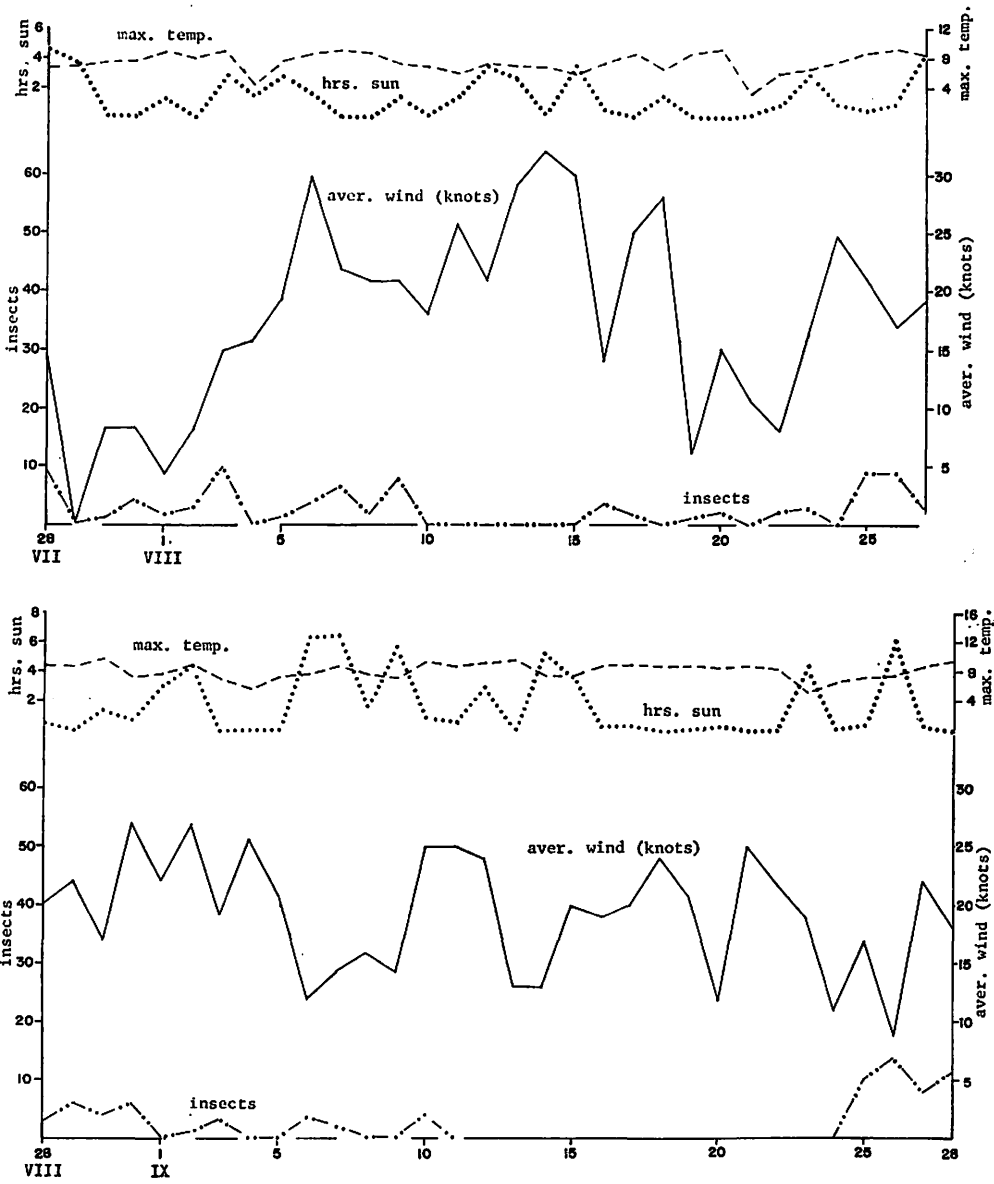


Fig. 18. Graphs of trappings at Beeman Pt., July to September 1962, as in fig. 14.

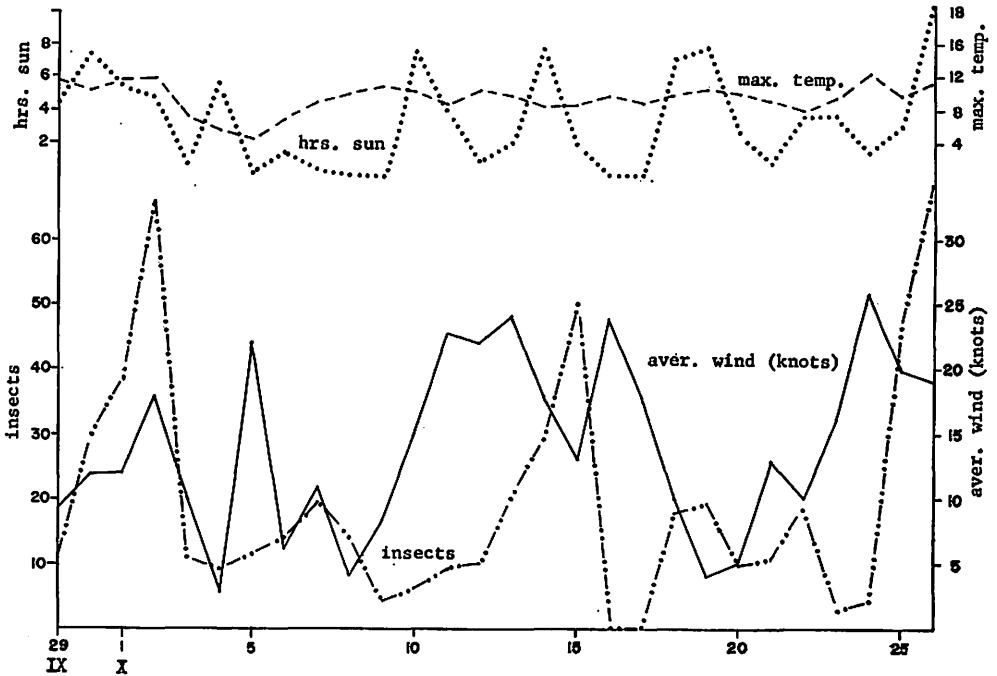


Fig. 19. Graph of trappings at Beeman Pt., September to October 1962, as in fig. 14.

By a study of the graphs it will be seen that in general insect catches were high when wind was low. It must be borne in mind that the winds in the Beeman area are often erratic and turbulent. This often caused reversal of the nets, resulting in loss of trapped specimens. Thus in very many cases the reported catches are far too low. Also, checking of the nets was in general done only twice a day, sometimes only once a day, because of pursuing field work on other parts of the island. During parts of the trapping period, the checking of nets was correlated with the 24-hour weather observation period, whereas in other parts the timing was less well coordinated. These discrepancies were largely dictated by circumstances. At any rate, the respective 24-hour periods do not all coincide, which is another reason for some apparent lack of correlation between trapping results and weather data. In other words, the results as observed by personal experience were much more strikingly coordinated with weather than is apparent from the graphs. Since differences existed in correlating insect catches with maximum, average and minimum wind speeds, in the graphs the catches have been plotted separately with average (figs. 14-19) and maximum (fig. 20) wind speeds. Figs. 14-19 also show maximum temperature and daily hours of sunshine. These two factors are of considerable importance relating to insect flight in such an environment, and in many cases the graphs show positive correlation. In many cases where average wind was low and maximum temperature and sunshine hours were high, but insect catches low, it must be assumed that the maximum wind speeds, or temporary erratic winds, caused reduction in insect flight and/or reversal of nets and loss of trapped specimens.

In order to further document weather conditions, to supplement the extensive general in-

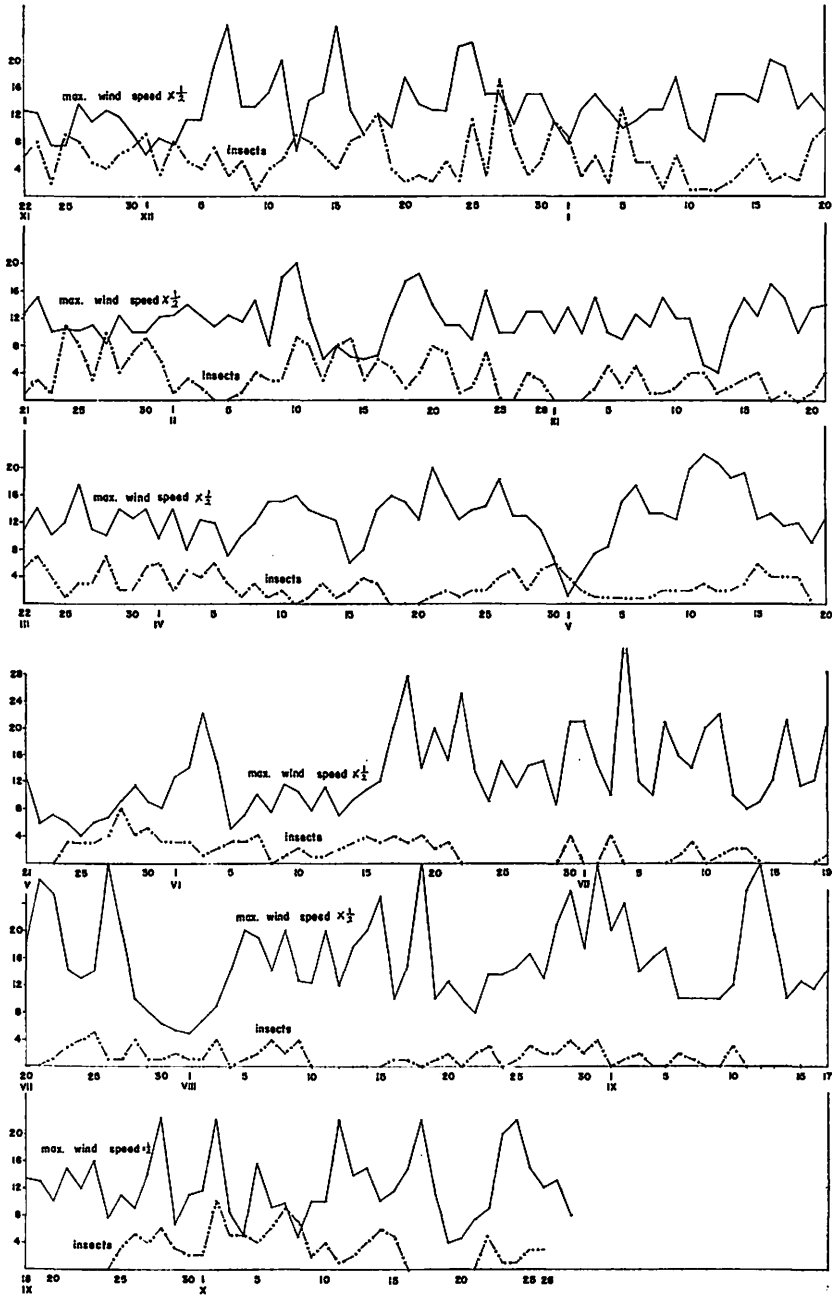


Fig. 20. Graph of complete period of trapping experiment at Beeman Pt., Campbell I., showing number of species trapped daily from 22 November 1961 to 26 October 1962, plotted against maximum wind speed (over factor of 2).

formation presented in the second chapter of this volume (de Lisle, p. 34), more extensive weather data is given in two graphs (figs. 12, 13), one for the month of December 1961 and the other for June 1962. These represent, roughly, early mid-summer and early mid-winter conditions; also, they represent the first full month of the trapping experiment, and a month just past the middle of the dispersal study period. By comparing these two graphs with the differences in trapping results (figs. 14-20), considerable correlation with weather conditions is obvious. In June (1962) the amount of sunshine was extremely limited, averaging less than half an hour per day; the maximum temperature was just over 11°C; and there was more precipitation. However, the wind speed and direction were not much different than in December. Figs. 14-19 show specimens; fig. 20 shows species.

There is a slight discrepancy between data in the table and the graphs. Accidentally, 313 specimens of Psychodidae were excluded from the data for the graphs. In figs. 16-19, the following should have been included: 73 specimens (March), 137 (April), 72 (May), 10 (June), 7 (July), 9 (August), 3 (September) and 2 (October). These data are included in Table 6.

In order to summarize some of the information resulting from the trapping experiment, and to compare with it some of the apparent negative aspects, some figures are presented in Tables 7 and 8. Table 7 gives the numbers of wingless, winged and flightless species in relation to trapping results. This includes both the Beeman and cliff-top trap nets, but not the Tucker Cove Malaise trappings. It should be noted that actually a smaller number may be truly fully winged than indicated on the table. Several apparently fully winged species were never seen in flight or trapped in the air. It is possible that some of these have reduced flight muscles and slightly reduced size or sclerotization of the wings. More study of habits and morphology is required to confirm these points. In certain cases, as noted in the next section, there appears to be good evidence that winged species are not making much use of their wings. Also, the trap collections include some of the introduced species.

Table 7. Ratios of wingless, winged, flightless and trapped species (excluding Malaise trap).

	Species known	Species trapped	Specimens trapped	Species not trapped
Normally wingless groups	198	4	12	194
Flightless (of normally winged groups)	74	1	1	73
Fully winged (see text)	109	40	4332	69
Totals	381	45	4345	336

Table 8 presents partial data on methods of collection of the apparently fully winged species which were not taken in the Beeman trap nets. This is included to indicate possible information on flying habits, although the information is incomplete. Unfortunately, in the general collecting, species actually netted in flight were not documented. However, few were taken in flight, and rather few were seen flying. Although a net was carried most of the time, it was generally used for catching specimens that dropped when roots, herbs, stones and mosses were examined. It was also used for sweeping herbs and beating scrub. However, vegetation was generally too wet for sweeping. Some of the winged species were taken only on rocky shores, or at scattered points around the island. The fact that numbers of specimens of certain species were taken in the Malaise trap is not



Table 8. Collection of winged species not taken in Beeman Pt. trap nets.

	No. species	Distr.	Method of collection				Average total per species		
			At light Total	At light Max.*	Malaise trap Total	Malaise trap Max.	General collecting Total	General collecting Max.	
Thysanoptera	1	wide	-	-	-	-	1	1	1
Aphididae	5 <sup>x</sup>	wide	-	-	-	-	16	6	3
Trichoptera	1	-	-	-	4	4	43	43	47
Microlepidoptera	2	wide	7	7	-	-	3	3	5
	3	N.Z.	3	1	34	33	12	9	16
Pyralidae	4	end.	-	-	25	20	32	16	14
	5	N.Z.	6	5	81	50	64	40	30
Geometridae	3	end., subant.	-	-	80	80	31	17	55
	3	N.Z.	-	-	12	9	41	22	17
Trichoceridae, Tipulidae	3	subant.	1	1	1	1	17	12	6
Psychodidae	1	intr.	-	-	-	-	1	1	1
Sciaridae	2	end.	-	-	71	70	17	17	44
Mycetophilidae	2	end.	-	-	32	30	31	25	31
	2	N.Z.	-	-	114	110	18	10	66
Ceratopogonidae	1	end.	-	-	-	-	1	1	1
Cecidomyiidae	1	end.	-	-	3	3	-	-	3
Empididae	2	end.	-	-	32	17	6	6	19
Syrphidae	1	N.Z.	-	-	28	28	3	3	31
Helomyzidae	2	subant.	-	-	17	17	29	20	23
Sphaeroceridae	1	end.	-	-	17	17	18	18	35
Ephyridae	2	N.Z.	-	-	92	52	820	800	457
Calliphoridae	1	N.Z.	-	-	16	16	5	5	21
Muscidae	3	end., N.Z.	-	-	119	113	79	51	66
Ptiliidae	1	end.	-	-	-	-	54	54	54
Curculionidae	1	N.Z.	-	-	-	-	65	65	65
Ichneumonidae	1	end.	-	-	110	110	35	35	145

\* *Max.* means maximum number of specimens of one species. *Total* means total specimens for the family. When numbers in one pair of columns are the same, it means only one species is involved. Thus for the first Microlepidoptera entry, one species was taken only at light, the other only in general collecting, whereas for the next entry, 1 specimen of each of the 3 species was taken at light, 2 species were taken in the Malaise trap, and 2 or 3 in general collecting. *General collecting* includes Berlese funnelling.

x Possibly some of these aphids lack winged formson Campbell. Most of these were taken by Berlese funnel.

necessarily of great significance as far as flight is concerned. Even flightless species are often taken in the Malaise trap, as the insects may crawl all the way up from the ground into the killing chambers, similiar to the way they might crawl up the trunk of a shrub. The base of the trap rested on ferns on peat and old rubbish, and was in contact with *Myrsine* shrubs and close to *Dracophyllum* shrubs. The clearing in the *Dracophyllum* scrub in which the trap was erected was an old rubbish dump of the former Tucker Cove Camp, close to the stream not far from its mouth. It is interesting to note that some of the moths were not taken at light, as well as most of them not having been taken in the trap nets. A few, however, were seen in day flight in good weather, as discussed further below. One

geometrid moth taken in a camp building might have been attracted to light.

## EVOLUTION

An island with the climate, isolation and faunal size of Campbell is of the greatest interest to students of evolution. If it were a more hospitable island it would be an ideal open-air laboratory of evolution. One gains the feeling that here evolution is proceeding at a rapid rate. On the other hand, certain indications suggest that this may not be the case. If evolution is rapid here, then the fauna must be very young, or there must be a very high extinction rate. However, the examination of peat samples did not suggest the latter. There are various indications that much of the Campbell I. fauna is young. The recent glaciation suggests this, as does the morphological and ecological plasticity of many of the species. On the other hand, the great faunal similarities between Campbell and the Auckland Is. and their common dissimilarities from Macquarie I. suggest some similarity of history for the former two as opposed to a more strictly over-ocean faunal origin for Macquarie. The answer to the problem may lie in a history involving for Campbell and the Aucklands some relics of common local land-mass and/or closer stepping stones, plus over-sea dispersal in recent times from a common source of certain species with the propensity for facile dispersal and establishment.

Another indication that much of the fauna is young is the disharmony coupled with the apparent meagre proliferation of species. The high ratio of genera to species plus the apparent separateness of phyletic lines indicate the slight proliferation in the historic sense. Possibly the great majority of species on the island represent separate evolutionary lines and thus separate colonizations. It is also possible that re-introductions of the same species result in gene dilutions from the parent populations and retardation of the evolution of new species through random fixation of genes.

As pointed out by Mayr (1963) the most important forces in the evolution of species are the factors of the environment functioning as selection pressures operating on the normal genic variability. In other words, natural selection (long somewhat mistakenly termed "survival of the fittest", whereas the important fact is the contribution made to the gene pool of the next and subsequent generations, and thus reproductive success). It has been suggested that the selection pressures of the environment are more severe under austere circumstances such as an inhospitable environment like that of Campbell I. It would appear that plants are more successful than land animals in this environment, for the ratio of numbers of species of land arthropods (the dominant land animals in general, and more particularly so on Campbell) to vascular plants (3.4 : 1) is much lower than in most temperate and tropical areas.

Since Campbell I. is small and in some senses the environment rather uniform, it is possible that the "competitive exclusion principle" (see Mayr 1963) or the Gause principle, is of great importance here. That is, proliferation of species is retarded by competition preventing the development of two closely related species in the same niche. However, the variation in niches would appear to be greater than in some I have seen in the tropics which appeared to support two or three species of the same genus or subgenus. No doubt the stringent nature of the Campbell environment plays a role here, and perhaps there has actually been little autochthonous speciation on the island in spite of the seemingly high endemism. The small number of established man-introduced cosmopolitan species is an

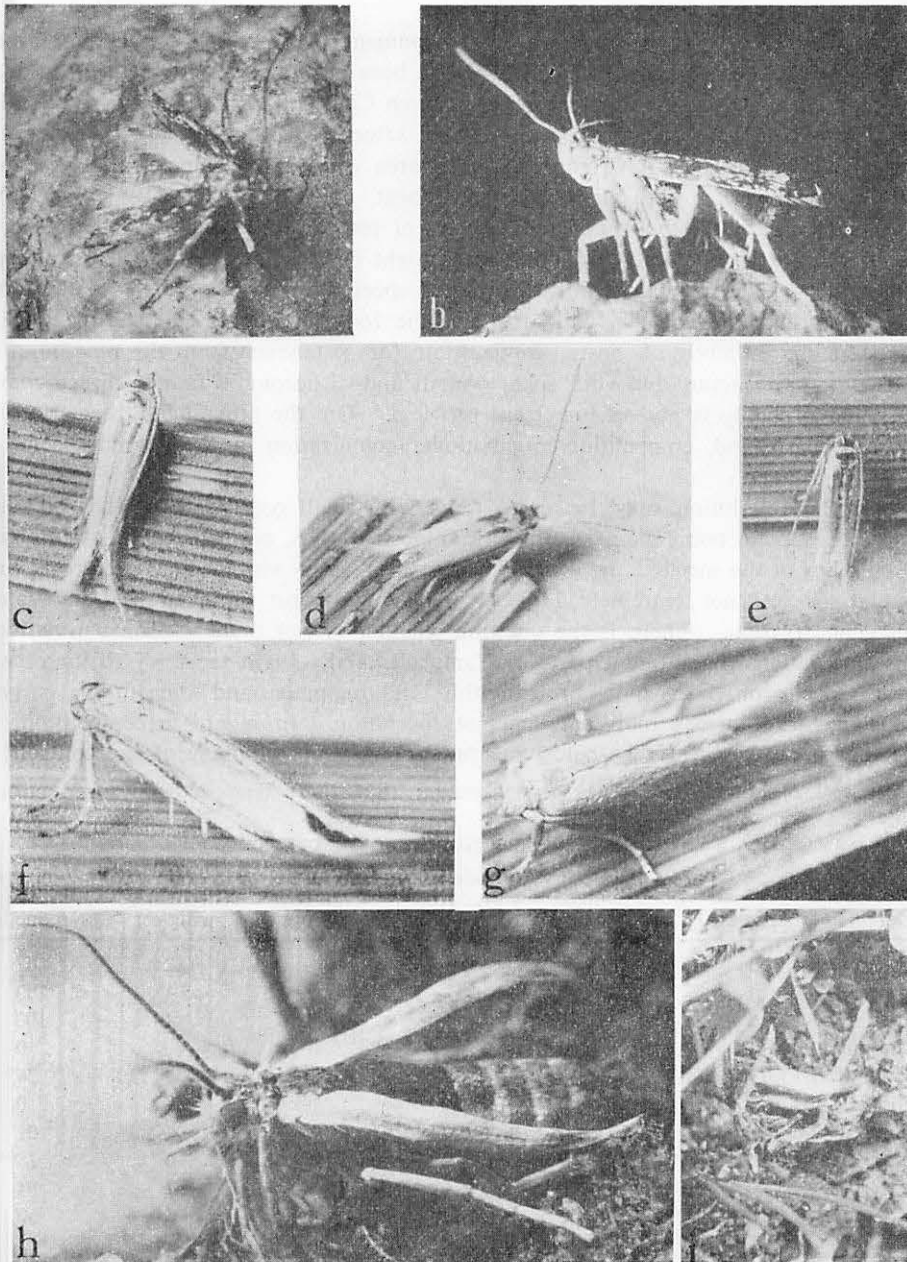


Fig. 21. *Tinearupa sorenseni* Salmon & Bradley on rock with lichens in upper splash zone, Monument Harbor, Campbell I. (hind wing appears much wider than in photograph of type specimen in Salmon & Bradley, 1956, fig. 10); b, same, side view; c, probably *Euproteodes galathea* Viette, on sedge leaf, Tucker Cove, 7.XII.1961; d, same; e, same or different species, same data; f, ditto; g, ditto; h, possibly *Exsilirarcha graminea* Salmon & Bradley ♀ on mossy ground, slope of St. Col Peak, 180 m, 7.XII.1961; i, unidentified flightless moth on mossy ground, Beeman area, I, 1962; all Campbell I. (photos by Rennell, partly with Gressitt).

indication of the stringent limitations of the environment. However, the number of species native to southern New Zealand which may have been introduced is a difficult question. A number of species are possessed in common between Campbell and southern New Zealand, and perhaps more will be found to represent the same species. To succeed on an island like Campbell, species must have come from an area with similar climate, or have evolved gradually to keep in step with changing environment, including climate and biota. With increase or decrease in the number of species of plants and animals on the island, the factors affecting a particular arthropod species might be greatly altered. Thus a species which depends on a particular plant or animal species for its existence would disappear when its host disappeared, but with less specific food habits it might survive. With a reduction in the number of hosts, competition for sustenance from the remaining ones might become more acute, but with such a small and disharmonic fauna, direct competition for food probably is not an important problem. On the other hand, because of the small size of the island, competition might hinder colonization by the second species of a genus.

It is said that evolution may be more rapid with small populations. It is difficult at this stage to estimate population size among Campbell species, partly because of the hidden nature of many of the species. In general it may be safe to assume that effectively breeding populations are not extremely large, which may permit a higher rate of evolution through gene fixation. There is the question whether or not there is some isolation of breeding populations on different parts of Campbell, and thus a tendency to increase the number of species on the island. Probably this is taking place, and some of the purported intra-specific variation may represent incipient speciation. In regard to competition, it is possible that populations may be below the functioning level of many of the controls.

Downes (1962) noted for far northern Canada, that there tended to be a reduction of

Table 9. Wing reduction of normally winged groups on Campbell I.

Order	No. species	Fully winged	Moderately reduced wings	Short or narrow wings	Totally (or nearly) wingless	% of species with wing reduction
Plecoptera	3	1(?)	-	-	2	67
Orthoptera	1	-	-	-	1	100
Psocoptera	3	-	-	2	1	100
Thysanoptera	1	1	-	-	-	0
Homoptera*	11	7(?)	-	-	4	36*
Trichoptera	1	1	-	-	-	0
Lepidoptera	29	23	1	5	-	21
Diptera**	81	67	5	3	6	18**
Coleoptera	43	4	-	2	37	91
Hymenoptera	10	5	1	1	3	50
Totals	183	109	7	13	54	40

\* Ratio is probably higher, as winged forms of some of the aphids may be lacking.

\*\* Probably more species have wing muscles and wings slightly reduced in size.

The winged plecopteran has not been taken in recent years, and may be extinct, or may represent a mistaken record. If the introduced insects are subtracted, the ratio of wing reduction might appear higher. But for a number of species, it is not certain whether they are naturally or artificially introduced.

mating flight and often the development of parthenogenesis. The wide, often circumpolar, distribution of arctic species is well known. Obviously, there is much more flight reduction in the subantarctic, where isolation and adversity of environment are more acute. No great tendency toward parthenogenesis has been noted here, however.

The most conspicuous aspect of the Campbell fauna is the high ratio of species which are unable to fly (see Table 9). Of a probable 170 native species of normally winged groups, 68 are flightless, having slightly or greatly reduced wings to no wings at all. This represents a flight loss of about 40 %, or close to the 43 % for the more isolated and apparently more ancient southern Indian Ocean islands. In addition, there are about 13 introduced species, of which 6 are flightless (of normally winged orders). Some of the groups which include flightless native species have a tendency to include flightless species elsewhere. However, in many cases this is not true. Among the groups having a tendency toward wing reduction are certain types of staphylinid beetles, weevils, the ichneumon wasp genus *Gelis* (fig. 22h), and diapiiid wasps. Of the rarely wingless groups, some of the examples on Campbell are striking, or even previously unreported or unparalleled as far as known. Among these are all the known male coccids (3 species), the striking cases in the six endemic moth genera (fig. 21), and others. Interesting cases include the two genera of dolichopodid flies (fig. 22 d, e), a muscid fly (fig. 22d), and two of the coelopid flies (figs. 22f, 23, 24).

Only four of the species of beetles (out of 43) are fully winged on Campbell, and two of these (*Uloma* and *Ptinus*) are probably introduced and may not be firmly established. One-half of the Hymenoptera are flightless (fig. 22h, i).

Some remarkable apparent intra-specific plasticity is evident in several Campbell species. This appears to involve both morphology and ecology. For instance, in the flightless dolichopodid fly genus *Schoenophilus* (fig. 22d, e) the variation is so great that the wings in some individuals are long and slender, and in others broadly expanded and spoon-like at tips. These are found in similar or somewhat dissimilar niches, and it is a question whether there is one or more species on the island. In the wingless diapiiid wasps there is great variation, but there appear to be separate populations differing in size, one in beached kelp and the other in tussock turf, parasitizing puparia of different families of flies. In the cynipid wasp *Kleidotoma subantarctica* (fig. 22i) there is great variation in wing size, from nearly complete to fairly small, but generally with distortion and weak sclerotization (see last paper by Yoshimoto). This suggests lack of use and selection for reduction in size.

In the trapping experiment, the fact that many of the trapped specimens would have been blown into the harbor had they not been trapped suggests that these species are subject to negative selection pressure for use of their wings. That certain abundant winged species were not taken in the trapping experiment seems significant. It suggests that these species may have developed the habit of dropping to the ground when there is an increase in wind speed above a certain rate, say of 15 or 20 knots. During the rare calm, sunny periods, a number of species were seen in flight in the Tucker-Beeman area, up-wind from the trap nets. These included some abundant species which were never caught in the traps. Among these were some of the pyralid moths, geometrid moths and the ichneumon wasp *Diadegma agens* (which appeared to be much more abundant than the smaller species *Campoplex disjunctus* which was taken principally in the trap nets). These species which were not trapped are weaker fliers than some of the types commonly caught in the nets,

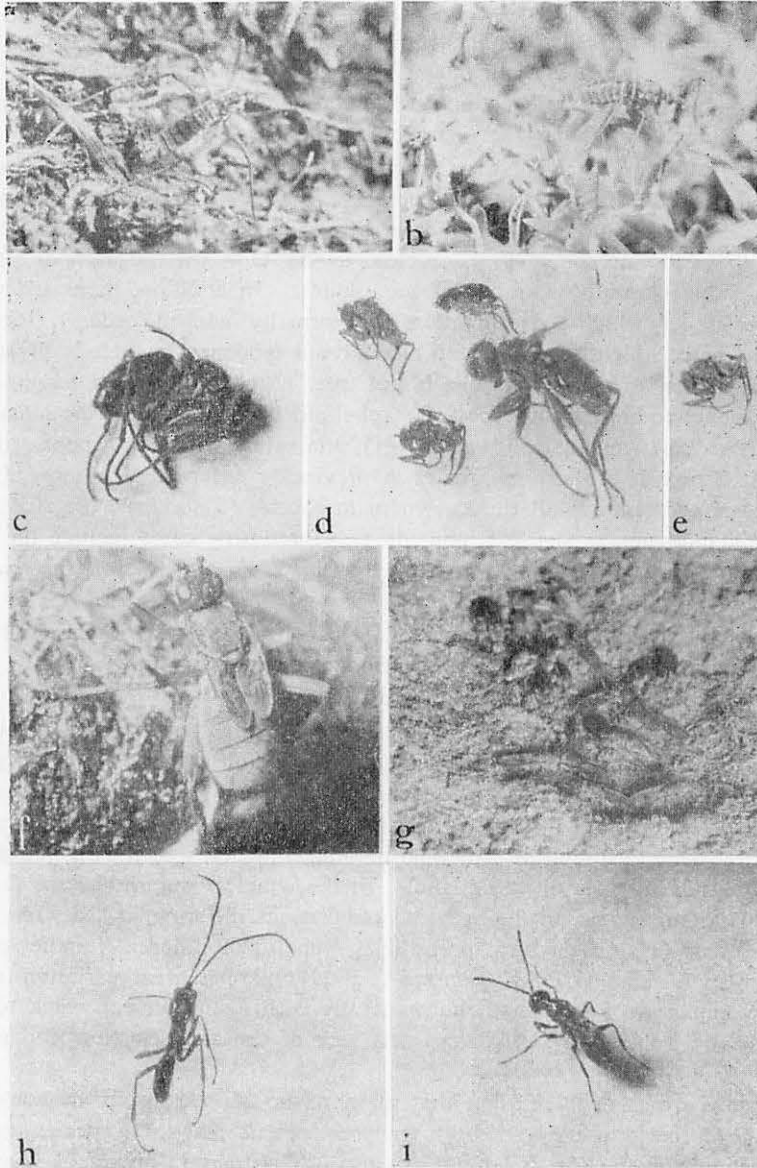


Fig. 22. a, wingless crane-fly, *Erioptera (Trimicra) brachyptera* Alexander, walking on debris near mollymawk nest, Courrejolles Peninsula, Campbell I.; b, same, on *Colobanthus*; c, probably *Schoenophilus* sp. (Dolichopodidae); d, 4 flightless flies: 2 *Schoenophilus* at left and below (*S. pedestris campbellensis* Harrison), *Acropsilus borboroides* Oldroyd above, *Coenosia filipennis* Lamb, from Beeman—Lyll area, below, XII.1961; e, *Schoenophilus pedestris campbellensis* Harr.; f, *Baeopterus robustus* Lamb ♀ on rotting kelp, shingle beach, Rocky Bay, 20.XII.1961; g, winged coeloid flies, probably *Coelopa debilis* Lamb, on underside of rock, Rocky Bay, 20.XII.1961, showing failure to fly when disturbed; h, wingless wasp, *Gelis campbellensis* Townes, Beeman area, XII.1961; i, brachypterous wasp, *Kleidotoma (Pentakleidota) subantarctica* Yoshimoto, from Lookout Bay, under *Stilbocarpa polaris*; all Campbell I. (photos mostly by Rennell, partly by Gressitt).

like calliphorid flies, muscids and others, yet are stronger fliers than some which were taken abundantly in the nets, like the aphids, psychodids, sciarids and others. Perhaps some of these were selectively trapped at different wind-speeds, and more precise observations in this direction are needed. It was noticed that aphids and psychodids were abundant in the nets when wind was weaker, or variable, but scarcer when wind was uniformly strong. In some groups representation in the trap catches appeared to be roughly proportionate to local population levels as indicated by all types of collections. However, in other cases the reverse was true, with abundant species lacking as mentioned above, and others taken largely, or solely in the nets (*Apanteles*, *Campoplex*, etc.). Some species, including some of the delicate flies like cecidomyiids, were taken only in the Malaise trap, which was in a very protected spot.

The situation in the fly family Ephydriidae is very interesting. Some of the species have reduced wings and have substituted hopping for flying. Some of them can make short flights with the aid of a jump. One of the species, *Hydrellia enderbii*, is among the most numerous species of insects on the island, yet it was never taken in the trap nets, and only 40 specimens were taken in the Malaise trap, as against 800 by other means of collecting. Most of the specimens were swept from tussock, sedge and *Bulbinella*, often near streams or elephant seal wallows. This appears to be a strong indication that these flies are rapidly dispensing with the habit of flying. The other species of ephydriids, including those incapable of sustained flight, were found largely in bird rookeries, around elephant seal wallows and in rotting kelp, all rather windy environments. Some of the moths with reduced wings, as noted by Sorensen (Salmon 1956) have also developed the habit of jumping, often resembling small grasshoppers by their activity. Also, they often sham death when disturbed, falling to the ground or within the tussock heads. This is interesting because of the apparent lack of predators (other than spiders which were not observed on the stems of tussock and sedge, or on the open rock where the various moths were observed). The only native truly insectivorous bird is the pipit, which is now rare.

The adaptation of habits of the flightless species is very interesting. Besides the jumping flies and moths mentioned above, there are many which crawl rapidly downward into

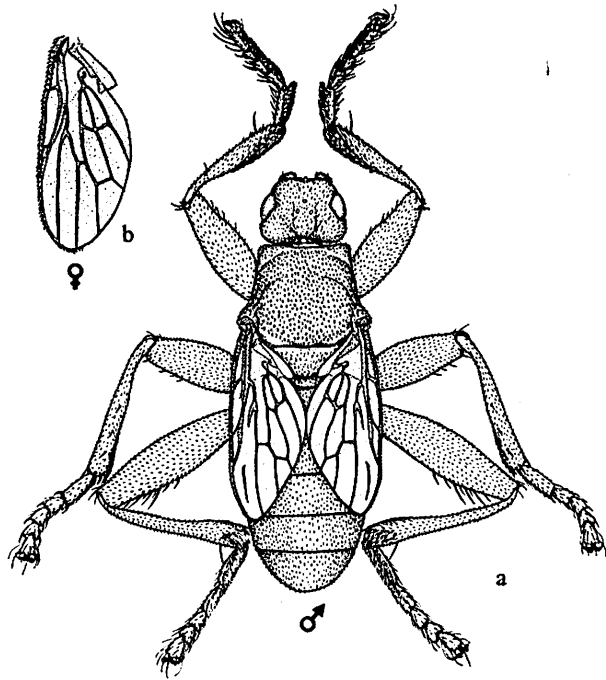


Fig. 23. Brachypterous coelopid fly, *Baeopterus robustus* Lamb ♂ (a) and wing of ♀ (b); Campbell I.

vegetation or other surroundings when disturbed. The large flightless coelopid flies (figs. 22f, 23, 24) are difficult to catch since they go downward rapidly under the rotting kelp and beach rocks where they occur. The winged coelopid flies (fig. 22g) often avoid flying when disturbed, crawling downward like the wingless species or remaining on the kelp or rocks. The flightless muscid and the totally wingless dolichopodid (fig. 22d), which often occur on the flower heads of *Bulbinella*, run downward when disturbed, jumping into vegetation on the ground.

It is significant to compare wing reduction on Campbell with that on other small islands or extreme environments. The situation is analogous to those on Macquarie, the Aucklands, the southern Indian Ocean islands and other subantarctic islands. There are analogies in high alpine areas. Jeannel (1940) noted some comparisons between African mountains and the Kerguelen area. I noticed striking superficial analogies (not necessarily closely related forms) between Macquarie, Campbell and Aucklands on one hand with the summits of

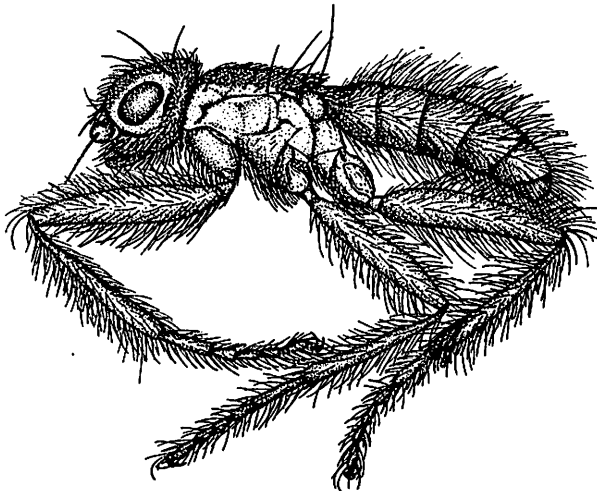


Fig. 24. Apterous coelopid fly, *Icaridion nasutum* Lamb, side view, Campbell I.

certain definite trends. These included larvae with thick skin, robust pharynx with rigid costae, long malpighian tubules, reduced gastric coeca, short hind intestine, abundant adipose tissue; tough puparia; and adults with heavily sclerotized mouthparts, atrophied notopleural callus, small thorax and reduced wing and leg muscles. In many of the Campbell species, however, the legs are greatly enlarged with wing reduction and the activity suggest saugmented leg muscles. Some, however, like the short-winged crane-fly (fig. 22a, b) move rather slowly.

## CONCLUSIONS

Final conclusions on the origin and history of the Campbell I. fauna cannot safely be presented at this time. Seemingly many conflicting ideas have been manifested in this volume. There is much evidence for oversea dispersal to the island, and this correlates with the extensive evidence for fairly recent glaciation. Other geological indications sug-

Mt. Wilhelm and Mt. Giluwe in eastern New Guinea on the other, though this may not have extended to wing reduction. Some analogies, as well as striking differences, were noted above between subantarctic and arctic areas. Again, the latter did not include striking wing reduction. Another analogy which might be significant is the appearance in temperate areas of early spring adults with reduced wings, whereas later appearing relatives are fully winged. Apterism is not highly developed on small tropical Pacific islands.

In regard to flies of the Kerguelen area, Seguy (1940) made morphological studies and noticed



gest that the island built itself up from a raised submarine plateau through volcanic action and does not necessarily represent a continental fragment left after drift or subsidence. Some of the apterous insects on the island are the only known wingless species in their respective groups. Some evidence suggests that evolution on such an island is very rapid, and that apterism may not be an indication of lengthy isolation. Among the evidence is frequent non-use of wings by winged species, the variation in wing size of some of the brachypterous species, and the general indications of great plasticity and intraspecific variation. The morphological variation appears to correlate with great ecological plasticity, perhaps both being influenced by scarcity of predators and competitors. Because of the great influence of the adverse climate, selection favoring loss of wings and the development of habits better attuned to the local environment is probably proceeding at a rapid rate. In some situations, wingless species (Diptera) appear to be less abundant than winged species. However, the former appear better adapted to the environment, are more cryptic in their appearance and habits and are less readily collected and less easily carried away by the elements.

Other evidence, such as the case of the two species of wingless stone-flies belonging to a genus represented only by wingless species and also occurring in the Aucklands and New Zealand, suggests greater antiquity. Undoubtedly there were at least closer stepping stones in the past, as the islands were once much larger. Also, some well-adapted species might have persisted through the glacial periods, as some free-living groups do now in Antarctica, possibly some of the latter actually having persisted through the periods of maximum glaciation.

It is quite clear that many of the groups now existing in Antarctica and the more southern islands are capable of air-borne dispersal. Representatives of many of them have been taken in trapping aboard ships in these general areas, primarily south of New Zealand and Tasmania, as far south as ocean extends in the Ross Sea, and off the coasts of the southern tip of South America. A few have been taken on the Antarctic continent. These include wingless forms such as spiders, mites and springtails, as well as winged insects. Trapping experiments on Campbell I. indicate that many individuals of the winged forms are blown off the island, whereas the wind has much less effect on the wingless kinds.

The subantarctic faunal make-up is different from that in the Arctic, where there are more Lepidoptera and Hymenoptera, and fewer Coleoptera.

The faunal contrast between Campbell I. and Macquarie I. is very great, both regarding faunal origin and extent of representation. This seems to correlate with submarine topography, the purely volcanic origin of Macquarie and its probable more complete glaciation. It is also slightly suggestive of the possibility that when continental blocks moved in these areas, Macquarie was more closely associated with Kerguelen and other southern Indian Ocean Islands and perhaps also with East Antarctica, while Campbell (and the Aucklands and New Zealand) was associated with West Antarctica and South America. However, as this would have been before the Cretaceous, it could not have had much effect on the present situation except as it related to the long-term isolation of New Zealand and the history of ancient groups.

When the fauna of the Auckland Is. (and New Zealand) is better known, and studied in conjunction with those of South Georgia, the Falklands and southern South America, much more light should be shed on the unsolved questions. By that time, more evidence

will be available on the geological history of the general area.

#### POSTSCRIPT

A few of the Campbell I. manuscripts were received too late for inclusion in systematic order in the body of this volume. These are included in the APPENDIX. In addition, four papers on Macquarie and/or Auckland Is. arthropods were received during the course of publication of this volume. They are included as a SUPPLEMENT, as some of them bear on zoogeographic matters discussed in the SUMMARY.

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#### ADDENDUM

When this volume was nearly through the press, an advance part of the collections made on Bird Island and the main island of South Georgia was received. These were collected between December 1962 and April 1964, by Harry Clagg.

A preliminary tally of this portion of the collection indicates the following numbers of species, which appear to represent an increase of more than 60% over the previously recorded fauna of South Georgia:

Acarina	18	Thysanoptera	1	Lepidoptera	1
Araneae	4	Anoplura	2	Diptera	12
Collembola	14	Mallophaga	10	Siphonaptera	2
				Coleoptera	10
				Total	74

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