The insects of sub-Antarctic Marion and Prince Edward Islands; with a bibliography of Entomology of the Kerguelen Biogeographical Province

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Twenty-six species of free-living insects representing eight orders (with Diptera, Coleoptera and Lepidoptera numerically dominant) have been recorded on the isolated, volcanic islands of the Prince Edward archipelago. Six are endemic to the islands and 11 are native to the sub-Antarctic. A further nine species with wide or cosmopolitan distribution occur on Marion Island. They are treated as naturalized aliens. Only four alien insect species are known from relatively pristine Prince Edward Island. The basic biology of all the insect species was studied between 1983 and 1986 during the course of an investigation of the role of insects in decomposition processes on Marion Island. The results of the former study are reported here. Biologies and diagnoses of the different life stages and short taxonomic discussions for each species are provided. The zoogeography of the insect fauna, which has many diverse affinities, is reviewed and the biogeographical unity of the Kerguelen Faunal Province is stressed. The role of insects in primary consumption and nutrient- and energy cycling in the terrestrial ecosystem on Marion Island is discussed. Ecological and evolutionary strategies employed by the insects are discussed with reference to various current theories such as adversity selection. An alternative approach to the standard theories on the origins of flightlessness in the insects (all the endemic species are flightless) is proposed. A list of insects parasitic on birds and mammals on the islands and a bibliography of entomology of the Kerguelen biogeographical province are provided.

Ses en twintig vrylewende insekspesies, wat agt ordes verteenwoordig, kom op die afgeleë vulkaniese eilande van die Prins Edward eilandgroep voor. Die ordes Diptera, Coleoptera en Lepidoptera oorheers getalsgewys. Ses spesies is endemies op die eilandgroep en 11 is inheems in die sub-Antarktiese gebied. Nege uitheemse spesies met uitgebreide of kosmopolitiese verspreiding word as gevestig op Marion eiland beskou. Slegs vier uitheemse spesies is tot dusver op die betreklik ongerepte Prins Edward-eiland aangetref. Tussen 1983 en 1986 is die basiese biologie van al die insekspesies bestudeer as aanloop tot die huidige langtermynondersoek na die rol van insekte in afbreekprosesse op Marion-eiland. Die resultate van eersgenoemde studie word hier weergegee. Vir elke spesie word 'n diagnose en 'n beskrywing van die biologie van elke lewensstadium, asook 'n kort taksonomiese oorsig, gegee. Die soögeografie van die insekfauna, wat uiteenlopende verwantskappe toon, word hersien, en die soögeografiese eenheid van die eilande van die "Kerguelen-provinsie" word beklemtoon. Insekte as primêre verbruikers en hul rol in die mineraal- en energievloei in Marion-eiland se ekosisteem word bespreek. Die ekologiese en evolusionêre strategieë waarmee insekte die ongunstige omgewingstoestande op die eilande die hoof bied, word bespreek met verwysing na die onlangse teorie van "A"- of ongunstigheidseleksie. 'n Alternatiewe benadering tot die ontstaan van ongevleueldheid onder die insekte (al die endemiese spesies is ongevleueld) word voorgestel in die plek van geykte teorieë oor die onderwerp. 'n Lys van insekte wat parasities leef op voëls en robbe op die eilande, asook 'n bibliografie van die entomologie in die Kerguelen-soögeografiese Provinsie, word verskaf.

Preface

We follow current taxonomic practice by excluding springtails (now Class Collembola) from the Insecta. Parasitic insects and their hosts from the Prince Edward Islands are listed in an appendix. Taxonomic revision of some taxa, and the possibility of new discoveries, will eventually render this account incomplete. At present it accurately reflects our current state of knowledge about the free-living insect fauna of the Prince Edward Islands, and provides a basis from which more detailed ecological studies can proceed.

Introduction

The two islands of the Prince Edward archipelago, Marion and Prince Edward, represent the summits of two closely related, coalescing shield volcanoes (Kable *et al.* 1971, Verwoerd 1971). They arose *c.* 2 million years ago just off the crest of the mid-Atlantic ocean ridge in a series of volcanic events. The nearest land is the Crozet archipelago 925 km to the east; Cape Town lies 2 300 km to the north. Marion Island (46°54′S, 37°45′E) is 290 km^2 in surface area and rises to a peak of 1 230 m a.s.l. Prince Edward Island (46°38′S, 37°57′E) lies 22 km NNE of Marion, is only one-seventh its size and rises to 672 m a.s.l. (Fig. 1). Their volcanic origin, their isolation from other land masses and the profound effect of the surrounding ocean on their climate and biota make the Prince Edwards "truly oceanic" islands (Verwoerd 1971). Biogeographically, the islands form part of the Kerguelen Province of sub-Antarctic islands, which is comprised of the Prince Edward, Crozet and Kerguelen archipelagos, and Heard Island (Fig. 1).

Marion and Prince Edward were annexed by South Africa in 1948, and since 1965 Marion Island has been the site of intensive, continuous scientific research. Inaccessibility and lack of facilities preclude intensive study of the Prince Edward Island biota. The advent of man had far-reaching effects on the terrestrial biota of Marion Island, chiefly through the introduction of alien species onto the island. Feral populations of cats (*Felis catus* L.) and house mice (*Mus musculus* L.) are well established on Marion Island. The cats take a heavy toll of small burrowing birds (Procellariidae); a few species have been decimated to the brink of local extinction. The subsequent indirect impact of cats on the nutrient status of plants and soils has not been fully assessed, but could be equally severe. The mice are primarily insectivo-

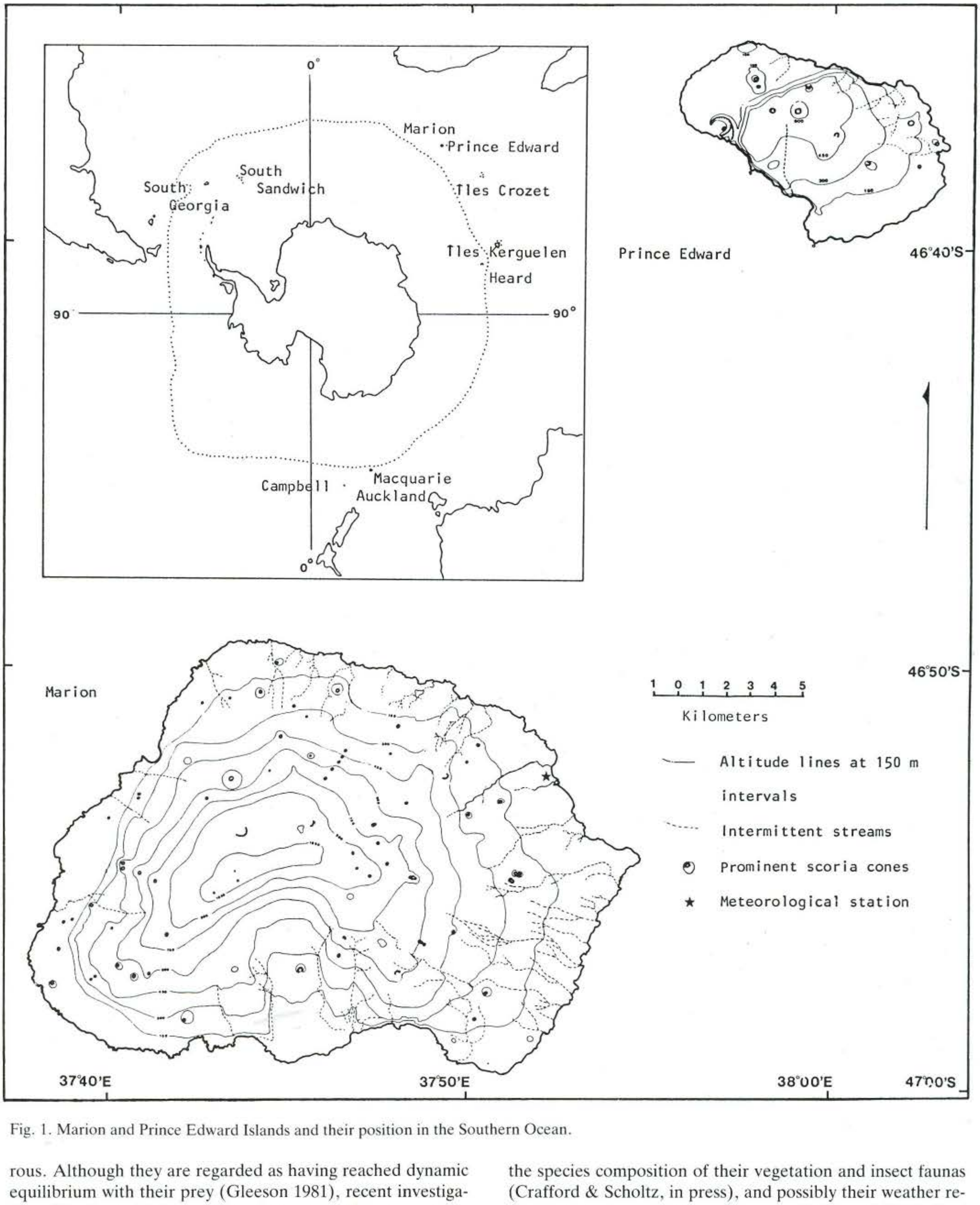


Fig. 1. Marion and Prince Edward Islands and their position in the Southern Ocean.

rous. Although they are regarded as having reached dynamic equilibrium with their prey (Gleeson 1981), recent investigations (Crafford & Scholtz, in press) suggest that, through the cumulative impact of their predation and the slow production rates of their prey species, mice have a severe impact on the population dynamics of prey species. The introduction of 13 species of alien vascular plants has substantially altered plant composition on Marion Island, especially in the vicinity of the meteorological base.

Prince Edward Island has so far escaped major manwrought changes; only one alien species of plant, (*Poa annua*) has been recorded from there. Bar slight differences in the species composition of their vegetation and insect faunas (Crafford & Scholtz, in press), and possibly their weather regimes, Marion and Prince Edward are essentially similar. The relatively pristine condition of Prince Edward Island and its terrestrial fauna makes it an ideal "control" site for monitoring further effects of the inevitably growing human impact on Marion Island.

Research over the past two decades at Marion Island has focused mainly on plant ecology, ornithology and mammalogy, and to some extent on their interrelationships on the island (see Siegfried *et al.* 1979 for a bibliography of scientific research carried out on the Prince Edward Islands). Recently, research has become geared towards gaining insight into energy, nitrogen and nutrient cycling in the island's terrestrial ecosystem. Although insects have long been recognized as important elements of these processes (e.g. Smith 1977b), and in spite of significant advances, lack of entomological studies has resulted in serious gaps in knowledge of the island's ecology. Prior to 1984, only three entomological studies of an ecological nature were published (Burger 1978, Smith 1977a, French & Smith 1983). Insect ecological studies are in turn hampered by a lack of basic information on the life histories and biology of the insects involved. This report was prompted by this lack of information.

History of entomological research at the Prince Edward Islands

In December 1873, a party from the Challenger Expedition, which included the naturalist H.N. Moseley, spent eight hours ashore at Marion Island. Their collections included insects; Waterhouse (1885) published the first description of insects from Marion Island based on the Challenger collections. Between 1875 and 1910 at least eight scientific expeditions explored the southern oceans. No one from these expeditions landed at the Prince Edward Islands, but descriptive studies of the insect faunas of Kerguelen and Crozet appeared during this period (see bibliography). The German South Polar Expedition of 1901-1903 passed close to the islands and its attendant entomologist remarked on the paucity of knowledge regarding the insects of the Prince Edward Islands and lamented the fact that he was "prevented from landing" (Enderlein 1909).

A party from the French Bougainville Expedition landed briefly on Marion Island's north coast in 1939. The only naturalist in the party was René Jeannel, an entomologist from the Natural History Museum in Paris. After the establishment of the permanent South African meteorological station on Marion Island in 1949, collections by the South African, Robert Rand, laid the basis for the first formal published account of the insect fauna of the islands (Jeannel 1953). The first South African biological and geological expedition to the Prince Edward Islands (1965 – 1966) resulted in a monograph (Van Zinderen Bakker *et al.* 1971) which incorporated descriptive studies of all the known insects from the islands, and firmly established the zoogeographical position of the islands' insect fauna within the sub-Antarctic province of Kerguelen. The first formal entomological study was launched in 1983, and focused on the role of insects as decomposers in Marion Island's terrestrial ecosystem. Autecological studies of four dominant insect decomposers have been completed, and form the basis of a current long-term study of energy flow through the invertebrate decomposer guild on Marion Island.

Description of the environment

Climate

The Prince Edward Islands have a cool, extremely oceanic climate, with the following outstanding features (Schulze 1971): predominantly strong westerly, and regularly, gale-force winds; high relative humidities (>80 %); low mean temperatures showing little diurnal and seasonal variation (mean air temperature of the coldest and warmest months are 3,2 °C and 7,3 °C respectively); heavy precipitation in the form of rain (>2 500 mm p.a.), snow and sleet; and a high degree of cloudiness.

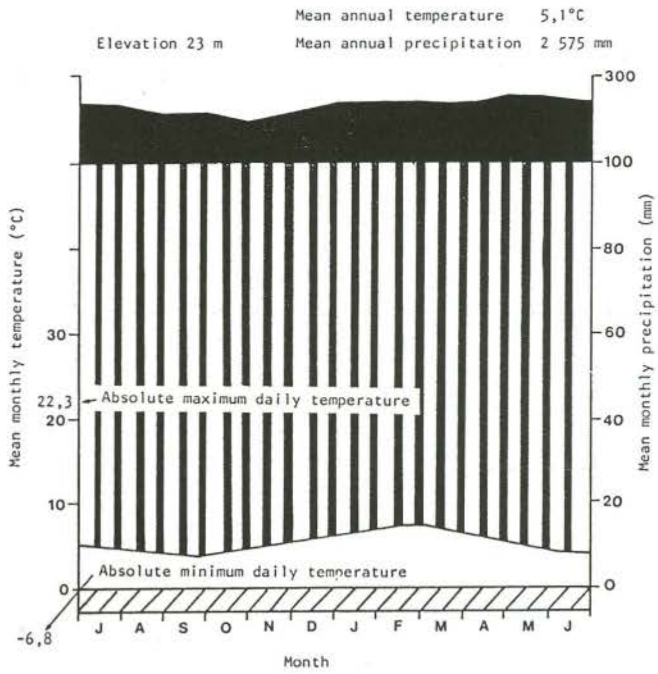


Fig. 2. Climate diagram of the weather recorded at the Marion Island meteorological station (after Gremmen 1981).

A climate diagram of the weather recorded at the Marion Island weather station is presented in Figure 2 (after Gremmen 1981). According to Walter & Leith's (1967) world atlas of climate diagrams, few other stations in the world have similar climates – these include Staaten Island, the sub-Antarctic islands Kerguelen and Macquarie, and some mountain stations in New Zealand. Air temperature measured at the weather station does not reflect "effective" temperatures prevalent at Marion Island. The chill factor (a combined effect of low temperature, high humidity and high wind speed) can reduce a measured air temperature of 5 °C to several degrees below zero. The average temperature lapse rate at Marion Island is about 4,5 °C and 4,0 °C per 1 000 m altitude in winter and in summer respectively (Schulze 1971). Life in the interior of the island is consequently exposed to vastly different environmental conditions from those on the coastal plain. Conversely, many favourable microhabitats exist and are utilized by invertebrates: these include habitats underneath "canopy vegetation" such as in *Poa cookii* tussock grassland; the interior of tussocks, "cushion" plants (*Azorella selago*) and moss balls; and wrack beds on the island's shores. No microclimatological data are available, however.

Geology

Two stages of volcanic activity, with an intervening period of glaciation during the Pleistocene, gave rise to two distinct types of lava on the Prince Edward Islands. Grey, pre-glacial lava formations (dated at 276 000 ± 30 000 yrs) are generally exposed, and have a smooth topography offering little foothold for vegetation. This formation supports a sparse flora consisting of open fjaeldmark and occasional patches of mire vegetation. Post-glacial black lava flows (15 000 ± 8 000 yrs) cover approximately 80 % of Marion Island's surface and form a hummocky, well vegetated mosaic of mire, herbfield and fjaeldmark (Verwoerd 1971, Smith 1978).

The central highland on Marion Island consists of bare, wind-blown scree slopes. It is permanently snow-covered in winter. A permanent central "ice plateau" approximately 5 ha in extent occurs above 1 000 m elevation, and may influence the island's climate.

Vegetation

Marion Island has a tundra-type biome. This is based on the definition of tundra as an area where the temperature is too low or precipitation and wind too great for natural forest vegetation to develop (Wielgolaski 1972). Smith (1976b) pointed out that the species composition of the Marion Island vegetation, the distribution of biomass among these species and the nutrient contents of the island's soils are typical of many tundra vegetation types.

Twenty-two species of vascular plants are indigenous to Marion and Prince Edward Islands. Most of these species are widely distributed throughout the temperate regions of the southern hemisphere; seven are restricted to islands of the Kerguelen Province. A total of 72 moss, 36 hepatic and about 100 lichen species are known from the Prince Edward Islands. Like the fauna, the vegetation has its closest affinities within the Kerguelen biogeographical province (Gremmen 1981).

Because of the harsh climate, only areas below 500 m a.s.l. on Marion Island support closed plant communities, but these communities support a higher phytomass than those in many temperate or tropical areas (Huntley 1972). The development of the high phytomass is partly the result of a long growing season and, in tussock grass, prolonged leaf longevity; the absence of large herbivores and the paucity of invertebrate grazers play a further role (Huntley 1971, Smith 1977b). Primary production on the island is channelled primarily through a detritus chain; most of the invertebrates on the island are litter-dwelling detritivores. Only one species (larvae of the flightless moth *Embryonopsis halticella*) is restricted to grazing, being a strictly monophagous stem-borer of the tussock grass *Poa cookii* (Crafford & Scholtz in press).

Huntley (1971) grouped the island's plant communities into five complexes:

1. Slope (consisting of open and closed *Blechnum pennamarina* fernbrake).
2. Mire (dominated by the grass *Agrostis magellanica*).
3. Salt spray (areas adjacent to the coast, dominated by the halophile *Crassula moschata*).
4. Fjaeldmark (exposed, sparsely vegetated "wind desert")
5. Biotically influenced (coastal areas heavily manured by birds and seals, dominated by the tussock grass *Poa cookii*).

Smith (1978) estimated the percentage surface area occupied by the various plant communities on black and grey lava flows below 300 m a.s.l. on Marion Island's eastern coastal plain (Table 1).

Table 1.
Percentage surface area occupied by the various plant communities on black and grey lava flows below 300 m a.s.l. on Marion Island's eastern coastal plain (from Smith 1978).

Community	Black lava %	Grey lava %
Closed fernbrake	18,0	0,04
Open fernbrake	21,6	1,1
Drainage line	0,3	0,0
Tussock grassland	0,6	0,4
Wind-desert	20,9	39,3
Mire and bog	37,4	59,0

The heavy rainfall on Marion Island causes constant leaching of minerals from the soil. In many areas the vegetation depends on a supply of nutrients transported from the sea by wind, birds and seals. Approximately two million seabirds belonging to 26 species annually visit the island to breed and moult (Siegfried 1978). The total annual guano production by 14 species of surface nesting birds on Marion Island amounts to 3 615 tonnes (dry mass), 98 % of which is voided by penguins on the coastal plain (Burger *et al.* 1978). Nutrient input in inland areas, by ten species of burrowing petrels (Procellariidae and Pelecanoididae) has not been quantified, but is probably substantial. The effect of manuring by birds largely determines the distribution of *Poa cookii* tussock grassland. Enhanced plant growth, and high soil and plant nutrient content in manured areas (Smith 1976a, 1976b) are accompanied by increased densities and biomass of associated invertebrate consumers (Burger 1978, Crafford & Scholtz in press). On the coast, three seal species (the southern elephant seal, *Mirounga leonina*, and the fur seals, *Arctocephalus tropicalis* and *A. gazella*) heavily influence the vegetation and local topography in their haulout areas. Panagis (1984, 1985) described the resulting effect on invertebrate populations in these areas.

Only 67 species of free-living invertebrates have been recorded on Marion Island (Table 2). The paucity of species is offset by high densities and biomass (Burger 1978, Crafford & Scholtz in press). Some invertebrate groups (mainly micro-invertebrates such as Collembola and Acarina) have received little attention and have probably not been adequately sampled. In the Antarctic and maritime Antarctic they are the dominant invertebrates (Block 1985); on Marion Island they probably form important links in terrestrial food webs (Smith 1977b). The Araneae (spiders) are the major invertebrate predators.

Table 2.
Numbers of free-living macro- and meso- invertebrates on Marion Island.

Group	No. of species
Phylum Arthropoda	
Class Insecta (insects)	26
Class Collembola (springtails)	13
Class Arachnida	
Order Araneae (spiders)	4
Order Acarina (mites)	19
Phylum Annelida	
Class Oligochaeta (earthworms)	3
Phylum Mollusca	
Class Gastropoda (slugs and snails)	2
Total	67

Methodology

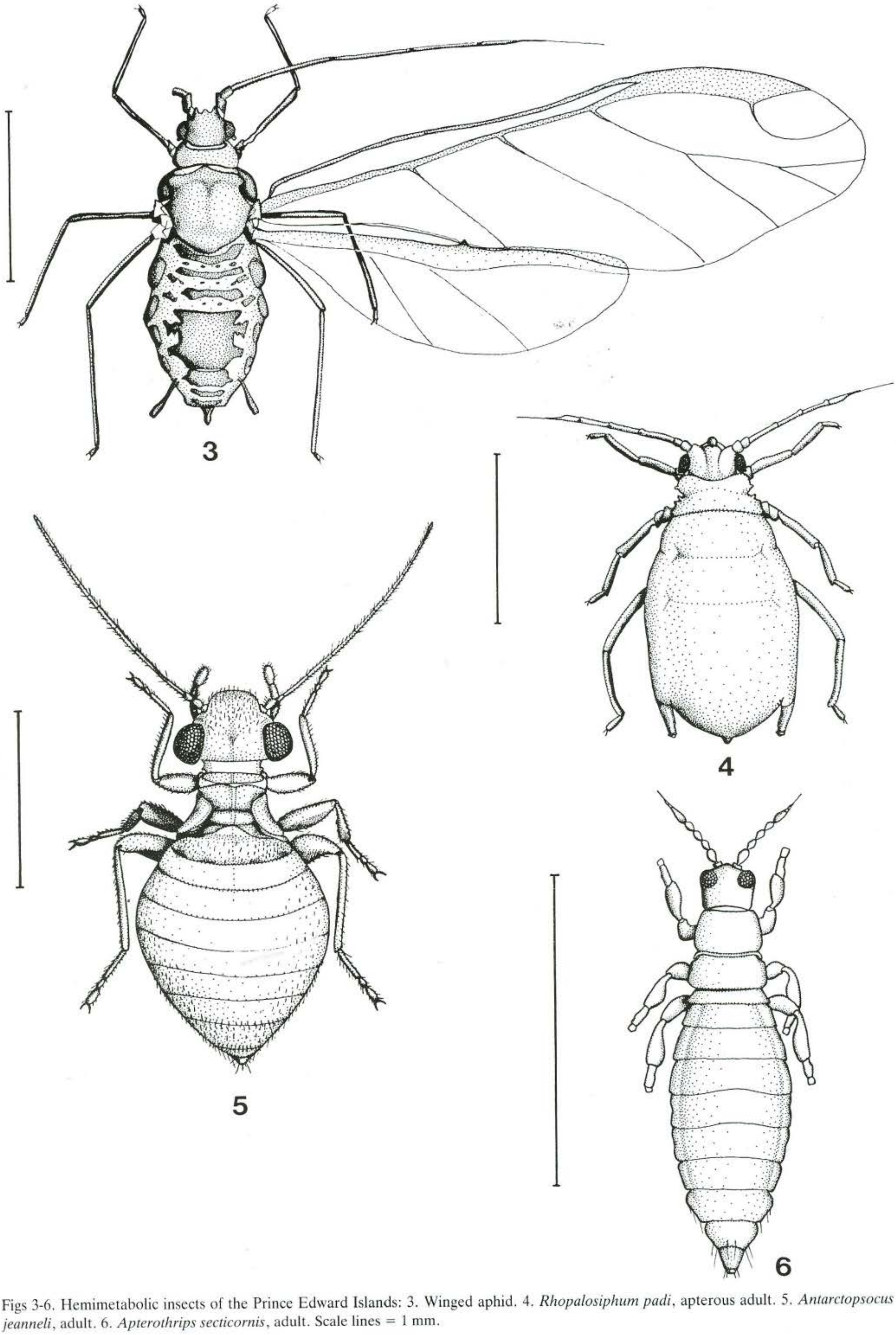
Fieldwork was done during a 21 month stay on Marion Island (April 1983-May 1984; September 1984-April 1985) and four, four-day visits to Prince Edward Island (May 1983, April 1984, September 1984, and April 1985). Insects were collected intensively and indiscriminately over the whole of each island and for the duration of the period(s). Collecting was done mainly with aspirators and by hand, although sweepnets were used in tall vegetation during dry spells. Berlese funnels were used to extract insects from peat and litter samples. The life cycles of rapidly breeding species were determined in incubators in the laboratory on Marion Island, as were food preferences and diets. Information on the basic biology and local distribution of species was derived from standard collecting data, supplemented by field notes.

The insects

Twenty-six species of free-living insects, representing seven orders, have been recorded on the Prince Edward Islands. Six are endemic to the islands and 11 are native to the sub-Antarctic. A further nine species with wide or cosmopolitan distribution occur on Marion Island and are treated as naturalized aliens. Five cosmopolitan tramp species, of which four are associated with man as household- or agricultural pests, have sporadically been recorded on Marion Island and are regarded as transient aliens. Only four alien species have become established on Prince Edward Island. The insect species recorded on the Prince Edward Islands, with their geographical distributions, are listed in Table 3.

Table 3.
The insects of the Prince Edward Islands and their geographical distribution.

	Marion Island	Prince Edward Island	Iles Crozet	Iles Kerguelen	Heard Island	
Indigenous insects						
Order Psocoptera						
Antarctopsocus jeanneli	+	+	+			
Order Coleoptera						
Ectemnorhinus similis	+	+				
Mesembriorhinus parvulus	+	+				
Antarctonesiotes elongatus	+	+				
Palirhoeus eatoni	+	+	+	+		
Bothrometopus randi	+	+	+			
Meropathus chuni	+	+	+	+		
Halmaeusa atriceps	+	+	+	+		Falklands, South Georgia
Order Diptera						
Paractora dreuxi mirabilis	+	+				
Listriomastax litorea	+	+	+	+		
Apetenus litoralis	+	+	+	+		
Halirytus amphibius	+	+	+	+		
Bradysia aubertii	+			+		
Order Lepidoptera						
Pringleophaga marioni	+	+				
Pringleophaga kerguelensis		+	+	+		
Embryonopsis halticella	+	+	+	+	+	
Order Hymenoptera						
Kleidotoma icarus	+	+	+	+		
Naturalized aliens						
Order Thysanoptera						
Apterothrips secticornis	+		+	+		Semi-cosmopolitan. Also South Georgia, Tierra del Fuego, New Zealand
Order Hemiptera						
Rhopalosiphum padi	+	+	+			Semi-cosmopolitan
Macrosiphum euphorbiae	+					Semi-cosmopolitan
Myzus ascalonicus	+					Semi-cosmopolitan
Order Diptera						
Psychoda parthenogenetica	+	+	+	+		Widespread in Southern hemisphere
Limnophyes pusillus	+	+	+	+		Cosmopolitan
Fannia canicularis	+	+				Cosmopolitan
Scaptomyza sp.	+					
Order Lepidoptera						
Plutella xylostella	+					Cosmopolitan; also New Zealand sub-Antarctic islands
Transient aliens						
Order Lepidoptera						
Vanessa cardui	"Painted lady"; cosmopolitan butterfly					
Heliotis armigera	American bollworm; cosmopolitan					
Agrotis ipsolon	Cutworm; cosmopolitan					
Phytometra orichalcea	Cereal moth, cosmopolitan					
Order Blattodea						
Blatella germanica	German cockroach; cosmopolitan					



Figs 3-6. Hemimetabolic insects of the Prince Edward Islands: 3. Winged aphid. 4. *Rhopalosiphum padi*, apterous adult. 5. *Antarctopsocus jeanneli*, adult. 6. *Apterothrips secticornis*, adult. Scale lines = 1 mm.

SYSTEMATICS AND BIOLOGY

Taxonomic references and synonyms under each taxon pertain only to the Prince Edward Islands and are only listed for native and naturalized species – for complete lists and information on tramp species, catalogues should be consulted.

ORDER PSOCOPTERA

This order is represented on the Prince Edward Islands by a single species, *Antarctopsocus jeanneli* which belongs to the family Elipsocidae.

Family Elipsocidae

This is a world-wide family of species which live in a variety of situations.

Genus *Antarctopsocus* Badonnel

Antarctopsocus Badonnel, 1947 : 26.

Antarctopsocus jeanneli Badonnel, Fig. 5.

Antarctopsocus jeanneli Badonnel, 1947; Dreux 1971 : 340.

DIAGNOSIS. Adults and nymphs occur together and, except for size (adults are about 2-3 mm long) are very similar. They are pale and globose with prominent dark eyes. Adults have very short wing stubs.

BIOLOGY. *A. jeanelli* occurs from the supralittoral to *c.* 300 m elevation on the coastal plains of Marion and Prince Edward Islands. It is a locally abundant but rather cryptic species which occurs on rockfaces covered with crustose lichen, and also in decayed and mouldy leaf litter, especially that of *Pringlea antiscorbutica* (Brassicaceae) growing in wet and sheltered areas. Both adults and nymphs feed on microflora (algae, lichens, fungi and fungal spores).

The reproduction mode of *A. jeanelli* at the Prince Edward Islands is not known. Parthenogenesis is obligatory in some Psocoptera and facultative in others (Smithers 1985). Asexual reproduction is an important pre-adaptation to sub-Antarctic conditions (Crafford in press), and may well contribute to the success of *A. jeanelli* at the Prince Edward Islands.

ORDER THYSANOPTERA

This order is represented on the Prince Edward Islands by a semi-cosmopolitan temperate species, *Apterothrips secticornis*, which belongs to the family Thripidae.

Family Thripidae

This is the largest family in the order with many, mainly plant-associated species.

Genus *Apterothrips* Bagnall

Apterothrips Bagnall, 1908 : 185

Apterothrips secticornis (Trybom), Fig.6.

Thrips secticornis Trybom, 1896 : 620
Apterothrips secticornis : Zur Strassen 1982 : 160

DIAGNOSIS. Adults and nymphs of this wingless species occur together and differ mainly in size; adults are about 1,5 mm long. They are uniformly brown.

BIOLOGY. On Marion Island, *A. secticornis* is associated chiefly with *Cotula plumosa* (Asteraceae) on the coastal lowland, but it has also been found on *Azorella selago* (Apiaceae) and *Poa cookii*. Host records on the Crozet and Kerguelen archipelagoes include *Acaena magellanica* (Rosaceae), *Ranunculus* spp. and *Crassula moschata* (Zur Strassen 1982). Adults and nymphs have similar feeding habits and are both foliage- and flower feeders. During summer large numbers of adults and nymphs occur on the inflorescences of *C. plumosa* where they appear to feed on pollen.

The mode of reproduction of *A. secticornis* on Marion Island is not known. Parthenogenesis is common in the order Thysanoptera. Sexual reproduction can be oviparous or ovoviviparous (Hartwig 1985).

ORDER HEMIPTERA

Suborder Homoptera

This large suborder of strictly plant-feeding insects is represented by three species of the family Aphididae on the Prince Edward Islands.

Family Aphididae

Three species of aphids occur on the Prince Edward Islands. Some of these species may become pests of various crops throughout the world and their catholic feeding habits and the ease with which they are dispersed by wind make them ideal candidates for transoceanic dispersal and establishment on isolated islands.

Dreux (1971) recorded four species on Marion Island but only two of these still occur there. They are *Rhopalosiphum padi* and *Macrosiphum euphorbiae*. Both species have a virtually world wide, but not cosmopolitan, distribution (Blackman & Eastop 1985), and may have been introduced by man. A third species, *Myzus ascalonicus*, is also common on the island. The species cannot be identified with certainty except after detailed preparation of specimens and the examination of microscopic structures. However, their general appearance and their host associations are usually very good indicators of the species. In April 1984, *Rhopalosiphum padi* was also recorded on Prince Edward Island – the first and so far the only record of an aphid on this island.

The two cosmopolitan species recorded by Dreux (1971), which can no longer be found on Marion Island, were probably introduced with fresh produce and did not become established.

Genus *Macrosiphum* Passerini

Macrosiphum Passerini, 1860:27

Macrosiphum euphorbiae (Thomas)

Siphonophora euphorbiae Thomas, 1878:61
Macrosiphum euphorbiae: Dreux 1971:340

DIAGNOSIS. Adult winged and wingless forms vary in length from 2,0-3,5 mm. They are spindle- or pear-shaped, usually green and often rather shiny. Eyes are reddish. Nymphs are slender, paler than adults, with a dark spinal stripe and light dusting of whitish-grey wax.

BIOLOGY. *M. euphorbiae*, commonly known as the potato aphid, is a polyphagous species that occurs primarily on dicotyledons and only rarely on grasses. Its primary hosts are members of the rose family (Blackman & Eastop 1984). On Marion Island, heavy local infestations of the flowers and seeds of *Acaena magellanica* (Rosaceae), by both winged and flightless forms of *M. euphorbiae*, occur during spring and summer. *Cotula plumosa* (Asteraceae) appears to be the only other major host plant, and is infested throughout the year. Although it has not yet been recorded on Prince Edward Island, it may occur there.

Genus *Rhopalosiphum* Koch

Rhopalosiphum Koch, 1854:23

Rhopalosiphum padi (L.), Fig. 4.

Aphis padi Linnaeus, 1758:451
Rhopalosiphum padi: Dreux 1971:340

DIAGNOSIS. Adult winged and wingless forms vary in length from 1,5-2,5 mm. They are broadly oval, dark green to purplish black. Nymphs are similar to but smaller than the adults.

BIOLOGY. The host plants of *R. padi* (oat aphid) include all the major cereals and pasture grasses of the world (Blackman & Eastop 1984). On the Prince Edward Islands, the wingless form occurs in small but dense colonies in *Poa cookii* tussocks, mostly on the lower parts of outside leaves. It also occurs on *Poa annua*. At present, infestations are localized but widespread on both Marion and Prince Edward Islands.

The life cycles of aphids are highly complex, with parthenogenesis and sexual reproduction alternating in successive generations. Several generations are usually produced per year and large populations may result after a short time. Nothing is known about the population dynamics of the aphids on the Prince Edward Islands. Natural enemies are absent, and it is not known to what extent abiotic factors are limiting. Heavy infestations by aphids may lead to retardation or distortion of growth in host plants, and most aphids are known to be vectors of plant virus diseases.

Genus *Myzus* Passerini

Myzus Passerini, 1860:27

Myzus ascalonicus Doncaster

Myzus ascalonicus Doncaster, 1946:29.

DIAGNOSIS. Adult winged and wingless forms vary in length from 1,2-2,4 mm. Wingless forms are greenish-brown to yellow and are strongly convex. Apices of the legs are black. Winged forms have a distinctive black abdominal patch.

BIOLOGY. This virtually cosmopolitan species is extremely polyphagous, colonizing plants in over 20 families and it is a proven vector of about 20 plant viruses (Blackman & Eastop 1984). On Marion Island the species occurs on *Cotula plumosa*.

ORDER COLEOPTERA

Family Curculionidae

The Curculionidae (weevils) is the largest and most successful family of beetles in the world. Many groups have wide ranges of tolerance for climatic extremes and food preferences, thus pre-adapting them for colonizing new regions. They range in size from very small to large and are among the few beetles suited to long-distance dispersal.

Subfamily Ectemnorhininae

The subfamily Ectemnorhininae is restricted to the sub-Antarctic islands of the Kerguelen Biogeographical Province. It is represented by eight genera and 32 species on the islands of the Kerguelen, Crozet and Prince Edward archipelagos as well as on Heard and McDonald Islands.

Five species belonging to five genera have been recorded on Marion and Prince Edward Islands.

Key to the Curculionidae (adults):

1. Labial palp 3-segmented. Epistome symmetric, its anterior margin transverse. Elytra without sparse erect setae 2
   Labial palp 2-segmented. Epistome asymmetric, its anterior margin distinctly oblique. Elytra with sparse, erect setae .... *Ectemnorhinus similis* Waterhouse
2. Claw segment distinctly longer than the first three tarsal segments. Tibiae mucronate. Intertidal .... *Palirhoeus eatoni* (Waterhouse)
   Claw segment distinctly shorter than the first three tarsal segments together. Tibiae not mucronate. Strictly terrestrial 3
3. Humeral area compressed, carinate. With hairs and scales. Size varies from 3,2-5,6 mm – with punctures on pronotum ..... *Mesembriorrhinus parvulus* (Waterhouse)
   Humeral area not compressed or carinate. Long transverse hairs on elytra and pronotum .... *Antarctonesiotes elongatus* Jeannel.
   Distinct pattern of dense scales on elytra. Size varies from 5,6-8,1 mm – without punctures on pronotum .... *Bothrometopus randi* Jeannel

Key to final-instar larvae:

1. Apical teeth on mandibles well developed, equal in size. Pronotum with 2 + 9 setae .... *Ectemnorhinus similis* Waterhouse.
   Apical teeth moderately to well developed, unequal in size. Pronotum with 2+8 setae 2
2. Thoracic lobes (excluding pronotum) unsclerotized. Airtubes of thoracic spiracle relatively broad .... *Bothrometopus randi* Jeannel.
   Thoracic lobes lightly to well sclerotized. Airtubes of thoracic spiracle relatively narrow 3
3. Thoracic spiracle with peritreme darkly sclerotized. Airtubes slightly shorter than diameter of peritreme .... *Palirhoeus eatoni* (Waterhouse).
   Thoracic spiracle with peritreme lightly sclerotized. Airtubes longer or equal to diameter of peritreme 4
4. Labial sclerotization with lateral arms broad at base. Airtubes of abdominal spiracles directed dorso-caudad. White .... *Mesembriorrhinus parvulus* (Waterhouse).
   Labial sclerotization with lateral arms narrow at base. Airtubes of abdominal spiracles directed dorsad. Bright yellow .... *Antarctonesiotes elongatus* Jeannel.

Genus *Ectemnorhinus* G.R. Waterhouse

Ectemnorhinus G.R.Waterhouse, 1853 : 184; Kuschel 1971 : 358
Dusmoecetes Jeannel 1940 : 161

Ectemnorhinus similis C.O. Waterhouse, Figs 8-10,14,15.

Ectemnorhinus similis C.O. Waterhouse,1885 : 122; Kuschel 1971 : 358
Ectemnorhinus marioni Jeannel 1940 : 179

This species is characterized by extreme intraspecific variation but can readily be distinguished from the other species by the key characters. The asymmetrical epistome and sparse, erect setae which are most easily visible in lateral view, are the most accessible characters but the 2-segmented labial palp is the most reliable for species identification.

Large specimens may be more than twice the size of the smallest ones and there are distinct size-linked differences in the colour of body scales. Kuschel (1971) could find no constant differences in either internal or external characters and regarded the whole complex as pertaining to a single species. On the basis of morphology, habitat preferences and differences in both temporal and spatial distribution patterns, we recognize three distinct ecotypes which correlate to three distinct morphs. They are most easily distinguished on the basis of size and colour. A small black (Fig. 8), intermediate green (Fig. 9) and large brown (Fig. 10) morph may be distinguished. Colour in the brown and green morphs is determined by scales of those colours on a brown integument whereas the black morph has a black integument basically devoid of scales.

Ectemnorhinus similis larvae (Fig. 14) are typical curculionid larvae – they are apodous and fleshy, with a darkly sclerotized head and pronotal sclerite. The species is characterized by the apical teeth on the mandibles which are well developed and of equal size. The pronotum has a setal configuration of 2+9. At present no morphological characters are known with which to separate the larvae of the different morphs. They can, however, be recognized on the basis of their habitat associations.

The pupa is a typical exarate weevil pupa showing details of the rostrum, antennae, legs and elytra (Fig. 15). The pupae of the different morphs, as with the larvae, cannot be separated morphologically.

Brown morph, Fig. 10.

DIAGNOSIS. Adults of this, the largest, morph (6,5-9,0 mm long) have a pale brown integument with a dense covering of brown scales, interspersed with sparse, erect setae.

BIOLOGY. Adults are associated mainly with *Azorella selago* and the tussock grass *Poa cookii*. On sunny days they occur in large numbers on *Azorella* plants, on which they have been observed to lay their eggs. During summer they may be found on the inflorescences of *Poa cookii*, where they appear to feed on pollen and seed. Throughout the year they also occur in the bases of tussocks where they feed on fungal growths in the moist litter layer. Other possible food plants include *Acaena magellanica* (Rosaceae) and mosses.

The polyphagous larvae are primarily detritus-feeders. Although associated chiefly with *Azorella selago* litter, they also occur in large numbers in albatross nests and in the litter of well manured vegetation. They are facultative feeders on mosses and lichens. Pupation takes place in well-drained ground, in a cell close to the surface.

Green morph, Fig. 9.

DIAGNOSIS. The adults of the intermediate, green morph, which vary in length from 5,0-7,0 mm, have a brown integument covered with rows of dense green scales which are interspersed with sparse, erect setae.

This morph superficially resembles *Bothrometopus randi* but can easily be distinguished from the latter by the presence, in the latter, of a very distinctive scale pattern on the elytra (Fig. 7). The scales on the elytra of the green *E. similis* morph lie in simple rows.

BIOLOGY. The green morph of *E. similis* has the widest local distribution of all weevils on Marion Island. Adults are ubiquitous, occurring in a wide range of habitats from the supralittoral to *c.* 800 m elevation. They are associated chiefly with *Poa cookii* grassland and drainage line communities on the coastal plain, reaching maximum densities of up to $220/m^2$ in March to April in the latter community (Smith 1977). *Acaena magellanica* (Rosaceae) and the moss *Brachythecium rutabulum* are major food plants. Large numbers are often found sheltering amongst the leaves of *Pringlea antiscorbutica* (Brassicaceae) but no direct feeding on the leaves has been observed. In summer they may be found with brown morphs on *Poa cookii* inflorescences. They are probably the most strictly herbivorous of the weevils, and Smith (1977a) regarded them as significant primary consumers.

The larvae are similarly ubiquitous and polyphagous litter dwellers. They are primarily detritivores, but also feed facultatively on mosses and lichens. Pupae may be found amongst moss fronds or in shallow cells in well-drained litter.

Black morph, Fig. 8.

DIAGNOSIS. The black morph is the smallest of the three *E. similis* morphs (4,0-5,5 mm long). It is furthermore characterized by its virtual absence of body scales and its black integument. This morph is similar in size and colour to *Palirhoeus eatoni* with which it often overlaps in distribution in low-lying coastal areas. It can, however, be easily distinguished from the latter by the characters listed in the key.

BIOLOGY. This morph is chiefly associated with *Agrostis magellanica* mire vegetation, but exhibits the same wide ecological range as do the two other morphs. The adults are less conspicuous than those of the others, occurring on the lower stems and among the roots of *A. magellanica* tufts on which they appear to feed. Adults, larvae and pupae are often found submerged in the saturated litter of mires and live essentially aquatic lives for most of the time. The larvae feed mainly on detritus, but fresh fragments of the mire-associated mosses *Jamesoniella* and *Drepanocladus* have also been found amongst their gut contents. Adults have also been recorded on *Azorella selago* and in drainage line communities adjacent to mires.

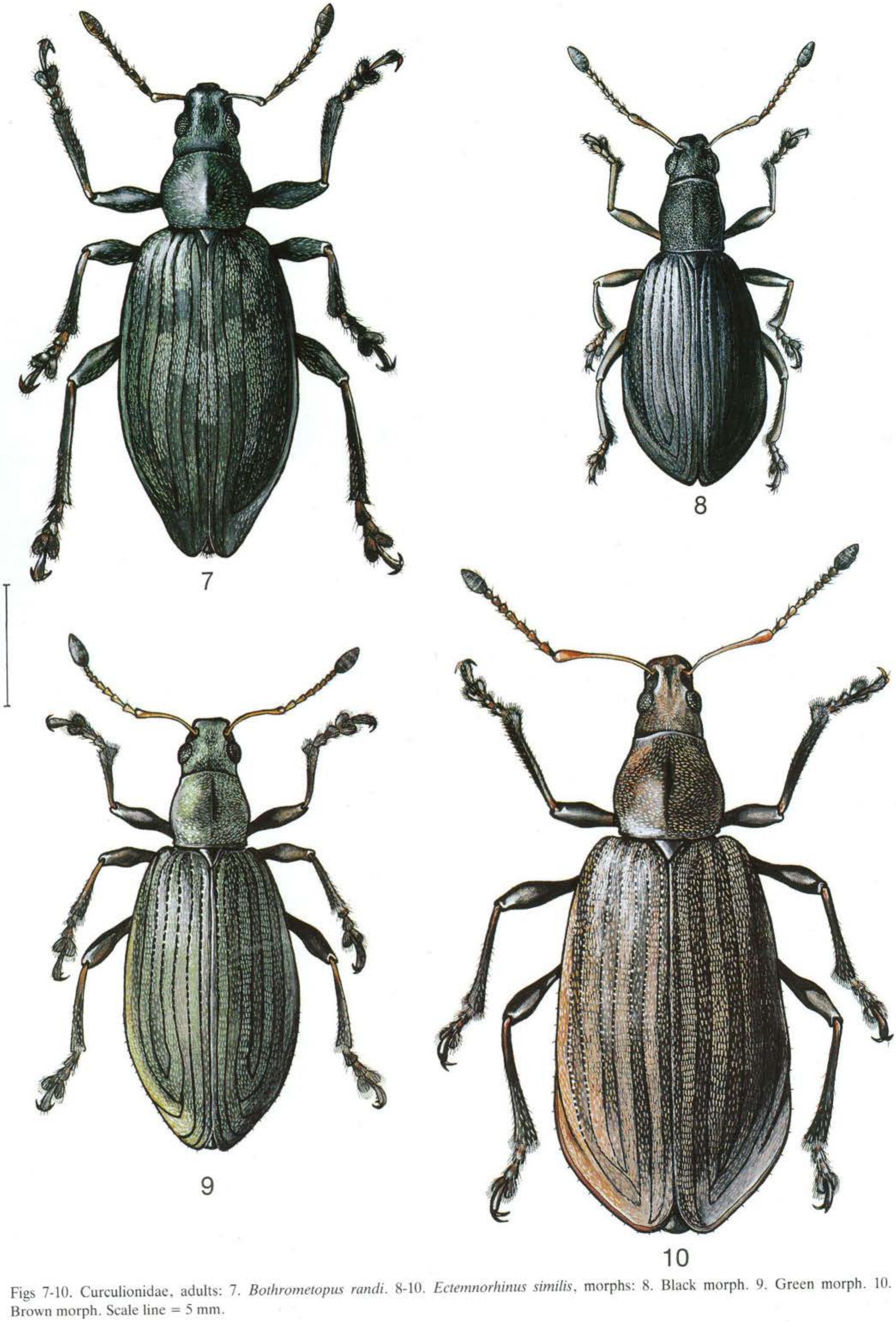
E. similis appears to be radiating and undergoing character release on Marion Island, with the ubiquitous, extremely generalized green morph possibly representing the plesiomorph from which the slightly more stenotopic black- and brown morphs are derived. A detailed ecological study of the species is underway.

Genus *Palirhoeus* Kuschel

Palirhoeus Kuschel, 1971 : 356

Palirhoeus eatoni (C.O. Waterhouse), Fig. 11.

Ectemnorhinus eatoni C.O. Waterhouse, 1879 : 234
Palirhoeus eatoni Kuschel 1971 : 356



Figs 7-10. Curculionidae, adults: 7. *Bothrometopus randi*. 8-10. *Ectemnorhinus similis*, morphs: 8. Black morph. 9. Green morph. 10. Brown morph. Scale line = 5 mm.

DIAGNOSIS. *Palirhoeus eatoni* adults, which vary in length between 4,0-5,5 mm, most closely resemble those of the black *Ectemnorhinus similis* morph (see above). They can easily be distinguished from the other weevil species by the presence of a tarsal claw segment which is longer than the first three tarsal segments. Furthermore, *P. eatoni* is the only species which lacks any vestiges of metathoracic wings or a lateral flange on the inner surface of the elytra.

Larvae are best distinguished from the other weevil larvae by the presence of a darkly sclerotized peritreme on the thoracic spiracle, as well as by their association with debris and vegetation in the intertidal and supralittoral zone.

Pupae cannot be distinguished from those of the other weevil species.

BIOLOGY. *P. eatoni* adults occur commonly on, and are restricted to, sea-facing rocks in the upper- to supralittoral zone which are regularly exposed to seaspray or are inundated with seawater. Small hooks on the tibiae, elongated claw segments and long claws enable them to get a firm grip on rocks; the adults are also often found wedged into narrow crevices in the rockface. Gut contents of adults have included fragments of the marine green algae *Enteromorpha bulbosa* and *Monostroma harioti* (Kuschel 1971).

Jeannel (1953) recorded larvae from clumps of *Enteromorpha* in the "intertidal zone", where they appeared to feed on this and other marine algae and where they are regularly inundated with seawater. We mostly found larvae wedged tightly into crevices (where they possibly also pupate). Jeannel (1953) found pupae in clumps of the supralittoral moss *Grimmia amblyophylla*.

The biology of *P. eatoni* is still not well known. Kuschel's (1971) description was based largely on conjecture. Doyen (1976) listed the species as one of only 50 species of Coleoptera known to be obligatory marine for at least some part of its life, and Kuschel (1971) stressed its uniqueness as the "sole weevil in the world that lives in the intertidal zone and feeds on marine algae". However, Marion Island has a very limited tidal range of 21 cm and 71 cm for neap- and springtides respectively (De Villiers 1976), and *P. eatoni* is essentially terrestrial. It simply exhibits the wide ecological tolerance characteristic of the weevil fauna of the islands, which in this case includes facultative marine habits and marked tolerance to immersion in seawater.

Genus *Mesembriorrhinus* Jeannel

Mesembriorrhinus Jeannel, 1940 : 186; Kuschel 1971 : 357.

Mesembriorrhinus parvulus (C.O. Waterhouse), Fig. 12.

Ectemnorhinus parvulus C.O. Waterhouse, 1885 : 22
Mesembriorrhinus parvulus: Jeannel 1940 : 190; Kuschel 1971 : 357.

DIAGNOSIS. Adults of this rather variable species (3,0-5,0 mm long) are probably the most difficult to identify. The best distinguishing character is the compressed and carinate humeral area.

Larvae are best characterized by the key characters.

Pupae cannot be distinguished from those of the other weevil species on the basis of current knowledge.

BIOLOGY. Adult *M. parvulus* occur mostly in low-lying coastal areas, but have been recorded up to 900 m elevation. In the supralittoral, where their range overlaps with that of *Palirhoeus eatoni*, they are clearly restricted to landward rockfaces. The adults feed mainly on lichens, algae and mosses, but inland they may occur, and apparently feed, on certain vascular plants (e.g. *Azorella selago*; Kuschel 1971). The larvae are detritivores, but may facultatively feed on mosses and lichens.

Genus *Antarctonesiotes* Jeannel

Antarctonesiotes Jeannel, 1940 : 183

Antarctonesiotes elongatus Jeannel, Fig. 13.

Antarctonesiotes elongatus Jeannel, 1953 : 166; Kuschel 1971 : 358.

DIAGNOSIS. Adults of this species are the smallest weevils (2,5-4,0 mm) found on the Prince Edward Islands. Besides their size they may easily be distinguished from the other black species by the presence of long transverse hairs on the elytra and pronotum. No other species has similar hairs.

Larvae are also very conspicuous, being bright yellow, thus allowing identification at a glance.

Pupae can be distinguished from those of the other species by their small size and, when alive, by the same yellow colour as the larvae.

BIOLOGY. *A. elongatus* is restricted to the central highlands of the Prince Edward Islands. It has only been recorded above 300 m and has been found as high as 1000 m elevation. Solitary adults are active in large numbers on snow and on rocks on sunny days. In the predominantly cold weather, clusters of up to 30 adults may be found in hollows and crevices on rocks. Clustering may be a behavioural thermoregulatory adaptation in this species. The adults feed on crustose lichens and on the epilitic moss *Andreaea acuminata*.

Larvae are both moss- and detritus feeders, and both larvae and pupae occur inside clumps and balls of moss (*Andreaea* and *Ditrichum* spp.) in the sparse vegetation of highland fjaeldmark.

A. elongatus can be expected to show physiological adaptations to low temperature, and the bright yellow colour of both larvae and pupae probably indicates the presence of cryoprotective substances in the haemolymph. An investigation of cold adaptation in this species is under way.

Genus *Bothrometopus* Jeannel

Bothrometopus Jeannel, 1940 : 180

Bothrometopus randi Jeannel, Fig. 7.

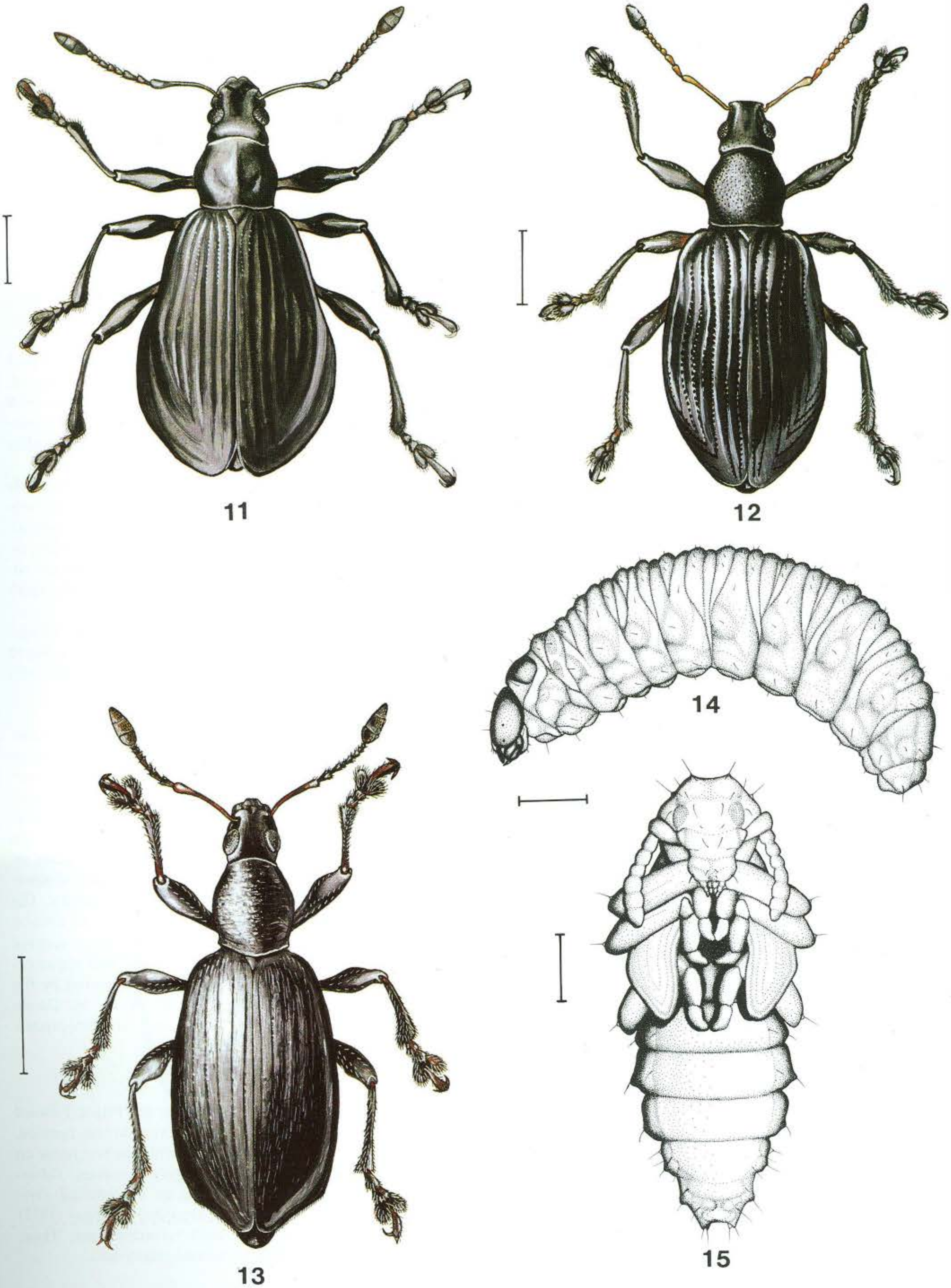
Bothrometopus randi Jeannel, 1953 : 165; Kuschel 1971 : 357.

DIAGNOSIS. Adults of *Bothrometopus randi* (5,0-7,5 mm long) can be distinguished from the other species, particularly the green *Ectemnorhinus similis* morph (see above), by the presence of a very distinctive elytral scale pattern.

Larvae are large and grey-green. Their size and colour are good characters for positive identification but confirmation therefor can be obtained by the presence of unsclerotized thoracic lobes.

Pupae, as with the other species, cannot be identified at present.

BIOLOGY. *B. randi* occurs from the coast to *c.* 800 m elevation. It is morphologically variable. Large adults with the



Figs 11-15. Curculionidae: 11. *Palirhoeus eatoni*, adult. 12. *Mesembriorrhinus parvulus*, adult. 13. *Antarctonesiotes elongatus*, adult. 14. Larva, probably *Ectemnorhinus similis*. 15. Pupa, probably *E. similis*. Scale line = 1 mm.

distinct green scale pattern (Fig. 7) are the most conspicuous weevils on the coast, where they occur abundantly on lichen-covered rocks above the splash-zone. A smaller form with a less conspicuous scale pattern occurs at higher elevations. Unlike the other weevils, *B. randi* is seldom found on vegetation, and it appears to be a relatively specialized algae or lichen-feeder in both the adult and the larval stage. Larvae occur in algae, on which they apparently feed. Mature larvae wedge themselves tightly into crevices prior to pupation, but may also pupate in the soil.

Family Staphylinidae

The family Staphylinidae is a very large and successful one and because of the wide diversity in feeding and habitat preferences found in the family and because of the small size of a great number of the species, members are ideally suited for colonizing new areas. Species may be phytophagous, predatory, scavengers, flower-frequenters or associated with bird nests and mammal burrows.

Subfamily Aleocharinae

Members of the subfamily Aleocharinae are often predatory on various stages of small insects such as fly eggs and larvae in decomposing organic matter or dung.

Halmaeusa atriceps is the only species known from the Prince Edward Islands.

Genus *Halmaeusa* Kiesenwetter

Halmaeusa Kiesenwetter, 1877 : 161; Steel 1970 : 241
Antarctophytosus Enderlein 1909 : 377

Halmaeusa atriceps (C.O. Waterhouse), Figs 16-19.

Phytosus atriceps C.O.Waterhouse, 1875 : 54
Antarctophytosus atriceps bougainvillei Jeannel, 1940 : 111
Halmaeusa atriceps: Steel 1970 : 241

Diagnosis. Adults (Fig. 19) are small, 3,4-4,5 mm long, dark brown without distinct sculpture but with the body covered in fairly dense, long pale setae.

Larvae (Figs 16 & 17) are pale, with dorsal and ventral sclerites slightly darker, the dorsal one on segment eight being much darker than the rest; the body, particularly dorsally, is covered with widely-spaced, long setae.

The pupae (Fig. 18) are elongate, with the head placed between the legs; appendages are clearly differentiated.

Biology. *H. atriceps* is a ubiquitous species occurring in a wide range of habitats on the coastal plain, but is always associated with nitrogenous decomposing plant material on which they feed. Adults and larvae are active foragers with the same diet, and occur together throughout the year. High up on pebbled beaches they may be found colonizing decayed kelp detritus washed in amongst the pebbles. Further inland they are particularly abundant in albatross nests and in the underground nest mounds of burrowing birds, but they are generally common in the litter layer in biotically influenced vegetation. In the laboratory on Marion Island, *H. atriceps* successfully completed its life cycle in detritus taken from an albatross nest. Although they are primarily detritus feeders, they are also known to prey on nematodes and possibly the eggs and small larvae of earthworms and flies.

Family Hydraenidae

Members of this family are small and are always aquatic or semi-aquatic in all stages. Adults and larvae feed on algae. Species may inhabit running or stagnant water, occur in water seepages on rock faces, live in supralittoral rock pools or even in hypersaline water in salt pans.

The ability to survive in salt water and the preference for algae as adult and larval food render hydraenids ideal candidates for trans-oceanic dispersal and island colonization.

A single species, *Meropathus chuni*, occurs on the Prince Edward Islands.

Genus *Meropathus* Enderlein

Meropathus Enderlein, 1901 : 121

Meropathus chuni Enderlein, Figs 20-23.

Meropathus chuni Enderlein, 1901 : 122; Janssens 1967 : 4.
Meropathus randi Jeannel 1953 : 163

Diagnosis. Adults (Fig. 23) are 2,0-3,0 mm long and dark brown. The dorsal surface is characteristically sculptured, with distinct pale setae. The elytra have a distinct humeral carina, costal ridges and punctate intercostae. Sexual dimorphism occurs on the head – males have two distinct hornlike processes on the clypeus; they are absent in the female.

Larvae (Figs 20 & 21) are distinctly segmented with darkly sclerotized dorsal sclerites and broad, unsclerotized intersegmental membranes; ventral sclerites are lightly sclerotized; meso- and metathoracic spiracles are raised on eversible tubercles; a pair of two-segmented, setose urogomphi are situated on the apex of the ninth abdominal segment; the tenth segment is eversible.

The exarate pupa (Fig. 22) is very compact, with irregularly-spaced long setae; the head and appendages are placed below the thorax; the abdomen is distinctly segmented, with long, lateral setae.

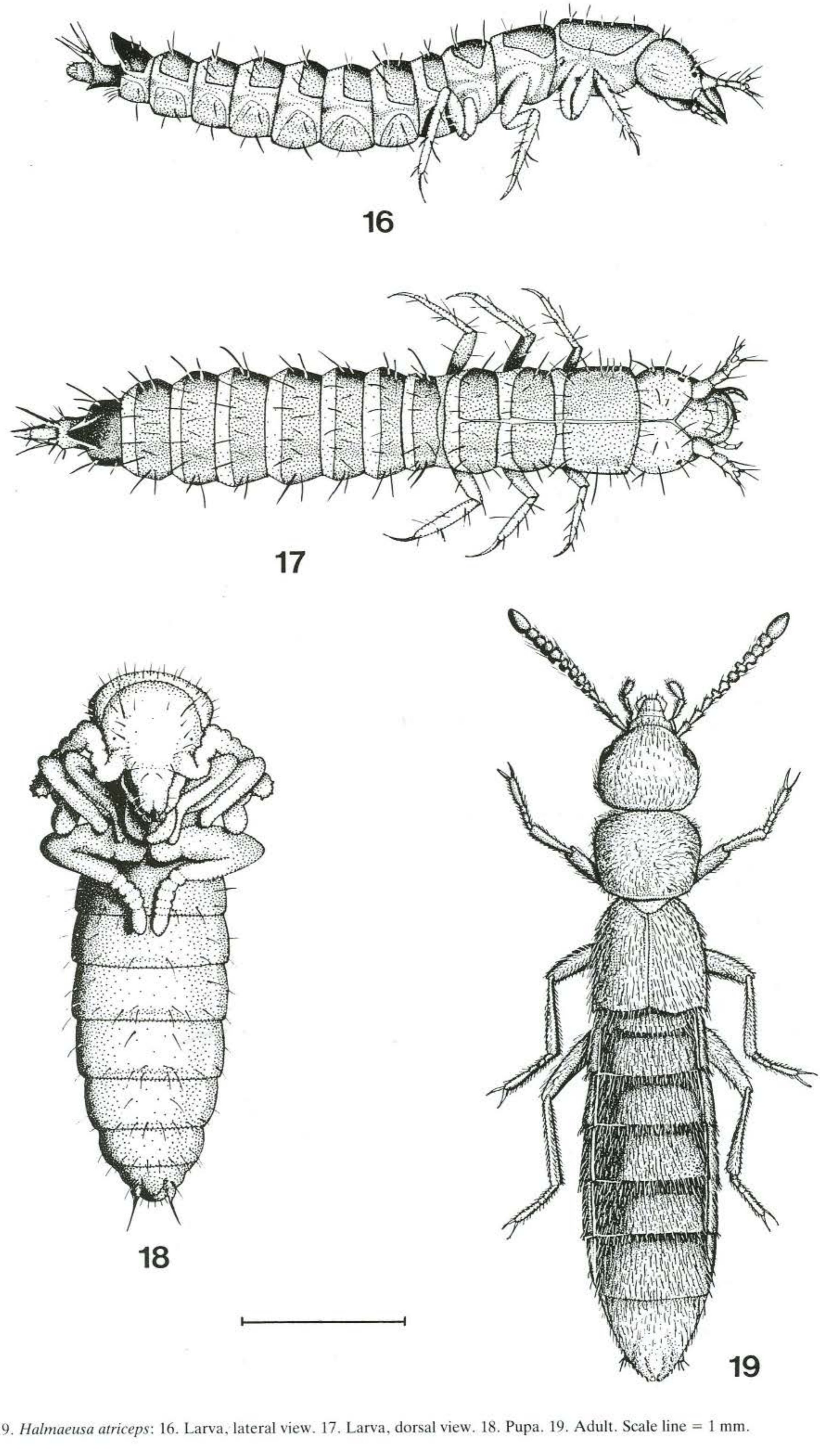
Biology. *M. chuni* is restricted to rockfaces on the coast, from the littoral to damp caves and overhangs up to 10 m inland. Adults and larvae occur together throughout the year, and are particularly abundant in the dense mats of filamentous algae which may completely cover protected rockfaces on the shoreline. Both adults and larvae feed on this and on other algae and diatoms. The adults are rather sedentary and strictly terrestrial, and are often rendered inconspicuous by a waxy layer on the pronotum and elytra. The active larvae may be semi-aquatic, tunnelling into an unidentified, gelatinous organic encrustation on water-seepage rockfaces and into watersaturated algal mats. The pupae occur in well-drained cells in the medium frequented by the larvae. Although classed as a marine beetle by Doyen (1976), *M. chuni* is at most eurihaline and only semi-aquatic in the larval stage.

Order Diptera

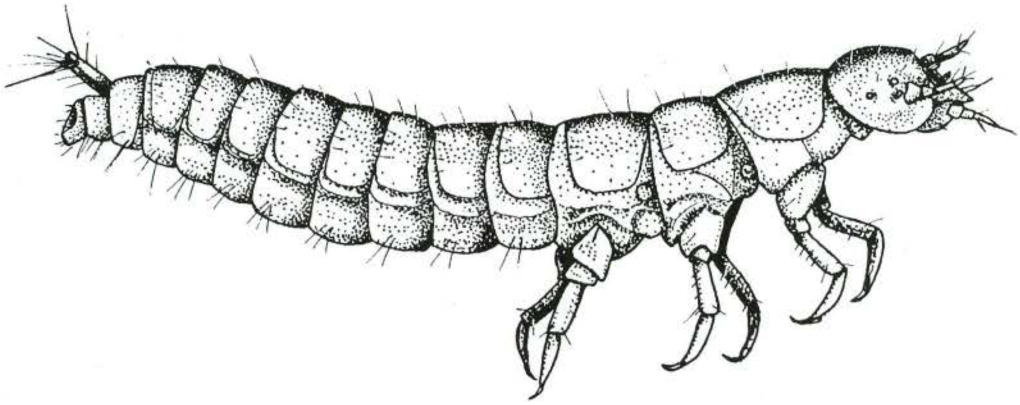
The nine species of flies recorded from the Prince Edward Islands represent two suborders and seven diverse families. Two of the species are cosmopolitan, while the rest occur on various subantarctic islands. A cosmopolitan species, *Telmatoscopus albipunctatus* Williston and an unidentified *Pericoma* species (both Psychodidae), recorded by Séguy (1971) from Marion Island have not been recorded since. These species have probably failed to become established.

Suborder Nematocera.

This primitive suborder is represented by three families and four species, one of the latter being cosmopolitan.



Figs 16-19. *Halmaeusa atriceps*: 16. Larva, lateral view. 17. Larva, dorsal view. 18. Pupa. 19. Adult. Scale line = 1 mm.



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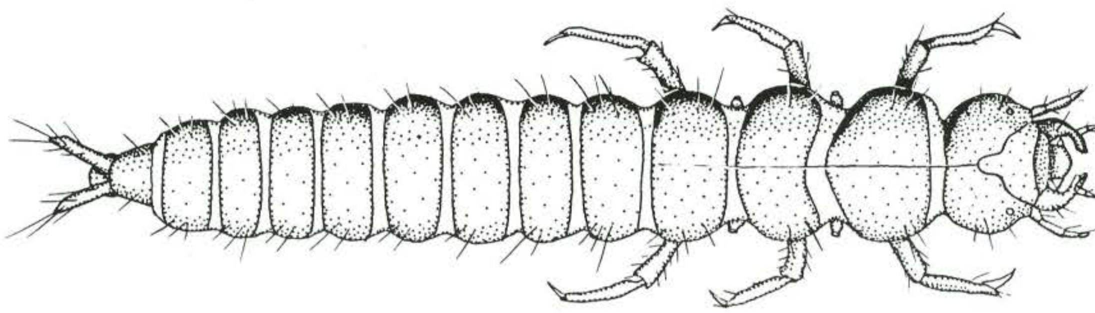

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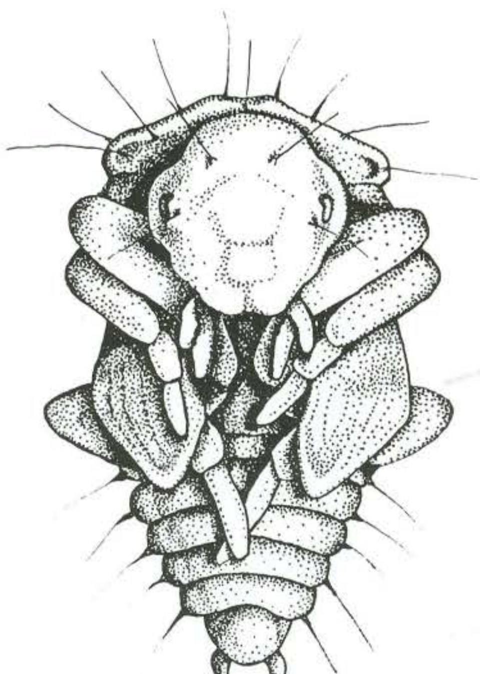

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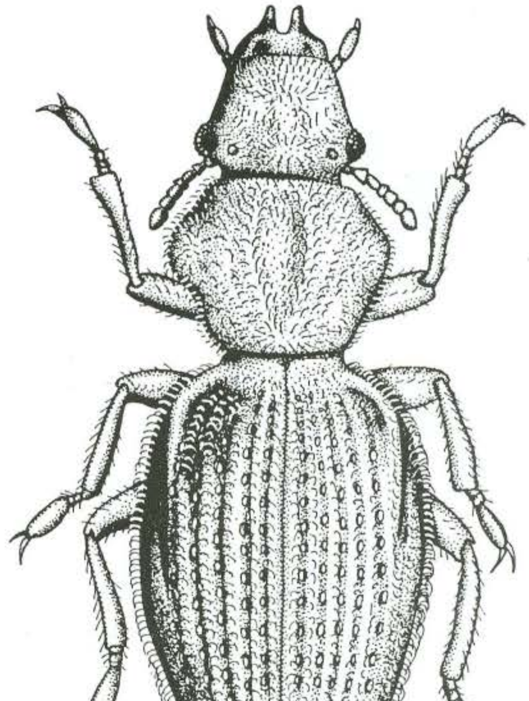

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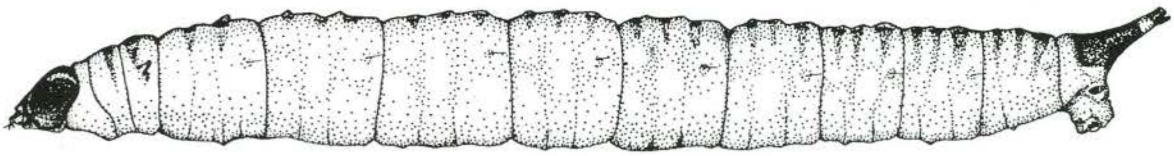
Figs 20-23. *Meropathus chuni*: 20. Larva, lateral view. 21. Larva, dorsal view. 22. Pupa. 23. Adult. Scale line = 1 mm.



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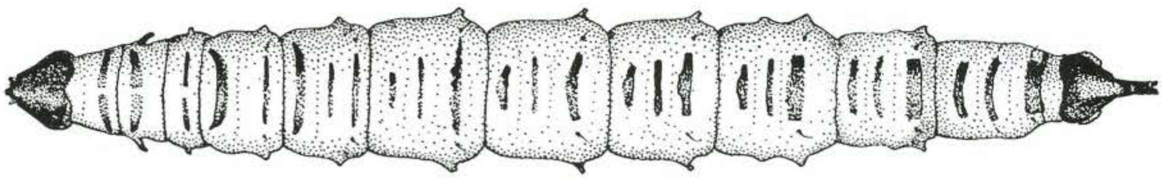

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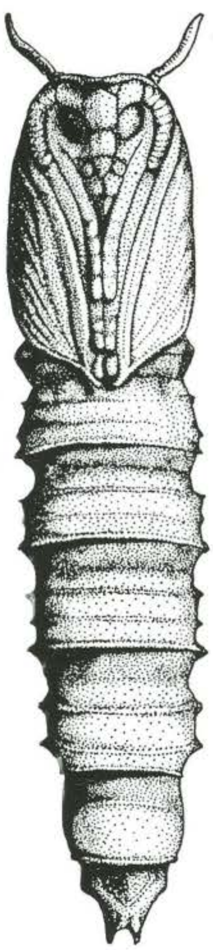

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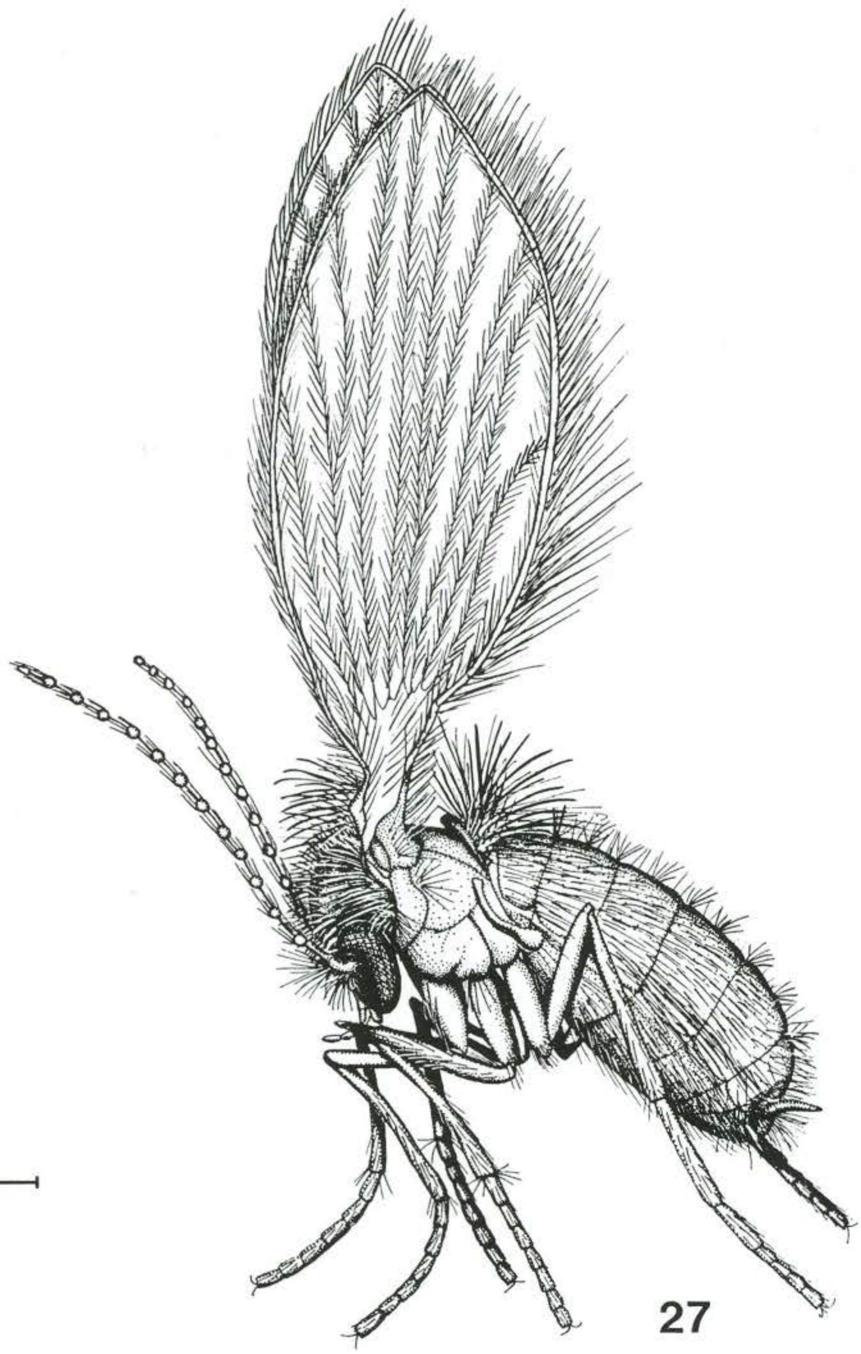

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Figs 24-27. *Psychoda parthenogenetica*: 24. Larva, lateral view. 25. Larva, dorsal view. 26. Pupa. 27. Adult. Scale line = 1 mm.

Members of the suborder are small, rather delicate flies which may become very abundant at certain times. The larvae have a distinct head capsule and may have terminal abdominal breathing tubes. Most are aquatic. The pupae are obtect with visible adhering sheaths of the legs and wings and they may have a pair of cephalic respiratory horns.

Family Psychodidae.

The family Psychodidae is represented on the Prince Edward Islands by a single species of the cosmopolitan genus *Psychoda*, thought to be *P. parthenogenetica*.

Genus *Psychoda* Latreille

Psychoda Latreille, 1796 : 152

Psychoda (?) *parthenogenetica* Tonnoir, Figs 24-27.

Psychoda severini parthenogenetica Tonnoir, 1940 : 53.
Psychoda parthenogenetica: Duckhouse 1962 : 428.

DIAGNOSIS. Adult females (Fig. 27) are small (wing-span about 5 mm). Males are unknown. The wings are broadly ovate, pointed and hairy and are usually held roofwise over the abdomen; this and the hairy body together give them a moth-like appearance, hence the common name of moth-flies.

Larvae (Figs 24 & 25) have a distinct, darkly sclerotized head capsule and breathing tube on the terminal abdominal segment. All body segments have distinct sclerotized dorsal sclerites.

Pupae (Fig. 26) are darkly sclerotized with distinct, adhering appendages and diagnostic cephalic respiratory horns.

BIOLOGY. *P. parthenogenetica* is primarily associated with rotting plant material on Marion Island. The larvae are semi-aquatic and sapropolyphagous. They reach maximum densities in highly decomposed kelp beyond the splash zone on the island's beaches, where they may occur together with *Paractora dreuxi* larvae. However, such infestations are sporadic and opportunistic, and usually result in the emergence of swarms of adult females which colonize other suitable habitats. The short-lived (1-2 weeks) and non-feeding adults are strong, active flyers. Eggs are laid in clusters on any wet, rapidly decomposing plant material, usually next to streams or wallows in biotically enriched habitats, on or near the coast. Generation turnover is rapid. Bred at 10 °C in decomposed kelp in the laboratory on Marion Island, egg, larval and pupal stages lasted 2-3, 21-30 and 8-12 days respectively. *Psychoda* was recorded on Prince Edward Island for the first time in April 1986.

Family Chironomidae.

Two species of small parthenogenetic midges occur on the Prince Edward Islands. One, *Limnophyes pusillus*, is cosmopolitan while the other, *Halirytus amphibius*, is restricted to the Kerguelen Province.

Adults of *L. pusillus* are common near water or seepage areas, but they are poor fliers and do not swarm. Their larvae are aquatic. *Halirytus amphibius* adults are brachypterous and are never found in large numbers; their larvae are semi-aquatic.

Genus *Limnophyes* Eaton

Limnophyes Eaton, 1875 : 60

Limnophyes pusillus Eaton, Figs 28-31.

Limnophyes pusillus Eaton, 1875 : 60; Séguy, 1971 : 345

DIAGNOSIS. Adult females (Fig. 31) are very small (wing-span about 3 mm), delicate midges with very sparse covering of hairs.

Larvae (Fig. 28) are long and thin and distinctly segmented with sclerotized mouth parts and "eye spots" but otherwise without darkly sclerotized sclerites. Thin anal tubes are present on the terminal abdominal segment.

Pupae (Fig. 30) are dark with distinct adhering appendages and black eyes. Anal macrosetae are borne on the terminal abdominal segment.

BIOLOGY. *L. pusillus* is a European species, but, paradoxically, it was first described by Eaton (1875) from specimens collected on Iles Kerguelen. It was probably introduced in the sub-Antarctic by man at a very early date (Jeannel 1953, Séguy 1971).

The biology and ecology of *L. pusillus* have been studied in detail on Kerguelen (Delettre 1978, Delettre & Tréhen 1977, Delettre & Cancela da Fonseca 1979). In a case study of selective advantages and pre-adaptations in a successfully established alien invertebrate on Marion Island, Crafford (in press) reviewed the biology of *L. pusillus* on Marion Island.

The parthenogenetic females lay their egg strings (Fig. 29) indiscriminately in any type of freshwater body, or even in saline rock pools on the coast. The larvae feed on detritus. The pupae are buoyant, and small "rafts" of pupae may form in running water. Adults can be locally abundant following eclosion, which may occur opportunistically in response to warm temperatures.

Genus *Halirytus* Eaton

Halirytus Eaton, 1875 : 60.

Halirytus amphibius Eaton, Figs 32-36.

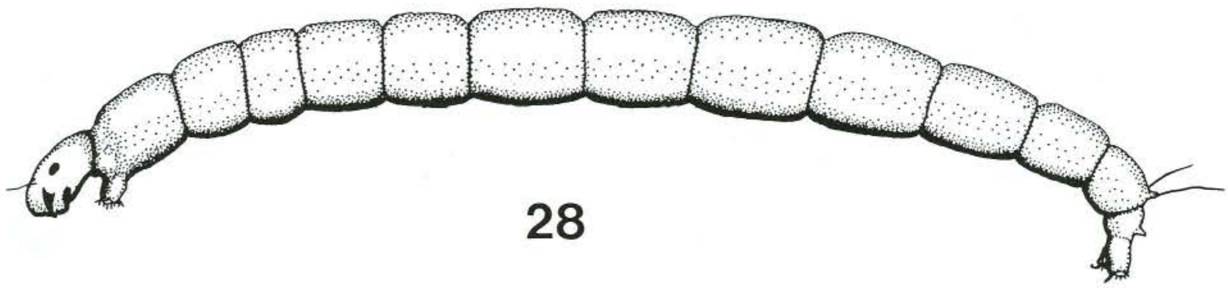
Halirytus amphibius Eaton, 1875 : 60.

DIAGNOSIS. Adult females (Fig. 36) are small (body length about 5 mm), and brachypterous.

Larvae (Fig. 32) are similar to those of *L. pusillus* but have a distinctly sclerotized head capsule and lack the terminal abdominal respiratory tubes.

Pupae (Figs 34 & 35) are very distinctive. They are dark, with distinct adhering appendages and characteristic terminal abdominal attachment disc. Small cephalic respiratory horns are also present.

BIOLOGY. *H. amphibius* was first recorded on the Prince Edward Islands in 1984. It is a semi-marine species restricted to the upper littoral- to lower supralittoral zone (*sensu* De Villiers 1976) on the islands' shores. The larvae are eurihaline, occurring amongst marine algae on rocks in the narrow intertidal zone, and also in mats of filamentous green algae on rocks in the lower supralittoral, which may become a temporary freshwater habitat after heavy rains. The larvae feed on green and red marine algae. The pupae attach themselves to the rockface in an upright position with their terminal "at-



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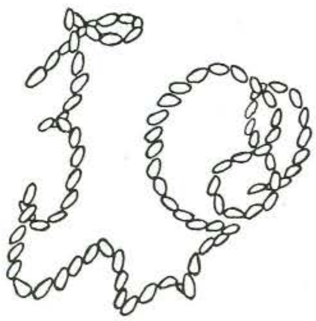

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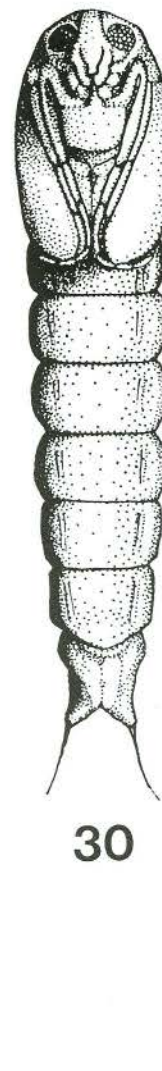

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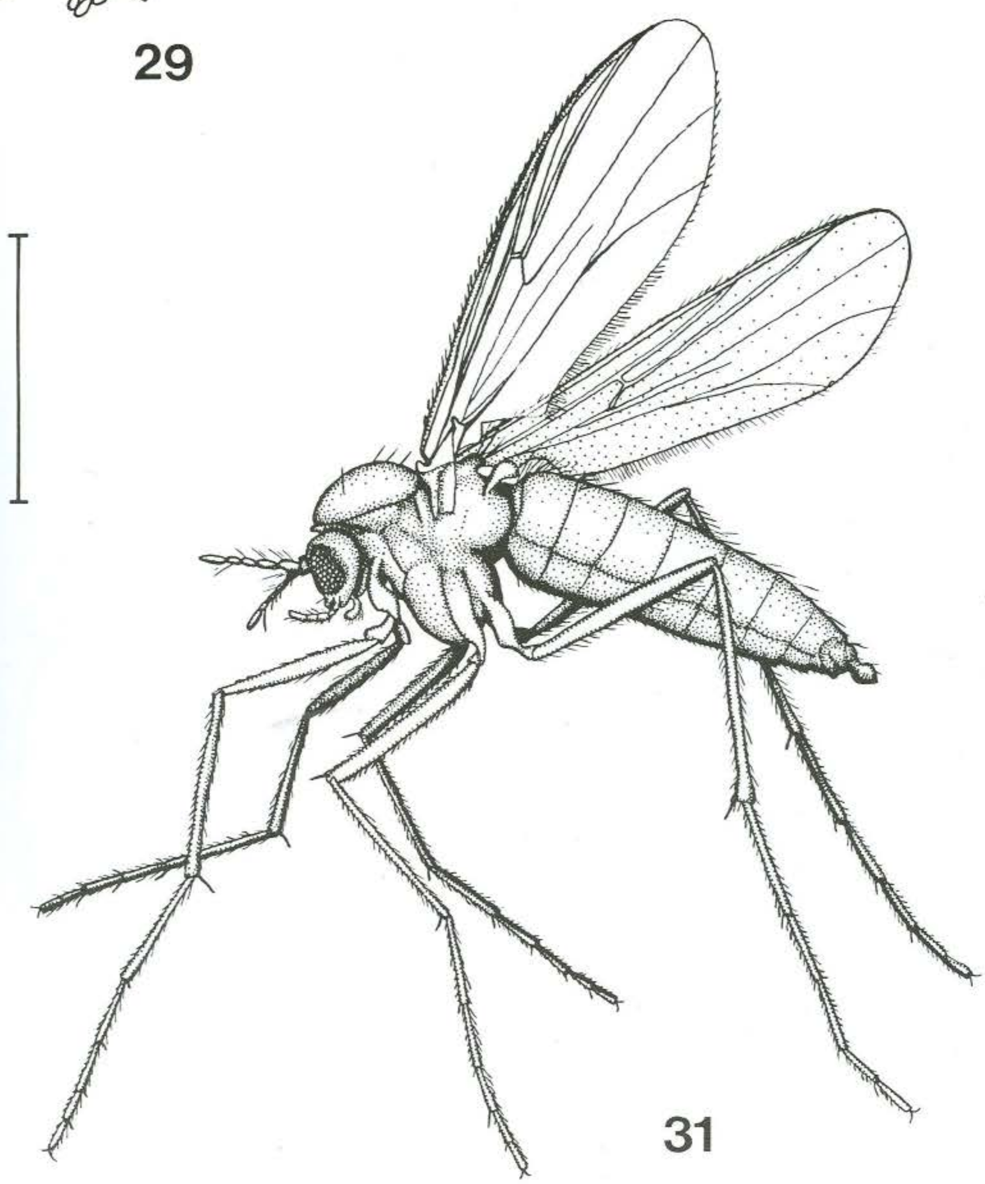

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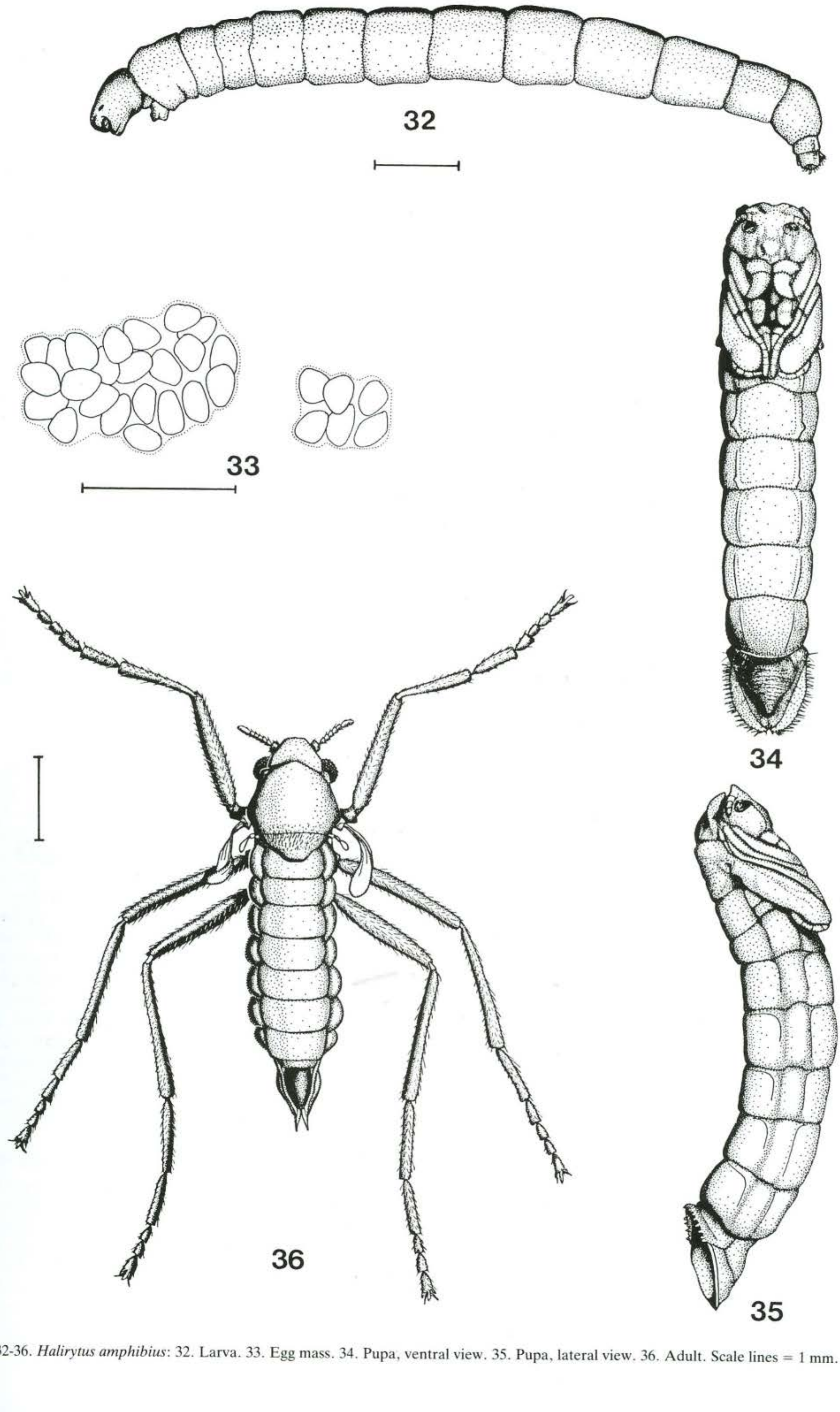
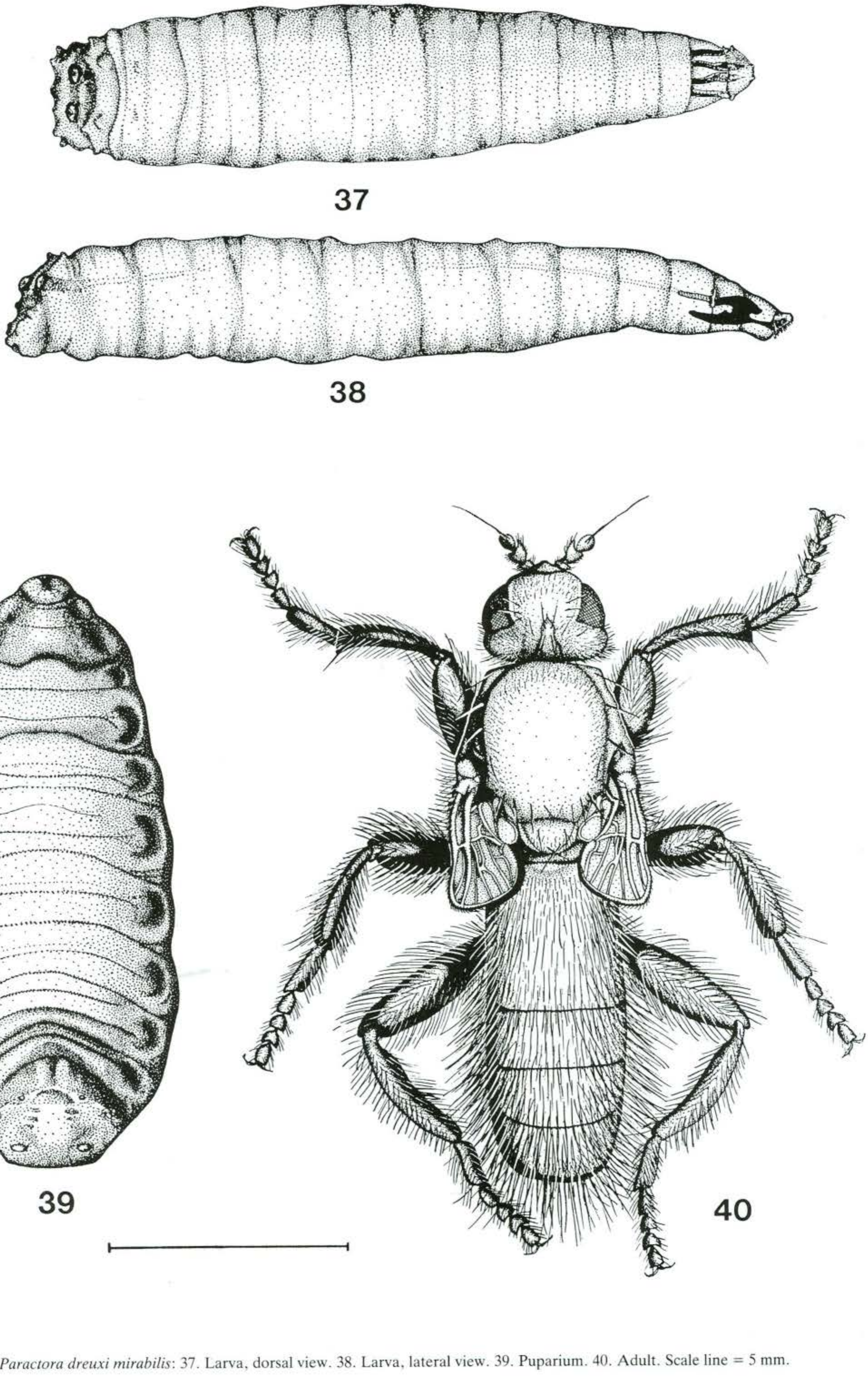
Figs 28-31. *Limnophyes pusillus*: 28. Larva. 29. String of eggs. 30. Pupa. 31. Adult. Scale line = 1 mm.



Figs 32-36. *Halirytus amphibius*: 32. Larva. 33. Egg mass. 34. Pupa, ventral view. 35. Pupa, lateral view. 36. Adult. Scale lines = 1 mm.



Figs 37-40. *Paractora dreuxi mirabilis*: 37. Larva, dorsal view. 38. Larva, lateral view. 39. Puparium. 40. Adult. Scale line = 5 mm.

tachment discs" (Figs 34 & 35). The spindly, mosquito-like adult females are short-lived, solitary, and never common. Frantic egg-laying activity commences shortly after eclosion. The bright yellow, oval eggs are laid in batches of 6-24 eggs each (Fig. 33) in the larval habitats, and are encased in a protective gelatinous layer.

Family Sciaridae.

This family is represented on the Prince Edward Islands by a single species of *Bradysia*, thought to be *B. auberti*. Larvae of the family in general are found in rotting vegetable matter where they appear to be gregarious. They are usually pale with a shiny black head capsule.

Genus *Bradysia* Winnertz

Bradysia Winnertz, 1867 : 180.

Bradysia (?) *auberti* Séguy, Fig. 45.

Sciara auberti Séguy, 1940 : 211

DIAGNOSIS. Adults are very small, with a wing-span of less than 4 mm but otherwise the species has very few accessible diagnostic characters.

No description of larvae or pupae is available.

BIOLOGY. *Bradysia* was first recorded on Marion Island in 1984, in only one locality and in low numbers.

Sciarids are commonly known as "fungus gnats". The Marion Island species was first found breeding in human excrement, and has since been found breeding in rotting *Pringlea antiscorbutica* leaves in swampy areas. It is now also known to be locally common, but not widely distributed on Marion Island.

Suborder Cyclorrhapha.

This suborder is represented on the Prince Edward Islands by four families and five species. One of the species is cosmopolitan whereas the others are all restricted to the sub-Antarctic islands.

Members of this suborder vary considerably in size but most are rather robust. The larvae are typical "maggots", without a distinct headcapsule but often with darkly sclerotized mouth hooks. They are mainly terrestrial and typically occur in decaying organic matter. The coarctate pupae are unique in that they lie within a puparium formed from the larval skin.

Family Helcomyzidae.

This family is represented by a single stranded-kelp-frequenting species, *Paractora dreuxi mirabilis*, on the Prince Edward Islands.

Genus *Paractora* Bigot.

Paractora Bigot, 1888 : 38

Paractora dreuxi mirabilis Séguy, Figs 37-40

Paractora dreuxi mirabilis Séguy, 1971 : 346

DIAGNOSIS. Adults (Fig. 40) of this, the largest dipteran species on the Prince Edward Islands (body length 9-13 mm) are black, brachypterous and hairy.

Larvae (Figs 37 & 38) are large and fleshy with darkly sclerotized mouth-hooks and prominent spiracles on the apex of the abdomen.

The puparium (Fig. 39) is dark, roundly pointed cephalad and broad caudad without any visible appendages. The terminal abdominal spiracles are visible as two paler areas.

BIOLOGY. *Paractora dreuxi mirabilis* larvae are the primary decomposers of stranded bull-kelp, *Durvillaea antarctica* (Crafford 1984). During heavy seas, masses of this prolific and highly productive intertidal phaeophyte (Haxen & Grindley 1985) wash up on the few and scattered pebble-beaches on the shores of the Prince Edward Islands. The short-lived (10-20 days) adults rapidly colonize, and lay their eggs on freshly stranded *D. antarctica* wrack. The eggs hatch after five days, by which time the tough, leathery epidermis of the fronds has decomposed sufficiently to allow burrowing by the young larvae. There are three larval instars; the first, second and third instars last 2-3, 5-7 and 40-50 days respectively. The larvae reach very high densities and biomass in diminishing piles of decomposing kelp. They are not very rapid feeders, and their major role in kelp decomposition, apart from direct consumption, appears to be the transfer and spreading of bacteria while feeding and burrowing in the kelp, and the subsequent enhancement of bacterial decay. Decayed kelp is washed in amongst the pebbles on beaches, which results in the build-up of a large reservoir of sub-surface kelp detritus (the "interstitial biotope" described by Tréhen & Vernon (1982) on pebbled beaches on Iles Crozet). In the absence of fresh wrack, *P. dreuxi mirabilis* larvae complete their development in this biotope and eventually pupate as deep as 50 cm beneath the pebbles. The duration of the pupal stage varies, and can last from 30 to 80 days. Eclosion appears to occur opportunistically in response to heavy seas and the beaching of fresh kelp; pharate adults may be able to detect osmotic changes in the environment.

Heavy seas occur most frequently in winter at the Prince Edward Islands. During summer, *P. dreuxi mirabilis* larvae colonize seal- and penguin carcasses on the islands' beaches, in the absence of wrack beds. They may also become, as was speculated for *P. dreuxi* on Iles Crozet (Tréhen & Vernon 1982), predators of oligochaetes and smaller fly larvae.

P. dreuxi mirabilis larvae are important prey for feral house mice (*Mus musculus* L.) on Marion Island's beaches (Gleeson 1981).

Family Tethinidae

This family is predominantly associated with stranded, decaying kelp in which the larvae feed. Two species occur on the Prince Edward Islands: *Listriomastax litorea*, which is fully-winged, and the apterous *Apetenus litoralis*.

Genus *Listriomastax* Enderlein

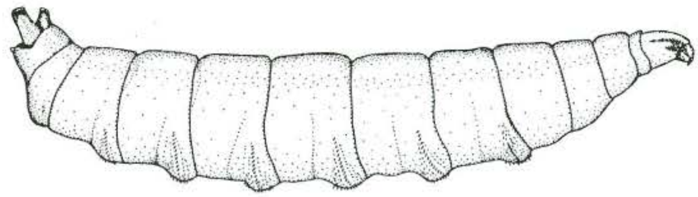
Listriomastax Enderlein, 1909 : 396; Séguy 1971 : 347.

Listriomastax litorea Enderlein, Figs 41-43.

Listriomastax litorea Enderlein, 1909 : 398; Séguy 1971 : 347.

DIAGNOSIS. Adults (Fig. 43) are quite small (wing-span about 6 mm) but fully winged. The abdominal sclerites are darkly sclerotized and contrast strongly with the white intersegmental membranes.

Larvae (Fig. 41) are fleshy with sclerotized mouth-hooks, terminal abdominal breathing tube and a field of stout spines dorsally on all the abdominal segments.



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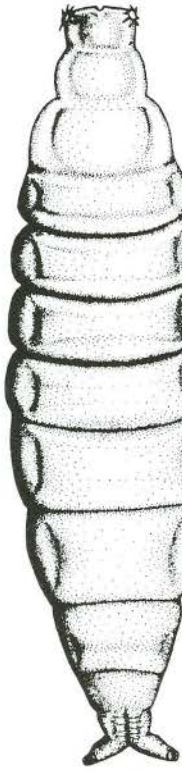

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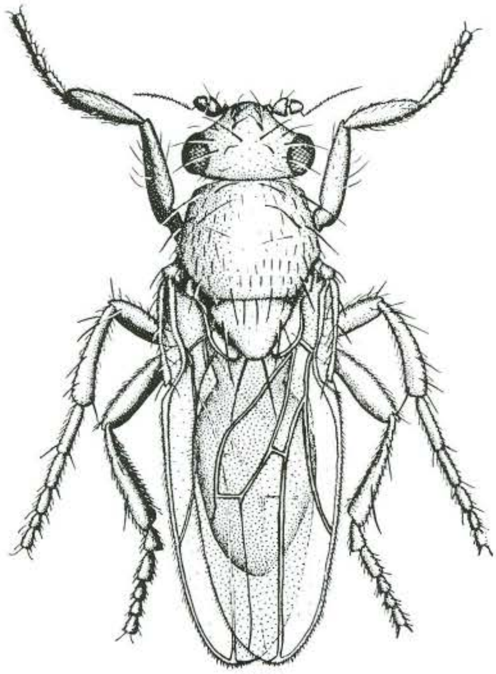

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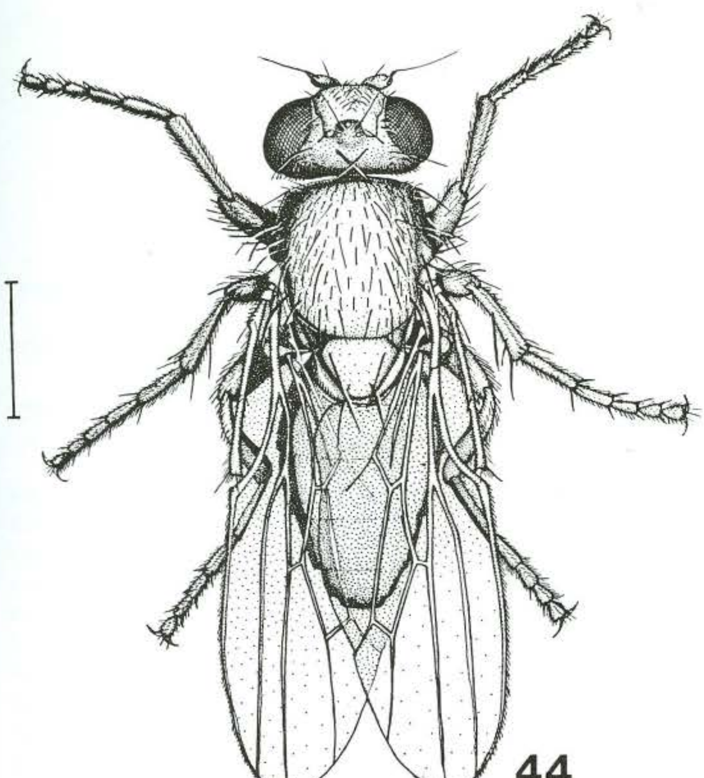

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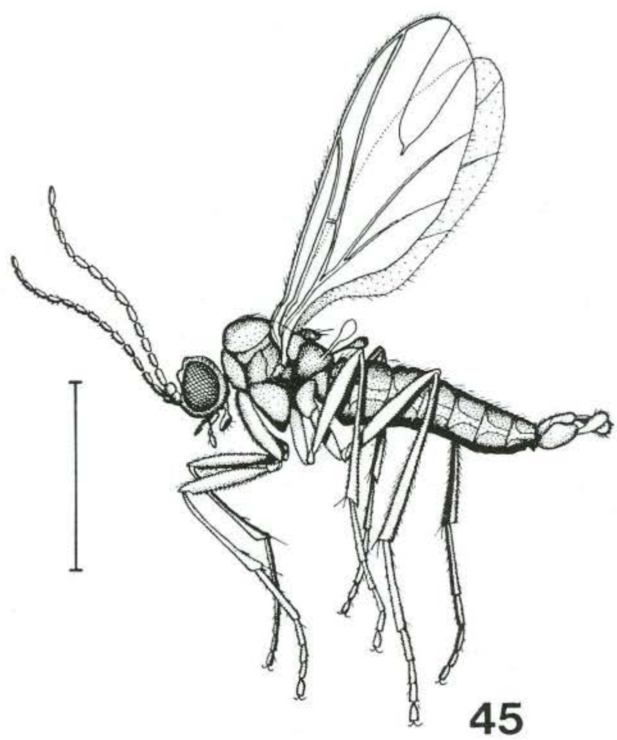

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Figs 41-45. Diptera: 41-43. *Listriomastax litorea*: 41. Larva, lateral view. 42. Puparium. 43. Adult. 44. *Fannia canicularis*, adult. 45. *Bradysia auberti*, adult. Scale lines = 1 mm.

The puparium (Fig. 42) is dark brown with forked terminal breathing tubes.

Biology. Apart from *Paractora dreuxi mirabilis*, *Listriomastax litorea* is the only other native dipteran involved in the decomposition of stranded *Durvillaea antarctica* on the Prince Edward Islands. *L. litorea* adults may occur in dense aggregations in stranded *D. antarctica* holdfasts and amongst fronds. Unlike *P. dreuxi*, however, *L. litorea* is also associated with the massive beds of small, mixed seaweeds which occasionally wash up on the islands' beaches after heavy storms. In these beds, *L. litorea* larvae reach maximum densities and are, with marine amphipods, the major invertebrate decomposers. Adults are strong fliers, forming large swarms over piles of rotting kelp on sunny days. Tréhen & Vernon (1982) found both brachypterous and fully winged *L. litorea* adults on Crozet, where, unlike on Marion, the species is associated primarily with penguin rookeries and moulting areas (Tréhen *et al.* 1985). Only fully winged adults have ever been found on Marion, and in the laboratory on Marion Island, *L. litorea* was reared successfully on decomposing *D. antarctica*.

Genus *Apetenus* Eaton

Apetenus Eaton, 1875 : 58

Apetenus litoralis Eaton, Figs 46-48.

Apetenus litoralis Eaton, 1875 : 58; Séguy 1971 : 347.

Diagnosis. Adults (Fig. 48) are small (body length 4-5 mm), black, brachypterous, and hairy. They superficially resemble the larger *Paractora dreuxi mirabilis* (see above) with which they co-exist in decomposing kelp.

Larvae (Figs 46&47) appear brown as a result of a distinctive, dense covering of minute hooks and spines. The mouth-hooks are darkly sclerotized and the terminal breathing tubes are coronate.

The puparium is typically globose with a coronate set of breathing tubes.

Biology. Although dense aggregates of *A. litoralis* adults may be found sheltering with *Paractora dreuxi* adults amongst fronds of stranded *Durvillaea antarctica*, the larvae are "strictly rock-dwelling" (Tréhen *et al.* 1985) in the supralittoral zone. The tough, leathery larvae feed on detritus and algae against rockfaces in the supralittoral zone, often coexisting with *Halirytus amphibius* larvae. The larvae are rather sedentary, wedging themselves into crevices where they eventually pupate. Single pairs of mating adults may occur against rockfaces in the same areas. In spite of the large temporary aggregations of adults in stranded kelp, eggs are laid in crevices and amongst algae filaments against rockfaces in the supralittoral zone, and larvae are never found in decomposing kelp.

Family Drosophilidae.

This family of largely fungivorous species is represented on the Prince Edward Islands by a single, probably introduced, unidentified species of *Scaptomyza*.

Genus *Scaptomyza* Hardy

Scaptomyza Hardy, 1849 : 361

Scaptomyza sp., Figs 50-53.

Diagnosis. Adults (Fig. 53) are fully-winged (wing-span about 7 mm) with distinctive reddish brown eyes.

Larvae (Figs 50 & 51) are white, fleshy with darkly sclerotized mouth-hooks. The terminal breathing tubes are in a coronate arrangement.

The puparium (Fig. 52) is pale brown with plumose cephalic horns and coronate terminal breathing tubes.

Biology. *Scaptomyza* may be a recent introduction on Marion Island. It was first recorded in 1984, but is well established over the whole island. It represents the first record so far of a drosophilid on the sub-Antarctic islands of the Indian Ocean (P. Vernon and E. Blanchard, *in litt.*); two brachypterous *Scaptomyza* species occur on Tristan da Cunha in the Atlantic (Holdgate 1965).

Adult flies are slow and sluggish and seldom fly. They are associated chiefly with dense stands of biotically influenced *Cotula plumosa* on the coast of Marion Island. Larvae tunnel into the slimy, decomposing stems and leaves of *C. plumosa* litter, and also occur in rotting leaves of *Pringlea antiscorbutica* near streams in biotically influenced areas. In the laboratory on Marion Island, *Scaptomyza* was successfully reared on rotting *C. plumosa* litter. However, it appears to be a sapropolyphagous species which utilizes a wide range of decaying organic matter. It has not yet been recorded on Prince Edward Island.

Family Fanniidae.

This family is represented on the Prince Edward Islands by the introduced cosmopolitan northern hemisphere lesser housefly, *Fannia canicularis*. It is typically synanthropic, occurring with man in his habitation.

Genus *Fannia* Robineau-Desvoidy

Fannia Robineau-Desvoidy, 1830 : 567.

Fannia canicularis (Linnaeus), Fig. 44.

Musca canicularis Linnaeus, 1761 : 454.
Fannia canicularis: Séguy 1971 : 348

Diagnosis. Adults are quite large (wing-span about 9 mm) typical houseflies.

Larvae are very characteristic. They are squat and very distinctly "spiny".

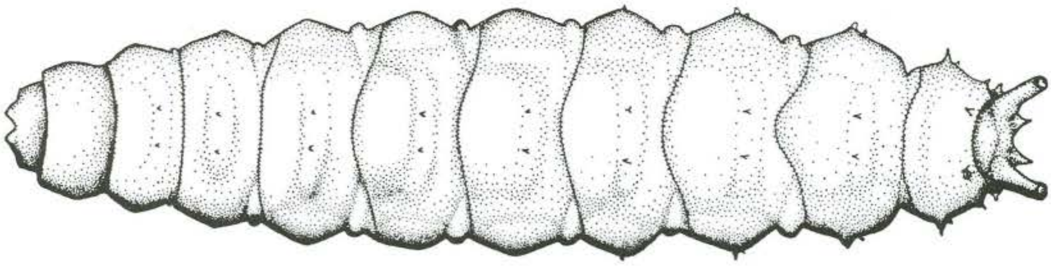
The puparium is pale yellow, typically without appendages but with slightly dark, tapered cephalic region.

Biology. *F. canicularis* usually breeds in nitrogenous wastes associated with human habitation. The larvae are well adapted to aquatic- or semi-aquatic life, and may even survive in urinals or urine-soaked ground. However, adult flies are not common inside the buildings of the base station on Marion Island, being associated chiefly with bird's nests and penguin rookeries further afield. Larvae and pupae have been found in the nests of gentoo penguins, *Pygoscelis papua*, and imperial cormorants, *Phalacrocorax atriceps*. Elsewhere, the larvae are known to cause secondary myiasis in vertebrates, including man.

Order Lepidoptera

Family Tineidae

The family Tineidae comprises many groups of biologically diverse taxa. Larvae vary in habitat and food preferences from tunnelling in fungi, feeding on leaves, bark and



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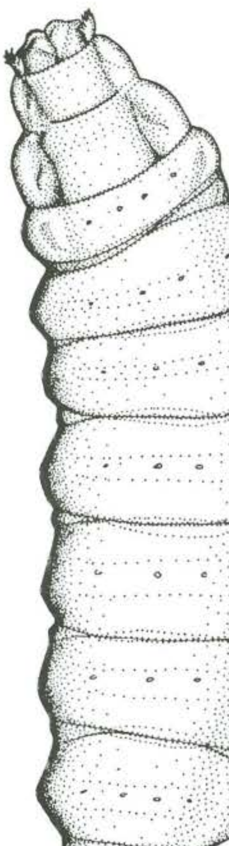

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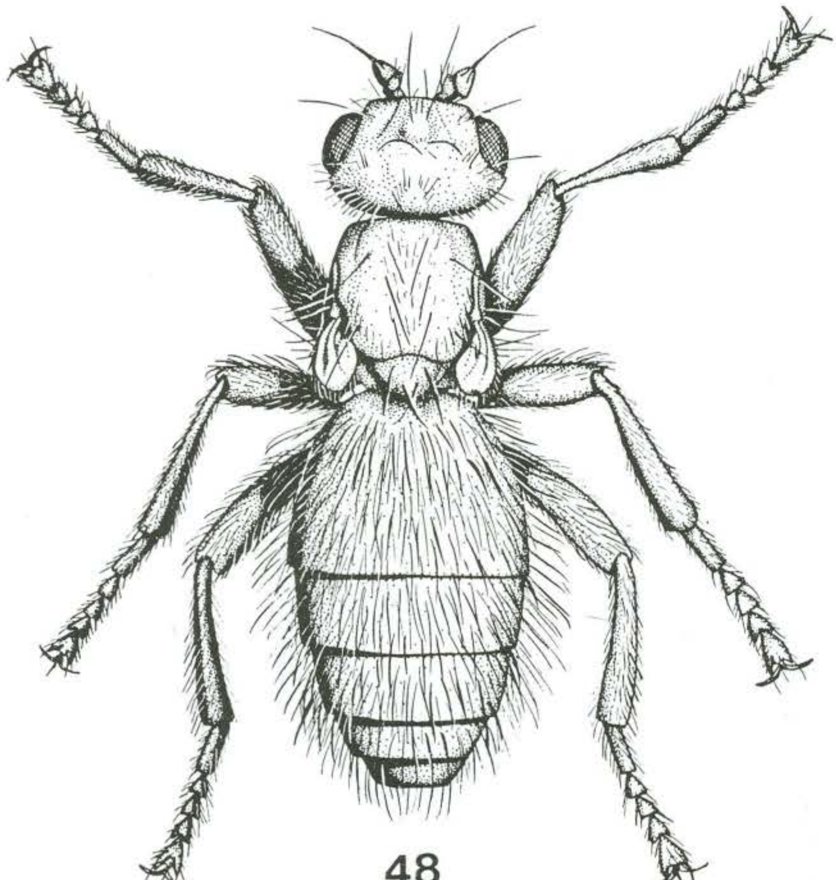

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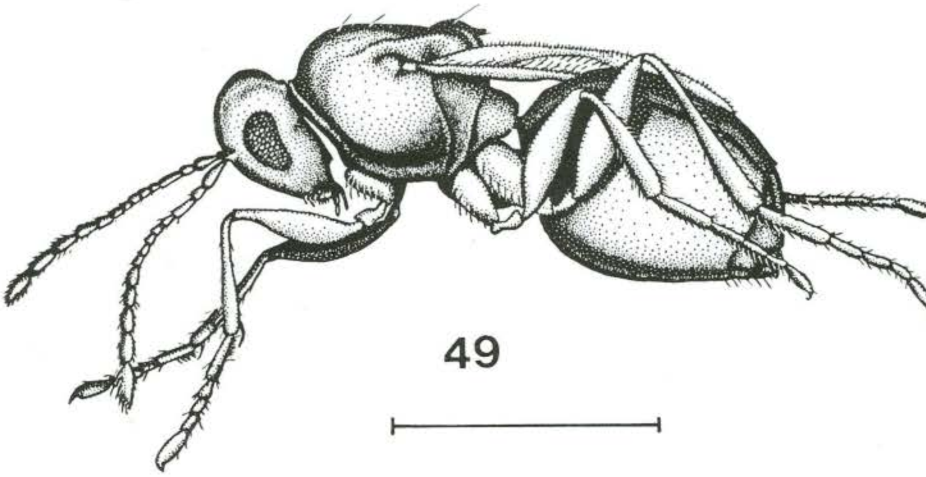

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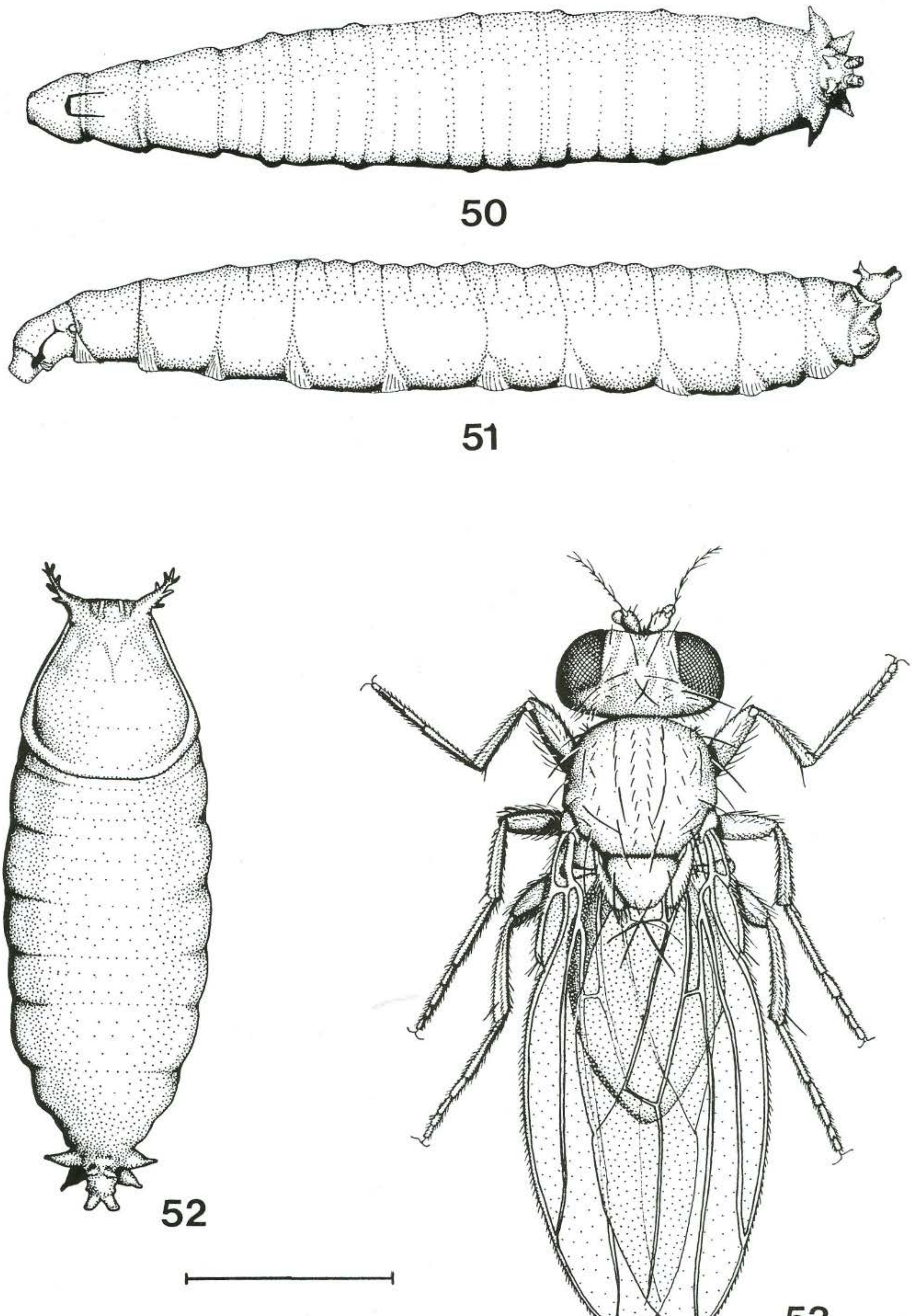
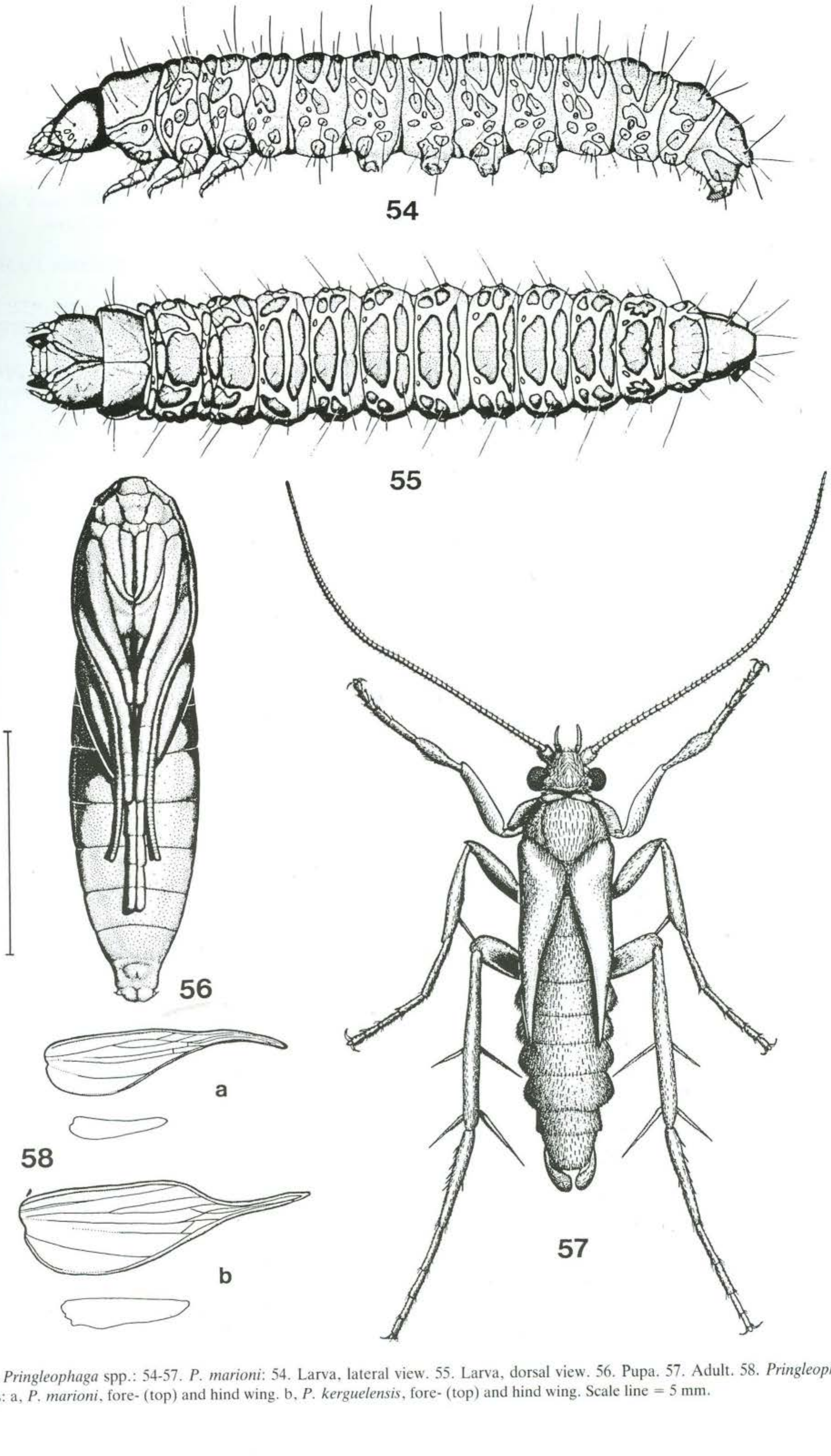
Figs 46-49. Diptera and Hymenoptera: 46-48. *Apetenus litoralis*: 46. Larva, dorsal view. 47. Larva, lateral view. 48. Adult. 49. *Kleidotoma icarus*, adult. Scale line = 1 mm.



Figs 50-53. *Scaptomyza* sp: 50. Larva, dorsal view. 51. Larva, lateral view. 52. Puparium. 53. Adult. Scale line = 1 mm.



Figs 54-58. *Pringleophaga* spp.: 54-57. *P. marioni*: 54. Larva, lateral view. 55. Larva, dorsal view. 56. Pupa. 57. Adult. 58. *Pringleophaga* spp., wings: a, *P. marioni*, fore- (top) and hind wing. b, *P. kerguelensis*, fore- (top) and hind wing. Scale line = 5 mm.

detritus to those which are case-bearers and feed on animal fibres.

Two species of the genus *Pringleophaga*, *P. marioni* and *P. kerguelensis*, occur on the Prince Edward Islands. *Pringleophaga marioni* occurs on Prince Edward and Marion Island whilst *P. kerguelensis* occurs only on Prince Edward.

The adults of both species have strongly reduced wings (Fig. 58) and well developed legs. The species are superficially very similar and differ only in size, wing venation and distribution.

Larvae of the two species are indistinguishable except for the size of the mature final-instar.

The pupae are typically lepidopteran and may be formed in a cocoon, or they may lie naked in a cell.

Genus *Pringleophaga* Enderlein

Pringleophaga Enderlein, 1905 : 119; Vári 1971 : 349.

Pringleophaga marioni Viette, Figs 54-57, 58a.

Pringleophaga marioni Viette, 1968 : 91; Vári 1971 : 351

DIAGNOSIS. Adult (Fig. 57) size is sex-linked, females being larger than males. Male forewing length varies from about 4,5-6,5 mm and that of the females from about 5,5-7,0. Wing venation is as in Fig. 58a.

Larvae (Figs 54 & 55) are heavily sclerotized, with isolated long setae evenly distributed over the body. Mature larvae grow to about 30 mm in length.

The pupae (Fig. 56) are as discussed above.

BIOLOGY. *P. marioni* adults are short-lived (10-14 days) and non-feeding. The life-cycle of the species is dominated and its ecological role fulfilled by the long-lived (>3 years) larvae. Attempts to determine the exact duration and number of instars of the larval stage have so far been unsuccessful. Similar-sized Lepidoptera in the Arctic (e.g. Lymantriidae: *Gynaephora* spp; Ryan & Hergert (1977)) may have a larval stage lasting up to ten years.

P. marioni larvae are ubiquitous litter-dwellers and are the major insect detritivores on Marion Island (Burger 1978; Table 4). However, they are unspecialized and indiscriminate feeders; their diet includes mosses, the foliage of several vascular plants, and even earthworms (French & Smith 1983). One of the few vascular plants excluded from the diet of *P. marioni* on the Prince Edward Islands is *Pringlea antiscorbutica* (the "Kerguelen cabbage") from which the generic name *Pringleophaga* is derived. Contrary to the reports by Paulian (1953), Viette (1968) and Vári (1971), there is no evidence to suggest that *P. marioni* is associated with *P. antiscorbutica* in any way.

Larvae of all ages, pupae, and adults, occur throughout the year on the Prince Edward Islands, although adult numbers tend to peak during late summer and early winter. The same trend has been described for *P. kerguelensis* and *P. crozetensis* at Iles Crozet (Chauvin & Vernon 1982).

Pupation occurs in the soil. Gonads develop and mature in the pupa, and adult females eclose gravid and with most eggs already ripe. Males are active walkers and are consequently more conspicuous than the sedentary females, which may explain the 5:1 sex ratio (Vári 1971) in most collections. However, no evidence of sexual attraction through pheromones has been found in these moths, and a preponderance of males, and high local densities of larvae, may act as compensatory mechanisms for the lack of dispersal ability and the absence of sexual attractants in this species.

Females use their extendable ovipositors to lay 150-200 relatively large eggs haphazardly on the surface of litter, or singly in the leaf axils of *Azorella selago* and *Poa cookii*.

P. marioni larvae are the preferred prey of feral house mice on Marion Island, and constituted up to 50 % of the stomach contents of trapped mice in a study carried out by Gleeson (1981). It has been calculated that mice may remove 14 % of the standing crop of *P. marioni* larvae annually (Crafford & Scholtz, in press). However, the cumulative effect of mouse predation may be much higher as a result of the low production rates of the larvae.

Pringleophaga kerguelensis Enderlein, Fig 58b.

Pringleophaga kerguelensis Enderlein, 1905 : 122; Vári 1971 : 351.

DIAGNOSIS. Adult size varies between the sexes. Male forewing length varies from about 6,5-7,5 mm and that of the females from 7,0 – 8,0 mm.

Larvae are identical to those of *P. marioni* (above) except that they grow larger, up to about 40 mm in length.

The pupa is identical to that of *P. marioni*.

BIOLOGY. The inaccessibility of Prince Edward Island has so far precluded detailed study of the biology of *P. kerguelensis*, but it appears to be essentially similar to that of *P. marioni*. Because of the similarity between the larvae of the two species, it has also been impossible to tell from the sampling programme carried out over the past three years on Prince Edward Island (Crafford & Scholtz, in press) whether the two species are ecologically separated in any way. Paulian (1953) considered *Pringlea antiscorbutica* to be the major host plant of *P. kerguelensis* on Iles Kerguelen, but, like *P. marioni*, *P. kerguelensis* is not known to feed on *P. antiscorbutica* at the Prince Edward Islands.

The absence of *P. kerguelensis* on Marion Island is curious (see Vári 1971). Zoogeographical factors may be responsible, but it has been hypothesized (Crafford & Scholtz, in press) that size-selective predation by mice on Marion Island could have caused the demise of an original *P. kerguelensis* population on the island. Block (1985) stressed the susceptibility of native sub-Antarctic species to disturbance. A long life cycle, low production rate and the cumulative effect of predation could have rendered *P. kerguelensis* particularly vulnerable.

Family Yponomeutidae.

This family is represented on the islands by two species – a Kerguelen Province native, *Embryonopsis halticella* and a cosmopolitan tramp species, *Plutella xylostella*. The former occurs on both islands whereas the latter is confined to Marion Island at present.

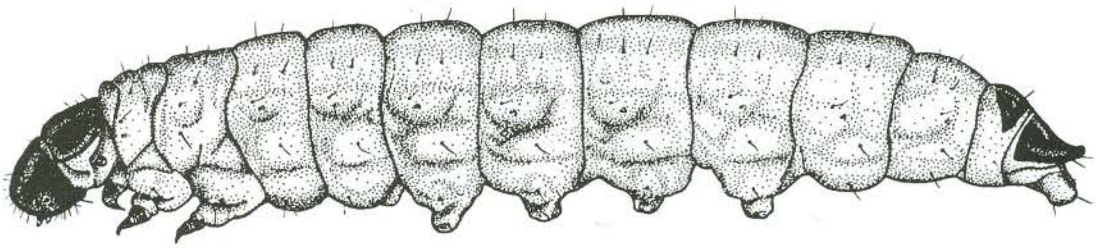
Genus *Embryonopsis* Eaton.

Embryonopsis Eaton, 1875 : 61; Vári 1971 : 353.

Embryonopsis halticella Eaton, Figs 59-61

Embryonopsis halticella Eaton,1875 : 61; Vári 1971 : 353.

DIAGNOSIS. Adults (Fig. 61) are small with reduced wings (forewing length 1,5-2,5 mm), and well developed legs. Specimens on Prince Edward are slightly larger than those on Marion Island, but otherwise identical.



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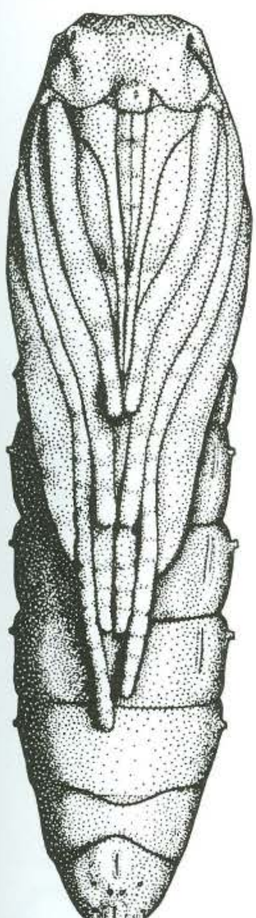

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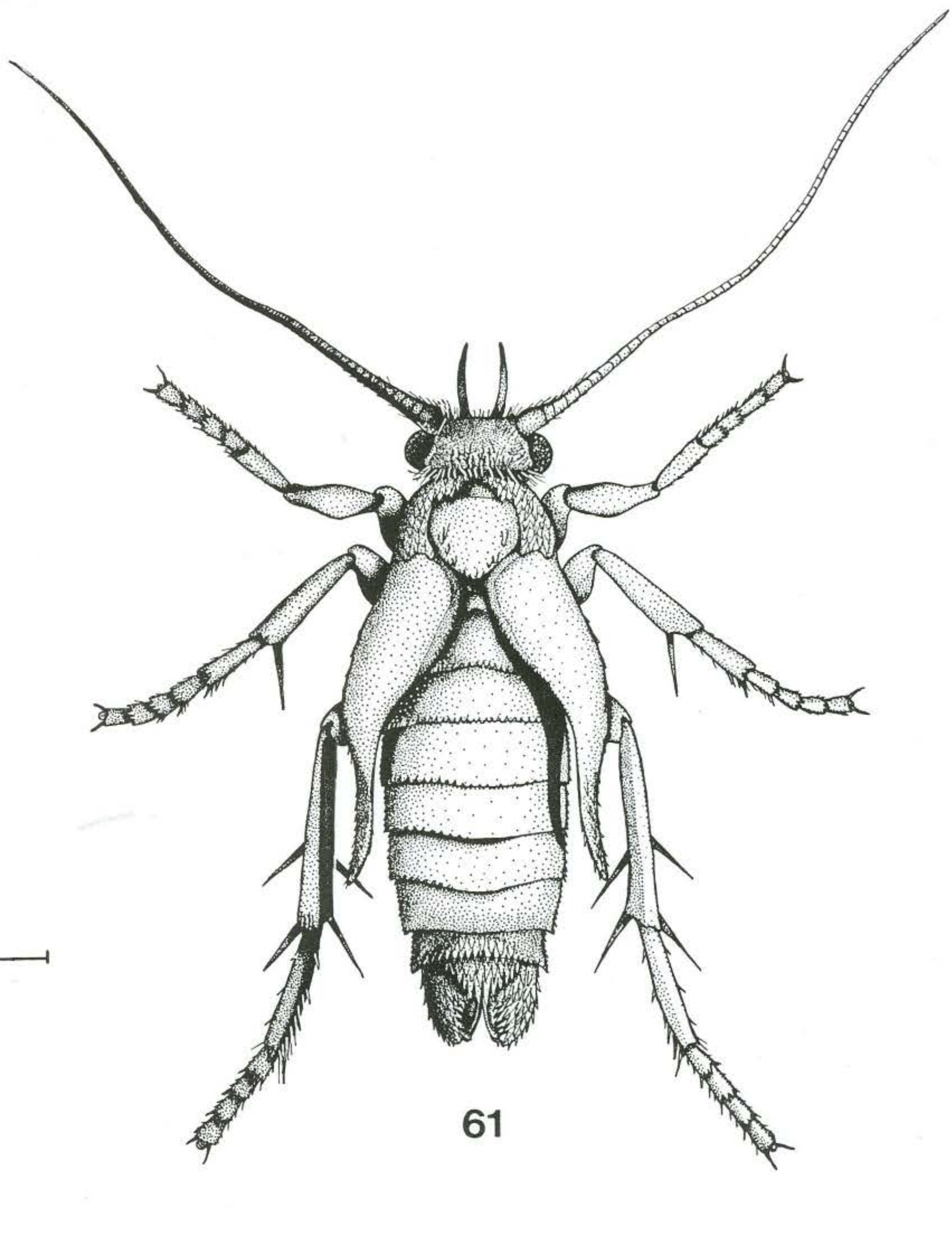

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Figs 59-61. *Embryonopsis halticella*: 59. Larva. 60. Pupa. 61. Adult. Scale line = 1 mm.

Live larvae (Fig. 59) are pale pink with two darker longitudinal dorsal stripes. Preserved larvae appear unpigmented except for the head capsule and dorsal sclerites on the prothoracic, penultimate and last abdominal segment.

Pupae (Fig. 60) are encased in a strong silk cocoon but are otherwise typically lepidopteran.

BIOLOGY. The geographical distribution of *E. halticella* is linked to that of its host, the tussock grass *Poa cookii*, which occurs on all the islands of the Kerguelen Province (Common 1970). The grass-boring larvae are strictly host-specific, and are the major herbivores on the Prince Edward Islands (Crafford & Scholtz in press).

Adults occur throughout the year on Marion Island, but, like on Iles Crozet and Iles Kerguelen, their numbers peak during spring and early summer (Chauvin & Vernon 1981). They are non-feeding. Females oviposit on the leaves and seeds in *P. cookii* tussocks, and also on *Azorella selago* "cushions" in mixed *P.cookii*/ *Azorella selago* communities.

The larvae are sedentary and cryptic, and spend the entire larval stage ensheathed in the inner fronds of *P. cookii* tillers. They feed both on the leaves and, in summer, on the inflorescences and seeds. *P. cookii* communities in biotically influenced areas support the highest biomass of larvae (up to 222 g/m, dry mass, in summer). The larvae are slow and erratic feeders, yet total annual consumption by larvae, of *P. cookii* foliage in coastal tussock grassland, may amount to 86 kg/ha (dry mass), or 2,5 % of annual *P. cookii* production (Crafford & Scholtz in press).

The exact duration of the life cycle of *E. halticella* is not known, but it probably does not exceed two years. There are five larval instars.

The pupal cocoons are attached to the outer, dead leaves of tussocks.

Genus *Plutella* Schrank

Plutella xylostella (L.), Figs 62-64.

DIAGNOSIS. Adults (Fig. 64) are fully-winged, small, with a forewing length of about 4,0-5,0 mm. They are grey with three pale triangular markings on the inner edge of each fore wing that form a diamond pattern when the wings are folded.

Live larvae (Fig. 62) are green but in preservative fade to pale yellow. They are only lightly sclerotized dorsally on the prothorax and last abdominal segment. The body is covered in widely-spaced long setae. Mature final-instar larvae are about 8,0 mm long.

Pupation occurs in a fine loose network of fine silk. The pupa (Fig. 63) is pale brown with darker longitudinal stripes.

BIOLOGY. *Plutella xylostella*, or the diamond-backed moth, is a cosmopolitan pest species. Its host plants include all the brassicas and a wide range of cultivated and other crucifers (Annecke & Moran 1982). It is an established species on most of the New Zealand sub-Antarctic islands (Dugdale 1971), but was recorded on Marion Island for the first time in April 1986. It attacks *Pringlea antiscorbutica* (Brassicaceae; Fig. 65) on Marion Island, but heavy local infestations appear to be confined at present to the southeastern part of the island. The larvae are voracious feeders on the leaves and growth tips of *P. antiscorbutica*, stunting and occasionally killing off individual plants. The damage is so noticeable that it can hardly be overlooked, yet it was observed only during the last year of our three-year study, suggesting a very recent introduction. The population appears to have built up rapidly and is still expanding, and may become a serious threat to the only indigenous brassica in this region of the sub-Antarctic. Some predation by mice on the larvae has been observed, but food may turn out to be the only limiting factor for *P. xylostella* on Marion Island.

ORDER HYMENOPTERA

This large order is represented by only a single species on the Prince Edward Islands. It is a tiny parasitic wasp, *Kleidotoma icarus*, which belongs to the family Eucoilidae.

Family Eucoilidae.

This family of parasitic wasps is almost exclusively associated with the puparia of cyclorrhaphous flies. The genus *Kleidotoma* is virtually cosmopolitan.

Genus *Kleidotoma* Westwood.

Kleidotoma Westwood, 1833 : 494.

Kleidotoma icarus (Quinlan), Fig. 49.

Aphiloptera icarus Quinlan, 1964 : 232.
Kleidotoma icarus: Quinlan 1967 : 5; Dreux 1971 : 338.

DIAGNOSIS. Adults are very small (total body length about 2 mm) black wasps with reduced wings.

Larvae and pupae are unknown.

BIOLOGY. The host of *K. icarus* has not yet been positively determined, and its biology thus remains poorly known. Presented with an array of larvae and pupae of the three native cyclorrhaphan flies in the laboratory, *K. icarus* females appeared to indiscriminately oviposit in all, but no parasitism resulted. However, adult *K. icarus* occur most abundantly in the same habitats occupied by the coelopid *Apetenus litoralis*, and the latter species is considered to be the most likely host.

ECOLOGY

The role of insects in the terrestrial ecosystem

The "simplicity" of sub-Antarctic terrestrial ecosystems, which could be inferred from the low diversity of species and habitats, is deceptive. Danks (1981) pointed out that there

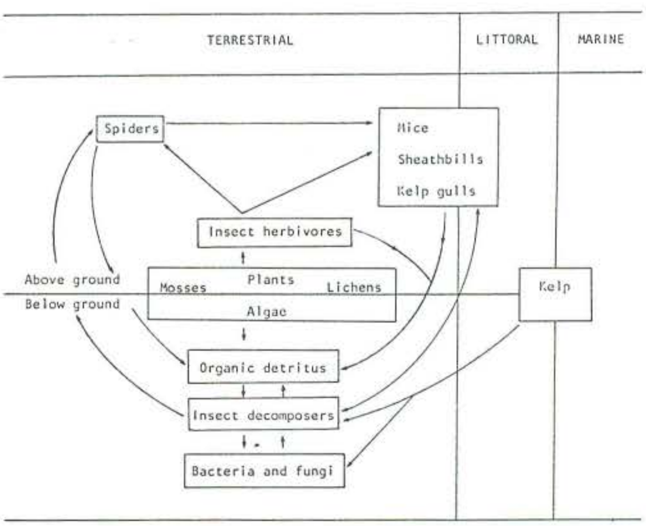
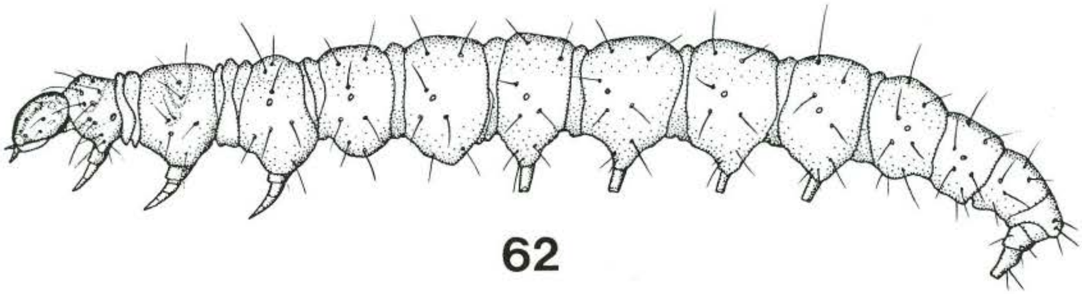
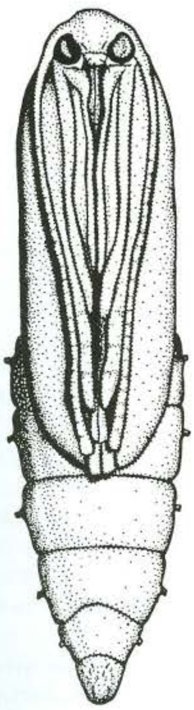


Fig. 66. Partial energy-pathway diagram showing inputs of insects in the Marion Island terrestrial ecosystem.



62



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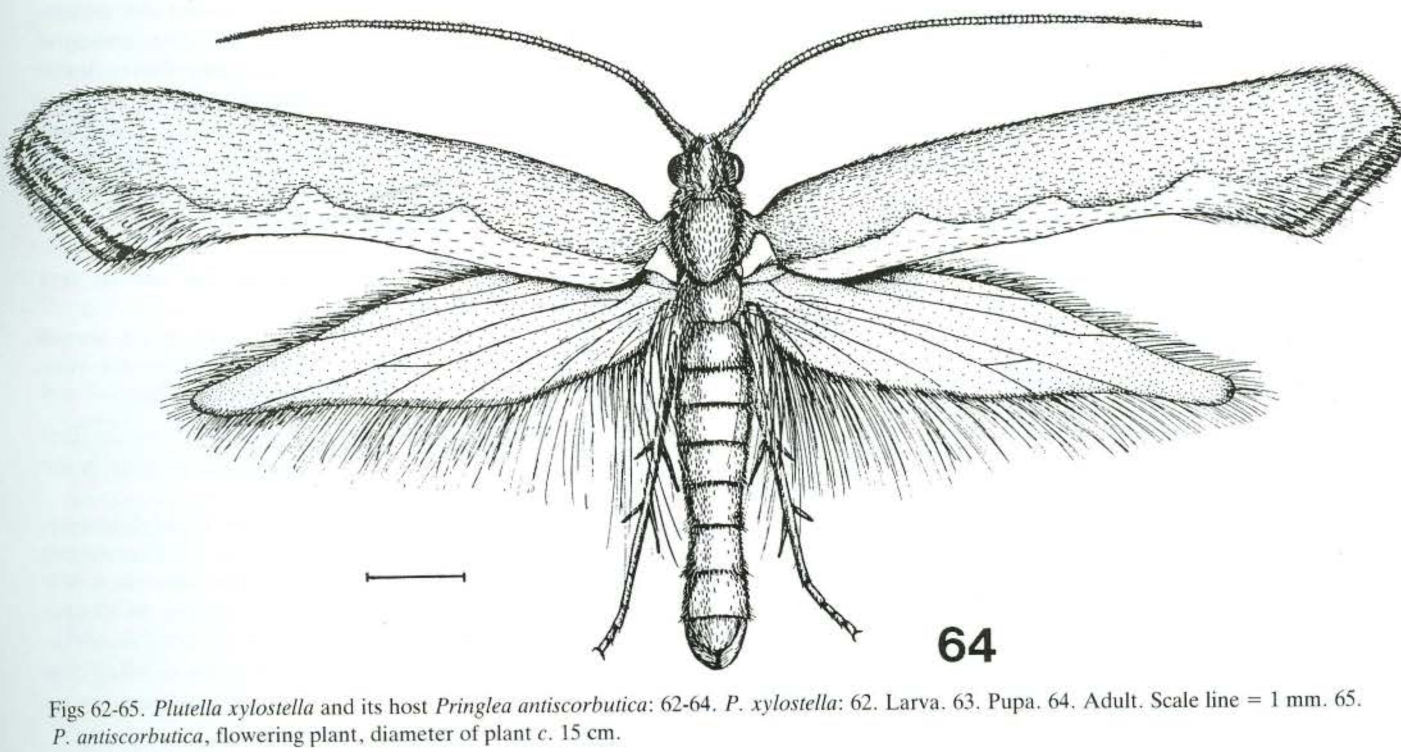

64

Figs 62-65. *Plutella xylostella* and its host *Pringlea antiscorbutica*: 62-64. *P. xylostella*: 62. Larva. 63. Pupa. 64. Adult. Scale line = 1 mm. 65. *P. antiscorbutica*, flowering plant, diameter of plant *c.* 15 cm.

are numerous cross-links of interactions within similar "simplified," low-diversity ecosystems in the Arctic. At Marion Island a single species may enter the system at different trophic levels and utilize the gamut of available habitats and resources (see Kuschel (1971) on physiological plasticity in native species, and Block (1984) and Crafford and Scholtz (in press) on the predominance of dietary generalists over specialists on the island). The result is an intricate cross-web of interactions across different trophic levels (Fig. 66). Smith (1977a) postulated that further important grazing chains should exist in the soil at the microscopic and sub-microscopic level. Figure 66 depicts the different inputs by insects in a partial energy-pathway diagram for the Marion Island terrestrial ecosystem.

Herbivores probably do not consume more than 3-5 % of above-ground net primary production at Marion Island. *Embryonopsis halticella* larvae annually eat 2,5 % of primary production in *Poa cookii* tussock grassland (Crafford & Scholtz in press). *Ectemnorhinus similis* adults consume 2-8 % of annual *Acaena magellanica* (Rosaceae) leaf production and 3-13 % of total production of the moss *Brachythecium rutabulum* (Smith 1977a). A few other insect species are facultative herbivores. Mice feed on the seeds of at least four plant species (Smith 1977b), but it is unlikely that they exploit the leaves of vascular plants to any degree.

With virtually all of plant productivity thus becoming dead organic matter (Smith 1977b) the emphasis of energy flow and nutrient circulation shifts to the below-ground, soil subsystem. At Marion Island the latter houses an essentially invertebrate community, which is dominated by the decomposer guild (*sensu* Root 1967) of saprovores and microbivores. Three macro-invertebrates dominate this guild: earthworms (*Microscolex kerguelarum*) and the larvae of *Pringleophaga marioni* and *Ectemnorhinus similis* account for *c.* 90 % of soil-invertebrate biomass in most vegetation types on Marion Island (Burger 1978).

Table 4

Mean annual biomass of the three dominant groups of invertebrate decomposers in 19 different vegetation types at Marion Island (after Burger 1978). Biomass given as g m^{-2} (dry mass).

Vegetation type	Earthworms	Lepidoptera larvae	Cuculionidae larvae
Mires			
Juncus/Agrostis	9,18	0,3	0,12
Drepanocladus/Agrostis	15,14	2,64	0,25
Blepharidophyllum/ Agrostis	0,1	0,14	0,44
Clasmatocolea/Agrostis	9,84	0,28	1,68
Jamesoniella/Agrostis	0,86	0,10	0,34
Mixed species mire	15,82	0,55	0,36
Degenerated bog	2,42	0,12	0,22
Uncinia/Ptychomnion	13,92	0,50	0,50
Slopes			
Blechnum fernbrake	11,9	0,66	0,51
Acaena herbfield	7,52	0,14	0,64
Agrostis bergiana	7,08	0,50	0,08
Saltspray			
Crassula moschata	3,06	0,68	0,40
Cotula/Crassula	8,54	0,64	0,24
Azorella-mixed species	8,00	0,94	0,46
Biotically influenced			
Callitriche	34,56	1,03	0,76
Poa cookii tussock	21,34	0,80	0,46
Clasmatocolea/ Marchantia mire	17,38	1,96	0,92
Cotula	43,14	0,97	1,10
Lowland fjaeldmark			
Azorella/Andraea	6,12	0,18	0,64
Weighted mean	14,63	0,64	0,54

Table 5

Numbers of free-living arthropods at Marion Island (sub-Antarctic), Devon Island (Canada; sub-Arctic) and Point Barrow (Alaska; Arctic), compared to invertebrate biomass at each site.

Site	No. of free-living arthropods	Invertebrate biomass (g m^{-2}dry)
Marion Island (47°S, 37°E)	67[a]	16,86[b]
Devon Island (75°N, 84°W)	167[c]	1,20[d]
Point Barrow (71°N, 156°W)	280[c]	3,80[e]

a This study.
b Macro-invertebrates only (Burger 1978).
c Ryan (1981).
d Macro- and meso-invertebrates (Ryan 1977).
e Macro- and meso-invertebrates (MacLean 1980).

Despite the low numbers of species, soil invertebrates attain higher densities and biomass at Marion Island than in Arctic and even temperate areas. Table 4 gives the mean annual biomass of the three dominant groups of invertebrate decomposers (earthworms, and the larvae of *P. marioni* and *E. similis*) in 19 vegetation types at Marion Island (after Burger 1978). Table 5 compares the numbers of free-living invertebrate species at Marion Island and two Arctic IBP Tundra sites with the biomass of soil macro- and mesofauna at the same sites.

Detritivores generally have low ecological efficiencies because of their inability to digest cellulose; they obtain their food energy largely from microflora (Odum 1971). At low temperatures, furthermore, both the digestion of cellulose and the action of microflora and internal symbionts are inhibited (Remmert 1980; see also Downes (1965) for detailed discussion on the slow-down of life processes at low temperatures). Block (1984) pointed out that an understanding of the interactions of soil-invertebrates and microbes is fundamental to any ecosystem analysis in the species-poor ecosystems of the Antarctic and sub-Antarctic. Through sheer biomass, though, soil invertebrates at Marion Island could be expected to process significant quantities of litter, and to speed up decomposition of the cellulose matrix mainly by:

a. Fragmenting litter, thus increasing the surface area available for microbial action.

b. Ingesting bacteria, thus stimulating bacterial growth and metabolic activity in the gut, and voiding into the environment faeces highly enriched by microbial activity.

P. marioni larvae are coprophagic; i.e. they ingest their frass after it has been enriched by microbial activity in the environment.

Lack of predation is one of the reasons for high invertebrate biomass at Marion Island. Sheathbills (*Chionis minor*) and kelp gulls (*Larus dominicanus*) annually consume *c.* 8 % of invertebrate standing crop, but, according to Burger (1978), they take mostly earthworms. Mice are the major insectivores and may consume up to 14 % of the standing crop of *P. marioni* larvae annually in areas of maximum mouse density (Crafford & Scholtz, in press).

Ecological strategies

The biotas of the sub-Antarctic islands are disharmonic and poorly integrated (e.g. Carlquist 1974), due mainly to their relative youth and strict isolation. Crafford (in press) pointed out that the Marion Island fauna is poorly integrated on the interspecific level (lack of competition and predation), and that many species also lack intraspecific interaction (expressed in wing reduction, loss of swarming, and parthenogenesis). With low biological selection pressure, adaptation is to the physical rather than to the biological environment. Block (1984, and in a series of earlier papers) has treated the adaptations of insects to cold in the maritime Antarctic, in detail. These adaptations include supercooling, cryoprotective substances and freezing tolerance. Similar adaptations have not been investigated for insects at the Prince Edward Islands, but are thought to exist.

Southwood (1977) first advanced the idea that ecological strategies and natural selection modes are constructed on a "habitat templet," and stressed that attributes of habitat can be quantified both in space and in time: habitats are spatially either favourable or adverse, and temporally either predictable or uncertain. The Marion Island macrohabitat is constantly and predictably severe (Fig. 2), which restricts biological integration but allows close adaptation to predictable factors of the physical environment (*inter alia* low temperature and high wind). The conservation of such adaptation has been termed adversity- or A-selection (Southwood 1977). Greenslade (1983) considers the high Arctic the exemplar of an environment dominated by A-selection. Block (1984) found several correlates of A-selection in Antarctic terrestrial habitats.

A-selected species combine attributes that are traditionally linked to r- and K-selected species (e.g. Odum 1971). Attributes of extreme A-selected species are summarized in Table 6 (after Greenslade 1983), and concur with, and explain, many characteristics of the Prince Edward Island insect fauna given in the preceding section on biology. In both ecological and evolutionary terms, r- and K-selection have been equated with, respectively, generalist (or pioneer) and specialist (or climax) species and ecosystems (Odum 1971, Holm 1985). With the notable exception of *E. halticella*, all primary consumers on Marion Island are consummate "specialists" in opportunism and variability. In a wider context, the ecosystem, though by its very nature a poorly integrated, low-diversity pioneer system, exhibits characteristics typical of a climax system (e.g. long, complex life cycles of organisms, weblike and predominantly detritus-based food chains, large total organic matter; Odum 1971).

Zoogeography

Knowledge of the zoogeography of the insects of the sub-Antarctic is incomplete. This is due mainly to fragmentary information on the fauna of many of its islands, and a lack of consistent taxonomic assessment of the insects. Danks' (1981) warning that zoogeographical speculation easily outstrips the evidence is pertinent.

Based on the assumption that the taxonomy of the sub-Antarctic insects is adequately studied (which we have reason to doubt), the fauna can be divided into five geographical groups:

1. Those native to Marion/Prince Edward
2. Those native to the Kerguelen Province
3. Those with South American/Falklands distribution
4. Those with Kerguelen/New Zealand distribution
5. Those with circum-Antarctic distribution

Group 1.

Six species are endemic to the Prince Edward Islands: *Ectemnorhinus similis*, *Antarctonesiotes elongatus*, *Bothrometopus randi* and *Mesembriorrhinus parvulus* (Curculionidae); *Pringleophaga marioni* (Lepidoptera) and *Paractora dreuxi mirabilis* (Diptera). Their close affinities lie within the Kerguelen Province.

There is no generic endemism on the Prince Edward Islands. The genera to which the six endemic species belong show no close affinity to any other known groups outside of the sub-Antarctic, and are probably of African or Antarctic Eocene origin.

Group 2.

This is the largest group with the same geographical affinities. The two genera of Lepidoptera, *Pringleophaga* (with two species, *P. marioni* and *P. kerguelensis*) and *Embryonopsis* (with one species, *E. halticella*), the weevil subfamily Ectemnorhininae (with eight genera), the psocid *Antarctopsocus jeanneli*, the fly *Listriomastax litorea* and the hydraenid beetle, *Meropathus chuni* are restricted to the Kerguelen Province.

None of these groups has a close affinity to any known continental group. They are probably of African/Antarctic Eocene origin with speciation having occurred on various islands subsequently.

Group 3.

The only taxon in this group is the dipteran genus *Parac-*

Table 6

Attributes of extreme r-, K- and A-selected species and populations (after Greenslade 1983).

Selection type	r	K	A
Population or species attributes:			
Capacity for dormancy	Variable	Low	Variable
Selection for migratory ability	High	Intermediate	Low
Geographical distribution	Wide	Restricted	Variable
Selection for parthenogenesis	Variable	Low	High
Length of life	Short	Intermediate	Long
Maturity	Early	Intermediate	Late
Rate of development	Rapid	Intermediate	Slow
Fecundity	High	Intermediate	Low
Rate of increase	High	Intermediate	Low
Key factors	Adult losses: mortality migration	Juvenile mortality: variation in fecundity	Mortality at all stages; variation in fecundity and rates of development

tora which is distributed from South America to Iles Crozet (excluding Iles Kerguelen).

This group, as well as the next two, are typically dispersed by the westerly trades. All are ecologically distributed in the intertidal zone and their geographical distribution is easily explained by drift.

Group 4.

The dipteran genera *Apetenus* and *Halirytus* are distributed from the Kerguelen Province to Macquarie Island and since the flies are intertidal, their distribution may be explained as above.

Group 5.

Only the staphylinid genus *Halmaeusa* has a circum-Antarctic distribution which can be explained by drift induced by the westerlies. It is also ecologically distributed from the intertidal zone, inland.

Sub-Antarctic zoogeography was treated in detail by Jeannel (1965) and Gressitt (1970); see also Darlington (1965) and Brundin (1965). However, subsequent geological evidence has rendered some of their primary hypotheses obsolete. Jeannel (1965) claimed, *inter alia*, that a Tertiary connection existed between the Crozet archipelago and South Africa. This formed part of his "Sudamadie" (a biogeographical area which included South Africa, Madagascar, and the Mascarene Islands). Gressitt (1970) mainly reviewed the theories of Jeannel, Darlington and Brundin. A pivotal postulate of all these authors was that Kerguelen, and possibly Crozet, were of continental origin (see also as recently as Brown & Gibson (1983)). However, the Kerguelen archipelago is undoubtedly of entirely volcanic origin, albeit of such age (*c*. 45 million years) that the oldest lava flows resemble continental granite (Dosso & Murthy 1980, Nougier 1972)

The isolated positions of the sub-Antarctic islands, the inclemency of their climates, and the diverse affinities of their insect faunas, led Gressitt (1970) to conclude that the models of MacArthur & Wilson (1963, MacArthur 1967), and the hypotheses of Darlington (1960, 1965), were "not applicable" (see also Tréhen & Vernon 1982, and Carlquist 1974). The Prince Edward Islands, at least, seem to form a special case which does not fit in well with classic biogeographical theory. The fact that species recently introduced by man have successfully colonized the islands indicates that natural immigration hardly occurs; conversely, the autochthonous fauna has remained small and, we submit, virtually unchanged and stable. There is also no empirical relation between species and island surface area, as shown by Diamond & May (1981) for several temperate and tropical islands.

Table 7 compares the number of species, island surface area, percentage endemism, and the occurrence of flightlessnesss (through either brachyptery or aptery) on the islands of the Kerguelen Province. For the distribution of the Prince Edward Islands' species, and the number of species shared with other islands of the Kerguelen Province, see Table 3.

We limit speculation about the zoogeography of the Prince Edward Islands to discussion of three salient points which are consistent with available fact, and which could explain the present geographical distribution of the sub-Antarctic insect fauna:

1. The Kerguelen archipelago, being by far the oldest (Nougier 1972), was the major source of colonization for all the islands within the Kerguelen Province; hence the close affinities between their faunas and the high degree of endemism within the Province.

Van Zinderen Bakker (1971) pointed out that, at the Kerguelen archipelago, a very old endemic fauna might well have survived Pleistocene glaciations intact because of the abundance of small islets, many of which probably served as ice-free refugia.

The Prince Edward Islands' insect fauna is an impoverished version of that of Kerguelen; so is that of Heard Island and, to a lesser extent, that of Crozet. This implies, in the case of the Prince Edward Islands, colonization against prevailing winds and drift. Van Zinderen Bakker (1971) found no evidence of a change in wind patterns over the past 16 000 years, so that the possibility of wind dispersal, at least in post-Pleistocene times, is slight. However, since all of the groups of obviously "mainland" origin dispersed westwards as opposed to post-Pleistocene dispersal, it is quite likely that major changes in wind patterns did occur in the Pleistocene. Transportation by birds is a possibilty; partly terrestrial oceanic birds (chiefly wandering albatrosses, *Diomedea exulans*; giant petrels, *Macronectes giganteus* and *M. halli*; and skuas, *Catharacta antarctica*) are known to move freely, swiftly and fairly regularly between the islands (e.g. Brown & Oatley 1982).

2. Affinities with South America, the Falklands and South Georgia is explained by aerial dispersal and westerly drift, probably in post-Pleistocene times.

3. Autochthonous species could be pre-Pleistocene relicts which survived in coastal refugia.

It is generally postulated (e.g. Van Zinderen Bakker 1978) that the biota of the Prince Edward Islands is largely of post-Pleistocene origin. The Antarctic convergence was to the north of the Prince Edward Islands 20 000 years ago; as a result average air temperatures were at least 3 °C lower than now (Schulze 1971). Marion Island was extensively glaciated in the Pleistocene (Verwoerd 1971), but it is possible

Table 7.

A comparison between island surface area, number of free-living insects species, percentage endemism, and the percentage occurrence of flightlessness (amongst native species belonging to normally flying groups) on the major islands of the Kerguelen Province (partly after Gressitt 1970).

Islands	Surface area (km^2)	Number of species			% endemism	% flightless
		Natives	Endemics	Naturalized		
Iles Kerguelen	7000	22	6	12	27	95
Heard Island	375	9	1	0	11	100
Marion Island	300	16	4	10	25	94
Iles Crozet*	150	46	31	5	67	89

*Ile Possession only

that at least some elements of the fauna survived. Kuschel (1971) postulated that this was the case with the Curculionidae. The current predominance of bryophytes and lichens in the diets of some species, coupled to their morphological and physiological plasticity (Kuschel 1971), bears out the theory.

No evidence of Pleistocene glaciation has been found on Prince Edward Island; it is smaller and has more vertical relief and lower elevation than Marion. *Pringleophaga kerguelensis*, which occurs only on Prince Edward, could have arrived during glaciation, and, unable to gain a foothold on Marion, survived on Prince Edward. *P. marioni*, which occurs on both islands, appears to be as well suited as the weevils to have survived glaciation.

Rates and modes of evolution in the sub-Antarctic

The long life cycles of the native holometabolous insects on the Prince Edward Islands reduce the opportunity for genetic change. Moreover, with long-lived individuals of different generations and many age groups co-existing at any given time, selection will not act from generation to generation but through a running mean of generations (Downes 1965). Genetic changes can therefore be expected to be slow and buffered.

Carson (1959) showed that, if selection favours the heterozygote, thus preserving both alleles, the organism will be less specialized and physiologically more versatile. Such a genotype can be "fixed" in the species by inversions, or, more completely, by parthenogenesis. Versatile, generalist species arise in this way; at the same time the opportunity for speciation is restricted (Downes 1965). Such a genetic system has been demonstrated for *Belgica antarctica* (Chironomidae), the most southerly holometabolous insect known: it is heterozygous, with several chromosomal inversions, and parthenogenetic (Martin 1962). Many phenomena observed in sub-Antarctic insects may be explained by such a genetic system. No cytogenetic studies have yet been undertaken on sub-Antarctic insects.

It must be stressed that the modes of natural selection that operate on, and the evolutional and ecological strategies followed by the insects of the Prince Edward Islands, are complicated trade-offs between the environment and the attributes of the different species. Accordingly, no single set of rules applies: the insects may have diverse strategies for coping with the environment, although the environmental side of the interaction is constant.

Evolution of flightlessness

The most striking feature of the native insect fauna of the Prince Edward Islands is the high incidence of flightlessness. Of the 16 native species, all of which belong to winged orders, 15 are grounded either through brachyptery (Lepidoptera, Diptera, Hymenoptera) or aptery (Coleoptera). Details of wing reduction in certain sub-Antarctic species have been discussed by Séguy (1965), Jeannel (1947, 1965), Hennig (1935) and Brauns (1951).

Brinck (1948) and Vári (1971) believed the pressure of constant high winds to be the major factor in the evolution of flightless insects on the islands of Tristan da Cunha and Marion, respectively. Darlington (1943) disagreed, and viewed flightlessness as an inevitable trend wherever flight is not of high selective value in order to maintain large, sparse, unstable populations over large, unstable areas. In small stable areas, where populations are dense and stable, flightless insects may in fact have an advantage over winged forms: Jackson (1928) regarded flightless insects as having inherent superiority due to "simplicity and vitality," and Brinck (1948) conceded that, on oceanic islands, "a flightless type may even oust the normal." Downes (1964) has pointed out that wing reduction and flightlessness represent "economy of effort" where adaptation to cold temperatures may not be complete on the metabolic level; and that the need for economy of effort selects against winged forms. Gressitt (1970) concluded that wind, temperature and the size of the island combined as the critical factors in the evolution of flightlessness.

We propose a new approach, which integrates our present knowledge of the insects with that of their physical and biological environment. Lack of wings in the native insects is a paedomorphic trait; a fact recognized by Jeannel (1947), who discussed neoteny in *Phthirocoris antarctica* (Hemiptera) from the Crozets. Paedomorphosis produces generalists (Holm 1985), in that the less specialized juvenile (or larval) phase becomes prolonged, and specialized end (adult) phases are reduced or omitted (compare the life histories of the indigenous Lepidoptera; also that of *Paractora dreuxi*, Diptera). Such changes in rate and timing of development, which lead to paedomorphosis, occur not because of selection but rather as a result of lack of selection (Holm 1985): insects able to adapt to the adverse physical environment in the sub-Antarctic face very little selection pressure from the biological environment (see elsewhere in this report). Such insects live, for all practical purposes, in the kind of protective environment which usually gives rise to paedomorphosis. Extreme intraspecific morphological variation, such as that in *Ectemnorhinus similis* (Curculionidae), is a typical trait of neotenic forms (Lorenz 1968), and a logical result of the lack of biological selection pressures. For background to this approach, see Holm (1985) on the evolution of generalist and specialist species. This view is not in conflict with that of Jackson (1928) and Downes (1965), but rather proposes a mechanism for the *origin* of flightlessness under certain environmental conditions. That this flightlessness may be reinforced by its adaptiveness in the sense of Darlington (1943) is also not excluded.

Conclusion

The flora and fauna of islands have played a central role in the development of ecological, evolutional and biogeographical thought (Diamond & May 1981). The sub-Antarctic islands are in many respects unique and on the whole poorly studied. Insects are the only true land animals of the sub-Antarctic, and the reviving interest in their study was long overdue. Studies on community assembly, ecological energetics and the role of insects in soil mineralization processes are now underway at the Prince Edward Islands. However, it is in the field of theoretical ecology that the major opportunity of the system lies. The islands are eminently suited for provoking and testing theoretical ideas. Structuring and funding of research should be undertaken in cognizance of this opportunity.

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Appendix A

(see Emerson in Marion Book p. 360)

Insect parasites of birds and seals at the Prince Edward Islands

(v. little change)*

Marion Island host	Species recorded
	Order Phthiraptera
	Suborder Ischnocera
Pterodroma macroptera	*Trabeculus schillingi* Rudow, 1866
	Naubates pterodromi Bedford, 1930
	Halipeurus procellariae (Fabricius, 1775)
Pterodroma mollis	*Naubates pterodromi* Bedford, 1930
	Halipeurus procellariae (Fabricius, 1775)
	Trabeculus schillingi Rudow, 1866
Pachyptila turtur	*Halipeurus turtur* Edwards, 1961
	Naubates prioni (Enderlein, 1908)
Pelecanoides urinatrix	*Pelmatocerandra setosa* (Giebel, 1876)
Halobaena caerula	*Naubates clypeatus* (Giebel, 1874)
Catharacta antarctica	*Saemundssonia stresemanni* Timmermann, 1949
Pachyptila salvini	*Naubates prioni* (Enderlein, 1908)
	Order Siphonaptera
* *Procellaria aequinoctialis*	*Notopsylla kerguelensis*
	Order Phthiraptera
	Suborder Anoplura
Mirounga leonina	*Lepidophthirus macrorhini* Enderlein, 1908

× addition

Appendix B

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