

CONTRASTING PATTERNS OF POLAR BIOGEOGRAPHY: NORTH AND SOUTH IN ATLANTIC ISLAND BIOTA

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with 3 figures and 3 tables

ABSTRACT. The terrestrial and freshwater faunas of North and South Atlantic island faunas are discussed in relation to the twin hypotheses of survival in refugia and postglacial immigration. The palaeoclimatological record and Holocene fossil assemblages are considered and a conclusion in favour of Lateglacial and early Holocene immigration is reached. The importance of driftwood mechanisms in the South Atlantic is contrasted with rafting on ice in the North. The importance of human transport in the immigration of various elements in the biota is also assessed.

"As icebergs are known to be sometimes loaded with earth and stones, and have even carried brushwood, bones and the nest of a land bird, I can hardly doubt that they must occasionally have transported seeds from one part to another of the arctic and antarctic regions, as suggested by Lyell; and during the Glacial period from one part of the now temperate regions to another."

CHARLES DARWIN (1859)

INTRODUCTION

The opposing models of *refugia*, locations where elements of a biota are able to survive through extended periods of adverse conditions, and *tabula rasa*, a clean slate, into which the flora and fauna re-immigrate after local extinction, are seminal to any discussion of the plants and animals of polar and sub-polar islands. In the Atlantic, a major dichotomy is evident in the nature of the biota at either end of the World. The Faeroes, Iceland and Greenland appear to virtually lack endemic taxa, whilst many of the circum-Antarctic islands show a high degree of endemism. In Greenland, one species amongst the Coleoptera, *Atheta groenlandica* Mahl., belonging to a large genus, in which the distribution of individual species

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is often poorly known, is the solitary apparently indigenous species recorded from the island (BÖCHER 1988); there are none recorded from Iceland and Faeroe. In contrast, the Falklands has perhaps 70% of its fauna endemic, including several unique genera of Curculionid (weevil) and a number of species in other groups apparently known only from the islands (ROBINSON 1984). South Georgia's flora contains no endemics (GREENE 1964), but the short list of nine species of Coleoptera (beetle) includes three possible indigenous species (GRESSITT 1970), including a Dytiscid (water beetle) and a darkling beetle (Tenebrionidae = Perimylopidae of WATT (1967)). Whilst at the core of this contrast may be the disparate state of knowledge of the Holarctic, as opposed to Neotropical faunas, there would remain, if all the putative endemics were shown to be synonymous with Patagonian or Fuegian species, differences in faunal composition which require evaluation. Figure 1 summarises the taxonomic composition of the faunas of Iceland and the Falklands for comparison.

Whilst the affinities of the biota of the South Atlantic islands clearly lie with the New World, the ground-living fauna and the flora of the North, despite the proximity of North America, across the Davis Strait, have an evident European connection (Figure 2). This is not merely a reflection of a generalised Holarctic distribution pattern, but includes animals like the large flightless weevil, *Otiorhynchus arcticus* (F.), which extends across all of the islands of the North Atlantic (LINDROTH 1957) and no further. If the principal agents of transfer, by wind and wave, are similar, essentially dictated by the spin of the planet, from west to east, then New World elements should preside over both ends of the globe. Whilst such a model might be seen to ignore the complex events of the Quaternary, with its multiple glaciations, it appears to hold for those species which are sufficiently light and vagile to enter what CROWSON (1981) has termed the aerial plankton. It fails, however, with the ground-based, often flightless fauna and, surprisingly, also with the North Atlantic marine littoral faunas (INGÓLFSSON 1993), which are clearly European in origin.

The *refugia* model would seek to combat this problem by claiming survival *in situ* through the late Tertiary and Quaternary, from a time when the Northern Ocean was narrower and a land bridge or island hopping a possibility. The principal exponents of the hypothesis in recent years have been perhaps the botanists EILIF DAHL (1987) and AXEL LÖVE (LÖVE & LÖVE 1979) and the entomologist CARL LINDROTH. LINDROTH, however, whose fascination with island biogeography began with his thesis on the origins of the Icelandic biota (LINDROTH 1931), was too exacting a taxonomist to erect new taxa on slight morphological variation and clearly felt some unease over species stability, in the face of multiple glacial-interglacial cycles, over millions of years. His own work on the Carabid fauna of the Azores (1960) had defined a series of indigenous species which had evolved from the chance dispersal of ancestors, but similar endemics were lacking on Faeroe, Iceland and Greenland. He therefore argued for the late survival of a land bridge into the mid-Pleistocene (LINDROTH 1963a), something which was unacceptable on geological grounds. The *tabula rasa* hypothesis has been favoured on geological and geomorphological grounds

at least since THORODDSEN's study of Icelandic geography (1898), although this seems less to be the case in Greenland (cf. FUNDER 1979). Postglacial re-immigration would appear the more effective option, yet Lindroth (1972), along with most botanists (e.g. LÖVE & LÖVE 1979; STEINDÓRSSON 1962), continued to favour survival in *refugia*, often employing the fauna and flora of modern nunatak or isolated areas adjacent to glaciers as potential analogue situations (LINDROTH 1965). In his last paper, edited posthumously by SVEN-AXEL BENGTSON and PEHR ENCKELL, LINDROTH (LINDROTH, BENGTSON & ENCKELL 1988, p.51) ends with the comment,

“Such refugia.....cannot be demonstrated beyond doubt except by dateable fossil remains.”

The differing pattern of South Atlantic islands, essentially part of a circum-Antarctic group (Figure 3), scattered around the continent and its ice cap, has led to a rather less integrated, if less contentious approach to the history of their biota. GRESSITT (1970) provides an excellent discussion but, unfortunately, rarely comes to grips with the geological and geomorphological evidence for the islands' Quaternary history. On balance, GRESSITT, himself, would appear to have favoured Postglacial aerial dispersal, either as aerial plankton or through the intermediary of birds, for the origins of the biota (Gressitt 1970). WATT (1970) and BARROW (1978), however, working on South Georgia, suggest survival of at least part of the fauna and flora in refugia. CHOWNE (1992) has recently considered the problem in relation to weevils on other circum-Antarctic islands. The North Atlantic islands, with their more extended history of human interference in their biota, are also better served with a palynological framework (cf. JÓHANSEN 1985; HALLSDÓTTIR 1987; FREDSKILD 1983). The islands of the southern ocean, lacking in trees and with few shrubs, provide rather less for the palynologist (cf. BARROW 1978). Peat and limnic sediments, are extensive on all the relevant islands and the context for discussion of the origins of both North Atlantic and Southern island biota is best approached through the Holocene macrofossil record, preserved in such deposits. The scale of accidental anthropochorous transport and deliberate introduction is frequently underestimated (GRESSITT 1970; SADLER 1990) and the base line for discussion has to begin with the pre-settlement landscape and its biota.

Whilst palynology, with its more established research tradition, has tended to dominate terrestrial palaeoecology, the Insecta also have an extensive Quaternary fossil record (BUCKLAND & COOPE 1991). Their chitinous exo-skeletons are sufficiently durable to survive in anaerobic sediments and even disarticulated fragments may retain sufficient diagnostic characters to be identifiable to the species level. Although the relatively robust Coleoptera (beetles) tend to dominate fossil assemblages, other groups are also recognisable and both Diptera, the true flies, and Hemiptera, bugs (in the English sense), may be equally frequent, the former often as puparia. The Coleoptera, however, have the advantage in

biogeography of including taxa which might be dispersed by a wider range of mechanisms than most, and it is upon this group that most of the ensuing discussion is based. After initial radiation during the Tertiary, species, at least in continental situations, have remained remarkably stable (BUCKLAND & COOPE 1991); in the face of climatic or other environmental stress, massive shifts in distribution pattern occur (cf. COOPE 1973). Such options are not available to the faunas of remote islands, which are thereby fated to be dominated by generalists, ecological opportunists and recent introductions.

THE NORTH ATLANTIC ISLANDS

Whilst only the northern part of Greenland and the small island of Grimsey, off the north coast of Iceland lie within the Arctic Circle, in terms of North Atlantic biogeography the Faeroes, Iceland, and Greenland can be considered together. The Faeroes consist of 18 small islands, separated by deep fjords, lying some 300km north west of the coast of Scotland and 600km west of Norway. At 62°N, the climate is cool oceanic, with July average temperatures of 12°C and winter, January averages of 3.5°C. The invertebrate fauna has been the subject of extensive recent study, particularly by SVEN-AXEL BENGTSON and PEHR ENCKELL (BENGTSON 1981; ENCKELL 1985) and a revised checklist is in preparation (BLOCH & ENCKELL, in prep.). Iceland has a land area of nearly 103,000sq km, with some small off-shore islands. At 64°N to 66°N, its climate varies from cool oceanic on the south coast, with July averages of 11°C and January ones of 1°C, to a more continental regime in the north, 11°C in summer and -2.5°C winter. The coast of Greenland lies some 400km west of the northwest peninsula, Scotland is 820km to the south east and Norway 950km east. A checklist of the invertebrate fauna has been published by ÓLAFSSON (1991) and the fauna, particularly along the south coast, has been extensively studied in connection with work on the new volcanic island of Surtsey (LINDROTH *et al* 1973). Greenland, with an area of 2,175,600sq km, largely occupied by the largest ice cap after Antarctica, essentially consists of a group of islands, divided by sea and ice. At Kap Farvel, its southern tip, 59° 45'N, the climate is subarctic, but the most extensive areas of land, in the north, are the true Arctic, with average summer temperatures of only 7°C and January falling to an average of -40°C below. A checklist of invertebrate fauna was provided by HENRIKSEN (1939) and BÖCHER (1988) has re-evaluated the Coleoptera; other groups, however, are in need of revision.

Although Greenland has evidence for Inuit occupation from North America extending back to the mid-Holocene (Meldgaard 1979), neither Iceland nor Faeroe has convincing evidence for settlement on any appreciable scale before Norse expansion in the eighth and ninth centuries A. D. (JONES 1986). Whilst Faeroe lacked forest (JÓHANSEN 1985) at Norse Landnám, Iceland's extensive birch and willow woods and scrub, forested from mountain top to seashore according to one medieval source, rapidly fell victim to the fires and sheep of

the settlers, leading to extensive soil erosion (DUGMORE & BUCKLAND 1991). In Greenland, the arrival of the Europeans, a colonising venture which was to fail after nearly five hundred years (MCGOVERN 1985; 1992), is marked, in many places, by a layer of charcoal at around the turn of the millennium (BUCKLAND 1988), followed by a progressive deterioration in the landscape (MCGOVERN et al 1988). Excessive use of fire was the hallmark of European expansion in the Atlantic, from Madeira (CROSBY 1986) through the Falklands (DARWIN 1834 in ARMSTRONG 1992, 129), to interwar Chile and the Amazon Basin (REVKIN 1990). The long term anthropogenic impact on the biota, in terms of changes in species frequency and local extinctions, is only slowly becoming apparent from the fossil record (BUCKLAND, PERRY & SVEINBJARNARDÓTTIR 1983; BUCKLAND, DUGMORE & SADLER 1991).

The establishment of the baseline fauna in Iceland is assisted by the tephrochronological sequence, with the so-called 'Landnám ash' (LARSEN 1984) occurring over much of the country ca A.D. 900, close to the period of Norse settlement. It has recently been used in the examination of putative pre-Norse, Irish settlement on the off-shore island of Papey (BUCKLAND et al. 1995), with negative results. In the Norse Western Settlement on Greenland, the charcoal horizon is sufficiently widespread to indicate European activity, although the possibility of earlier Inuit fires has always to be considered (FREDSKILD & HUMLE 1991). The Faeroese situation is more difficult and remains the source of some contention (JÓHANSEN 1986; BUCKLAND 1992). In particular, a claim for occupation during the European Bronze Age, based upon palynology (JÓHANSEN 1989) has been disputed (HANSOM & BRIGGS 1992). The list of indigenous taxa is therefore based upon samples from contexts with early dates, defined by radiocarbon assay and lacking any species which might be considered synanthropic.

The techniques of recovery and identification of Quaternary fossil insects have been described elsewhere (COOPE 1986a; BUCKLAND & COOPE 1991). Table 1, summarising the data from the North Atlantic islands, includes faunas from four sites in the Faeroes, ten in Iceland, and one each in the east and west of Greenland. No single succession yet covers the whole of the Holocene, but the nature of the pre-Landnám faunas is evident, ranging from small Staphylinids (rove beetles) which could easily have formed part of the aerial plankton to large, heavy Carabids (ground beetles) and Curculionids (weevils), whose means of dispersal is more problematic; whilst some of these are parthenogenetic, the presence of several bisexual beetles should also be noted. The palaeoecological record also indicates the establishment on all the islands of a well developed community by the early Holocene; the biota has not been accumulated by progressive chance dispersal over the nine thousand years before the arrival of Europeans. Although dispersal in the air during periods of atypical airflow has been provided for a number of dragonflies (Odonata) and moths (Lepidoptera) (e.g. ÓLAFSSON 1975); other transport mechanisms for the majority of the biota must be sought. Despite largely botanical arguments to the contrary (LÖVE & LÖVE 1979), the absence of the evolution of endemic taxa in the face of multiple Pleistocene glaciation and frequent,

often precipitate swings from temperate to Arctic climate and back again should negate the refugia hypothesis. The extent of maximum glaciation has also entered into the discussion, in terms of whether there were areas available for refuges. There seems general agreement that Faeroe was completely covered by an ice cap during the last glaciation (ENCKELL 1985), but debate upon Iceland (HOPPE 1982; SIGURVINSSON 1983) and Greenland (FUNDER 1982) continues. BUCKLAND (1988) and BUCKLAND & DUGMORE (1991) have argued that the extent of ice-free areas is unlikely to be relevant, when, as far south as Midland England, there are no organic sediments over the period of maximum ice extent during the last glaciation, ca 18,000-15,000 B.P. Locked in permanent sea ice and surrounded by ice sheet, any land areas would have resembled the cold arid valleys of Antarctica (e.g. LLANO 1962), where the only life is algal, in the surface of rock and snow. Postglacial immigration therefore requires a mechanism which not only reverses at least part of the flow in the North Atlantic Drift, but which also allows the dispersal of flightless animals, as well as the supporting ecosystem to allow the rapid colonisation and expansion which is evident from the pollen diagrams (cf. JÓHANSEN 1985).

The probability that ice rafting has contributed extensively to the biota of oceanic islands was discussed by several leading nineteenth century biogeographers and Darwin, a visitor to the Falklands in 1833-4 on the *Beagle*, had extended the model to warmer latitude islands, like the Azores, at the maximum of glaciation (DARWIN 1859). LINDROTH (1963b) was prepared to accept ice rafting for the fauna of Newfoundland, but not the Atlantic islands. COOPE (1969) applied the model to the origins of the insect fauna of Scandinavia and later (1979; 1986b) expanded it to the Atlantic preferring a Lateglacial interstadial, rather than early Holocene dispersal, a viewpoint also taken by BÔCHER (1988). BUCKLAND and others (1986), after extensive work upon fossil insect assemblages in Iceland, hypothesised a short term event during the precipitately rapid warming event which began the present interglacial. The model has been expanded to all the North Atlantic islands (BUCKLAND 1988; BUCKLAND & DUGMORE 1991) and recent re-evaluation of the limits of Lateglacial and early Holocene ice in Iceland (INGÓLFSSON 1991) would support the later date for the origins of the island floras and faunas. New data from Greenland ice cores implies that the switch from high Arctic to temperate conditions may have taken place in less than a decade around ca 11,640 \pm 250 b.p, calendar years (ALLEY et al. 1993); the fossil insect evidence from the British Isles (OSBORNE 1980), although limited more by sample resolution, has long suggested very rapid warming to an early Holocene maximum (BISHOP & COOPE 1972; ASHWORTH 1972). In this scenario, the rapid decay *in situ* of the Fennoscandian ice cap would have provided the mechanism for the westward transport of the biota from the south west coast of Norway on sediment-laden shelf icebergs out across the Norwegian Sea, on a freshwater slick and a North Atlantic Drift turned back along the retreating edge of the pack ice (BUCKLAND & DUGMORE 1991). The one relevant fossil assemblage from Norway so far published, from Godøy in Ålesund, (BIRKS et al. 1993) provides a list surprisingly similar to

that of the Atlantic islands. The island faunas, disharmonic, dominated by cool temperate generalists, reflect the inevitable consequence of a very short rafting period, leaving little time for hosts to become established before their monophagous feeders. After early Holocene immigration, the biota shows remarkably little change until the arrival of European settlers late in the first millennium A.D., although, with the decay of the Laurentide ice sheet in North America, Greenland became progressively more open to Nearctic elements. The relative inertia in this decay must also be part of the reason why the littoral faunas of the Canadian Maritimes still maintain a Palaearctic connection (INGÓLFSSON 1993), a relict of the tail of the turned back North Atlantic Drift, for perhaps less than a decade, ten thousand years ago.

HUMAN IMPACT

Notwithstanding the evident differences of opinion regarding the early European settlement of the North Atlantic region (JÓHANSEN 1986; BUCKLAND 1992; BUCKLAND et al. 1995), the first largescale settlement venture occurred as a result of the Norse migrations during the eighth and ninth centuries (JONES 1986). The Norse exported an essentially pastoral cultural system based around the overwintering of domestic stock, mainly cattle and sheep. With the exception of Norse Greenland, where the settlements became extinct during the fifteenth and sixteenth centuries (GAD 1970; 1973; MCGOVERN 1994), remnants of this early system can still be seen in the present-day landscape. Settlement continuity has led to the continuity of habitats and the preservation of many elements of the introduced fauna (SADLER & SKIDMORE 1995). The pollen records from Faroe (JÓHANSEN 1985), Iceland (HALLSDÓTTIR, 1987) and Greenland (FREDSKILD 1973) highlight the often severe impact that these early colonists had on the their island environments. The palaeontomological record indicates that, at this time, the majority of the modern-day Coleopterous fauna was introduced to the islands (BUCKLAND 1988; SADLER 1990). This suite of synanthropic or 'stowaway' (= serfs of ENCKELL et al. 1987) insects were passively dispersed by the colonists and is associated with the general detritus of rural life around the settlements. Many of these species such as the Lathridiid beetle, *Lathridius minutus* L. and the Staphylinid beetle, *Quedius mesomelinus* Marsham, and parasites of domestic animals, notably those of sheep, have now attained near cosmopolitan distribution patterns. Others including most of the dung fauna, are widely distributed both East and West of the North Atlantic (BUCKLAND, ASHWORTH & SCHWERT 1995).

Later evidence for late- and post-Medieval transport of insect species has been admirably summarised by LINDROTH (1957), and much of it, like the shared elements in the Flora, is largely a result of the development of North Atlantic fisheries. Boats left Western Europe, particularly the ports of Southwest England, Brittany and the Basque Country of Spain, in ballast, sailed to the fishing grounds around Newfoundland, where they unshipped

ballast before stocking with fish and returning to Europe. This occasioned a considerable westward movement of species in ships' ballast and dunnage. Of the 40 species of ground beetles (Carabidae) and 69 species of weevils (Curculionidae) considered to be European introductions in North America, 36 species of Carabids and 61 species of weevils belong to the British fauna (LINDROTH, 1957: 143-145; BUCKLAND, ASHWORTH & SCHWERT 1995). This contrasts markedly with the South Atlantic islands where early pre-European human contact is presently unknown and the amount of later settlement is slight.

THE SOUTH ATLANTIC

In comparison with the North, the South Atlantic has relatively little land and the few islands lie in the path of the circum-Antarctic gyre, with air and water masses moving consistently west to east. The Falklands (Malvinas) consist of two major islands and about two hundred smaller ones, with a total land area of 12,000 km², lying at 51-53 °S and 450 km from the coast of South America. The climate is cool oceanic, with January averages of 10°C and July ones of 7°C. The natural history is reviewed by STRANGE (1992). MOORE (1967) provides a flora, and an insect checklist has been published by ROBINSON (1984). South Georgia is some 1450 km out from the Argentine coast, with a land area of 3755km², of which 56% consists of glaciers and permanent snowfields. Close to the edge of the Antarctic pack-ice at 54°S, it has a far more rigorous climate than the Falklands, with January averages of only 5°C and July falling to -2°C. Lacking permanent human settlement, its introduced reindeer have had considerable impact on the biota (VOGEL et al. 1984). The flora was studied by GREENE (1964) and the invertebrate fauna formed the core of research on South Georgia and Heard Island organised by GRESSITT (1970). Additions to the insect lists for both the Falklands and South Georgia are provided by ORAM (1992) and BLOCK (1988), respectively; ANDREWS (1995) has considered beetles of the Lathridiid genus *Aridius* on both island groups. None of the islands, however, has had the level of research afforded to the North Atlantic islands, although there are several detailed studies of the ecology of individual species (e.g. BLOCK & SØMME 1983), or particular habitats (e.g. WELLER 1975), carried out under the auspices of the British Antarctic Survey. The potential source areas of Patagonia and Tierra del Fuego have even more limited entomological data (cf. KUSCHEL 1960).

HUMAN IMPACT

European expansion into the South Atlantic begun in the late sixteenth century (CROSBY 1986), with the inevitable trail of accidental and deliberately introduced vertebrates (GRESSITT 1970; STRANGE 1992), but the first permanent settlement on the Falklands did not take place until 1764, when the French, under Bourgainville, built a fort at Port Louis on

East Falkland to protect their sealing and whaling interests (STRANGE 1987). The present largely anthropogenic rangelands reflect the move over from cattle ranching to sheep, which took place in the latter part of the nineteenth century under the control of the British government. An earlier phase of settlement appears to have left one trace in the warrah, the Falklands fox or wolf, *Dasycyon australis* (Kerr), which was finally hunted to extinction in 1876 (ARMSTRONG 1992). In contrast with the Arctic, where the arctic fox follows polar bears out onto the ice scavenging on their seal kills, no similar association exists in the southern hemisphere, where the main predators, leopard seals, are more strictly marine. In a review of the World Canidae, CLUTTON-BROCK (1977) favoured the introduction of a domesticated animal from South America at some time before European contact; any supporting archaeological evidence has yet to come to light, although the samples examined for fossil insect remains contain significant quantities of charcoal.

Regularly visited by sealers and whalers from the late eighteenth century onwards, South Georgia had several whaling stations around its edge, the last, Grytviken, being finally abandoned in 1963 (STRANGE 1992). Whilst these sites were always orientated towards the sea and largely supplied from outside, two introduced animals, rats from ca. 1800, and reindeer from 1913 have had considerable impact (GRESSITT 1970; VOGEL et al., 1984). The flora also contains a number of alien elements (GREENE 1964). BONNER and HONEY (1987) record the virtually cosmopolitan moth *Agrotis ipsilon* (Hufnagel) from the island, suggesting a chance arrival by aerial dispersal but the probability remains that the records reflect assisted passage on ships.

The evidence for introduced insect species is limited, although ROUX and VOISIN (1982) whilst adding an additional three species to the Falkland species list comment that several of the species of Carabidae (ground beetles) are likely to have been introduced. ROBINSON (1984) records *Aridius nodifer* (Westwood), *A. ? subfasciatus* (Reitter) and *Ptinus tectus* Boieldieu from East Falkland and *Quedius mesomelinus* Marshan from East Point and East and West of the islands. *A. nodifer* has also been found in the Davis Australian Antarctic station and was introduced to Campbell island prior to 1942 (ROUNSEVELL 1976). The Lathridiid beetles, *Dienerella* (= *Cartodere*) *apicalis* Blackman and *Lathridius minutus*. Were recovered from moss close to bases on Signy Island (South Orkney), King George Island and South Shetland. These species of beetles, along with two species of sheep lice, *Linognathus ovillus* (Neumann) and *Bovicola ovis* (Schränk), were introduced with Europeans and there are clear parallels with the situation in the North Atlantic. The exact timing of the movement of these species can only be satisfactorily resolved with recourse to the fossil record.

THE FOSSIL RECORD

The Falklands and South Georgia have extensive organic sediments suitable for

palaeoecological analysis and, over twenty years ago, COOPE (1963) examined samples taken by the British Antarctic Survey on South Georgia. BARROW (1978) provides pollen diagrams for both island groups. A visit to the Falklands in 1992 by one of us (RFS) allowed samples to be obtained for macrofossil study from two sites on East Falkland. A succession from Port Louis lies close to the original French settlement and one from Sapper Hill, 2km WSW of Stanley, is similarly placed in relation to British occupation. Both sites have been cut over for domestic fuel and are currently given over to rough grazing for sheep. Although there is no dating evidence for either site, the successions are likely to predate wholly European settlement. The fossil insect faunas from Sapper Hill (Table 2) is dominated by two species of weevil, of the indigenous genus, *Falklandius*. These are sufficiently numerous throughout the sequence to form the basis of a numerical taxonomic study. Like the North Atlantic island assemblages, the faunas contain a large number of flightless elements, including at least two Carabids, Byrrhids and the large weevil, *Listroderes salabrosus* Enderlein. Several of the fossil taxa have few modern records, a feature shared with North Atlantic findings (BUCKLAND, DUGMORE & SADLER 1991). Two of the bugs, *Sigara* sp. and *Nysius* sp. have yet to be described from adequate specimens. The Falklands have one described species of the circum-Antarctic Salpingid genus, *Poophylax*, *P. falklandicus* CHAMPION (1918). This animal does not appear to be represented among the fossils, but a similar, smaller, as yet undescribed species occurs in the lower part of the succession. Fragments of charcoal occur in several samples and the material from immediately beneath the modern vegetation layer contains several charred seeds; whether these reflect long distance transport from bush fires in Patagonia, or a local anthropogenic event has yet to be established.

BARROW's (1978) pollen diagrams from both West Falkland and South Georgia imply that suitable conditions for peat accumulation had become established by the middle of the tenth millenium BP, although evidence from South America would suggest that the window of opportunity for ice-rafted dispersal should have occurred some four or five thousand years earlier. Despite arguments to the contrary (e.g. HEUSSER & RABASSA 1987), a Lateglacial, Younger Dryas event has yet to be demonstrated effectively to occur in South America, where the initial warming from ca.14,000 radiocarbon years B.P. is not followed by any subsequent cooling (HOGANSON & ASHWORTH 1982; 1992; LUMLEY & SWITZER 1993). The evident disharmonic nature of the island faunas may more reflect the short span of initial colonisation rather than *refugia*, competitive pressures or later chance dispersal.

In contrast with the North, the South Atlantic offers more opportunities for passive transport in driftwood and this may go some way towards explaining the diversity of *Cylindrorhinine* weevils on the islands from the Falklands north to the Tristan group (37°S) (HOLDGATE 1960). Table 3 summarises the probable composition of the faunas before European settlement. In the Arctic, the bulk of the driftwood originates along the great Siberian rivers and is stripped of bark and ground in the Arctic pack for several years before being spread out into the North Atlantic (EUROLA 1971). Driftwood from South America

has no such destructive intermediary and southern beech, *Nothofagus* spp. and other trunks are widespread on the beaches of the circum-Antarctic islands (LEWIS SMITH 1985) and further north (BARBER *et al.*, 1959). Darwin and his former colleague on the *Beagle*, Sullivan corresponded on the prolific amounts of driftwood on the Falklands littoral and this was after a hundred years of scavenging for ships' fires and sealers' camps (ARMSTRONG 1992, 123). DARWIN (1860, 59) also notes the occasional canoe amongst this material. LEWIS SMITH (1985) provides a list of localities on South Georgia with extensive beached timber. Direct evidence for long distance transport of a Cossonine weevil, *Pentarthrum carmichaeli* Waterhouse in driftwood to the Falklands, apparently from New Zealand is provided by Kuschel; the same species is reported from Tristan da Cunha (THOMPSON 1989).

It is perhaps ironic that, in the Northern Hemisphere, the arguments in favour of endemic taxa and *refugia* have largely been advanced by botanists (e.g. LÖVE & LÖVE 1979), whilst, in the South, it is the entomologists who find numbers of indigenous species. WATT (1970) was prepared to regard the Tenebrionid *Hydromedion sparsutum* Müller on South Georgia as a Holocene immigrant, since some specimens were indistinguishable from Tierra del Fuegan *H. magellanicum* Fairmaire, whilst *Darwinella* (?= *Hydromedion*) *amaroides* Enderlein on the Falklands is 'sufficiently distinct to have arrived earlier'. The South Georgian apparent endemic *Perimylops antarcticus* Müller is thought to have arrived 'sufficiently long ago to permit distinctive characters to have evolved' and therefore must have survived the Pleistocene in a *refugium*. South Georgia appears to have been covered entirely by an ice cap during the last glaciation (SUGDEN & CLAPPERTON 1977), although BARROW (1978) suggests that some species may have survived in refuges below present sea level. The Falklands seems to have had less extensive ice cover (CLAPPERTON & SUGDEN 1978) and this could be used to support arguments in favour of survival in *refugia* and the evolution of extensive endemism amongst the insect fauna. It is probable, however, that, trapped in an extensive frozen sea, the islands, like Iceland, would have been reduced to conditions similar to the ice-free areas of the Antarctic Continent, where life, beyond the unicellular stage, is impossible away from the coastal fringe. Only a more extensive analysis of the fossil record can provide the answers.

CONCLUSION

Despite some extensive palaeoecological research, no convincing evidence for survival of plants and animals in *refugia* has been obtained from the North Atlantic islands and a similar pattern seems to be emerging in the South. Previous workers have tended to under-estimate the amount of accidental transport of both synanthropic and accidental travellers around the Oceans since European expansion began across the Atlantic over a thousand years ago. The only effective basis on which models of dispersal and colonisation

can be based is that provided by the fossils; these provide the means by which even the wildest dreams can be checked.

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TABLE 1

Insect remains from pre-European settlement deposits on the North Atlantic Islands

	Faeroes	Iceland	Greenland
Hemiptera			
Aphidioidea indet.		√	
Trichoptera			
Limnephilidae			
<i>Limnephilus</i> cf. <i>elegans</i> Curt.		√	
<i>L. griseus</i> (L.)		√	
<i>L. sparsus</i> Curt.		√	
cf. <i>Limnephilus</i> sp.			√
<i>Apatania zonella</i> Zett.			√
Coleoptera			
Carabidae			
<i>Carabus problematicus</i> Hbst.	√		
<i>Nebria rufescens</i> (Ström.)	√		
<i>Patrobus atrorufus</i> (Ström.)	√		
<i>P. septentrionis</i> Dej.	√	√	
<i>Trechus obtusus</i> Er.	√	√	
<i>Bembidion grapei</i> Gyll.			√
<i>Pterostichus diligens</i> Sturm		√	
<i>P. nigrita</i> (Payk.)/ <i>rhaeticus</i> Heer	√	√	
* <i>Calathus micropterus</i> (Duft.)	√		
<i>Trichocellus placidus</i> (Gyll.)	√		
<i>T. cognatus</i> (Gyll.)			√
Dytiscidae			
<i>Hydroporus gyllenhali</i> (Sch.)	√		
<i>H. pubescens</i> (Gyll.)	√		
<i>H. morio</i> Aub.			√
<i>H. nigrita</i> (F.)		√	
<i>Agabus solieri</i> Aub.	√	√	
<i>Colymbetes dolabratus</i> Payk.			√
Hydrophilidae			
<i>Helophorus ?aequalis</i> Thoms.	√		
<i>H. cf. flavipes</i> F.	√		
<i>Cercyon</i> sp.	√		
<i>Megasternum obscurum</i> (Marsh.)	√		
<i>Anacaena globulus</i> (Payk.)	√		
Hydraenidae			
* <i>Hydraena britteni</i> Joy		√	
Ptiliidae			
<i>Acrotichis</i> sp.	√		
Staphylinidae			
<i>Philonthus</i> spp.	√		
<i>Quedius umbrinus</i> Er.	√	√	
<i>Q. felmanni</i> Zett.			√
<i>Tachinus</i> sp.	√		
<i>Oithus angustus</i> Steph.	√		
<i>O. punctulatus</i> (Goez.)	√		
<i>Lathrobium brunripes</i> (F.)	√	√	
<i>Olophrum fuscum</i> (Grav.)	√		
<i>Eucnecosum brachypterum</i> (Grav.)	√		
<i>Lesteva heeri</i> Fauv.	√		

<i>L. longoelytrata</i> (Goez.)	√		
* <i>Ochtheophilus omalinus</i> (Er.)	√		
<i>Gymnusa brevicollis</i> (Payk.)		√	
<i>Atheta graninicola</i> (Grav.)		√	
<i>Atheta</i> (s.l.) spp		√	
Aleocharinae indet.	√		
<i>Stenus carbonarius</i> (Marsh.)		√	
<i>S. impressus</i> Germ.		√	
<i>S. umbratilis</i> Casey		√	
<i>Stenus</i> spp.	√		
Pselaphidae			
<i>Bryaxis puncticollis</i> (Den.)		√	
Byrrhidae			
<i>Similocaria</i> (?) <i>semistriata</i> (F.)			
<i>S. (?)metallica</i> Sturm.			√
<i>Byrrhus fasciatus</i> (Forst.)			√
Elateridae			
<i>Hypnoidus riparius</i> (F.)		√	
Scirtidae			
(?) <i>Cyphon</i> sp.	√		
Apionidae			
<i>Apion cruentatum</i> (Waltl.)	√		
Curculionidae			
<i>Otiorhynchus arcticus</i> (F.)			√
<i>O. nodosus</i> (Müll.)	√	√	
<i>Barynotus squamosus</i> Germ.		√	
<i>Tropiphorus obtusus</i> (Bons.)		√	
<i>Dorytomus taeniatus</i> (F.)		√	
<i>Ceutorhynchus contractus</i> (Marsh.)		√	
Diptera			
Bibionidae			
<i>Bibio/Dilophus</i> sp.		√	
Chironomidae			
indet.	√	√	√
Simuliidae			
<i>Simulium</i> sp.			√
Ceratopogonidae			
indet.			√
Indet Puparia	√	√	√
Hymenoptera			
Parasitica indet.	√	√	

TABLE 2

Insect remains from Holocene sediments on the Falklands and South Georgia.

- Coleoptera
Carabidae
 indet.
Dytiscidae
 Lancetes sp.
Leioididae
 Falkocholeva/Falkonemadus sp.
Staphylinidae
 Halmaeus atriceps (Waterhouse)
Byrrhidae
 Chalcosphoerium enderleini Champion
 C. ?solox Enderlein
Tenebrionidae
 Hydromedion sparsutum Müll. (South Georgia)
indet.
Salpingidae
 **Poophylax* sp.
Curculionidae
 Listroderes salebrosus Enderlein
 Falklandius antarcticus (Germain)
 F. turbificatus Enderlein
Hemiptera
Corixidae
 Sigara (Tropocorixa) sp.
Delphacidae
 Nothodelphax atlanticus (China)
 ?*N.* sp.
Jassidae
 Acocephalus (?)falklandicus Enferlein
Lygaeidae
 Nysius (?Anorthuna) sp.
Diptera
indet.

* Not recorded in the modern fauna. Taxonomy follows ROBINSON (1984) and GRESSITT (1970).

TABLE 3

Probable composition of the pre-Settlement beetle (Coleoptera) faunas of Iceland, Greenland, the Falklands and South Georgia.

	Iceland	Greenland	Falklands	S. Georgia
Carabidae	19	4	15	3
Gyrinidae	0	1	0	0
Haliplidae	1	0	0	0
Dytiscidae	5	3	3	1
Hydraenidae	1	0	1	0
Hydrophilidae	2	0	0	0
Catopidae	1	0	2	0
Scydmenidae	1	0	0	0
Staphylinidae	29	5	5	2
Pselaphidae	1	0	0	0
Elateridae	1	0	0	0
Byrrhidae	2	3	2	0
Coccinellidae	2	2	0	0
Salpingidae	0	0	1	0
Tenebrionidae	0	0	8	2
Chrysomelidae	3	0	0	0
Curculionidae	15	5	19	0

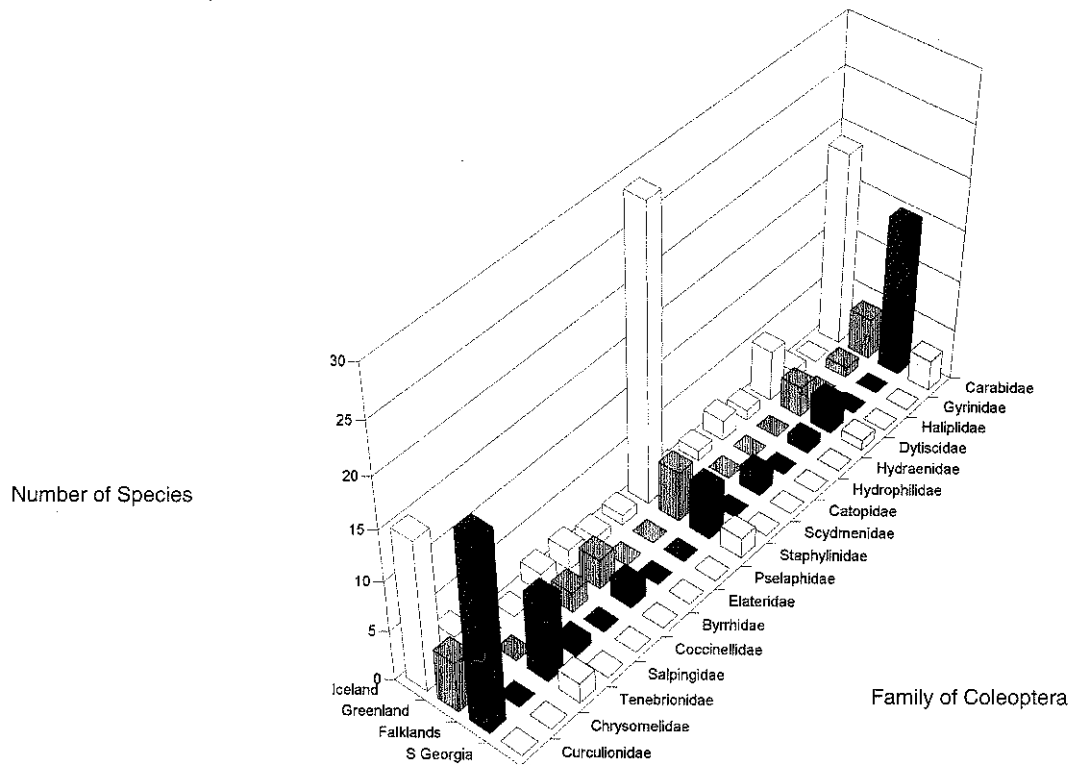


Figure 1 - The composition of the Coleopteran faunas of Iceland (a) and the Falklands (b) compared (excluding strictly synanthropic taxa). Data from ÓLAFSSON (1991) and ROBINSON (1984).

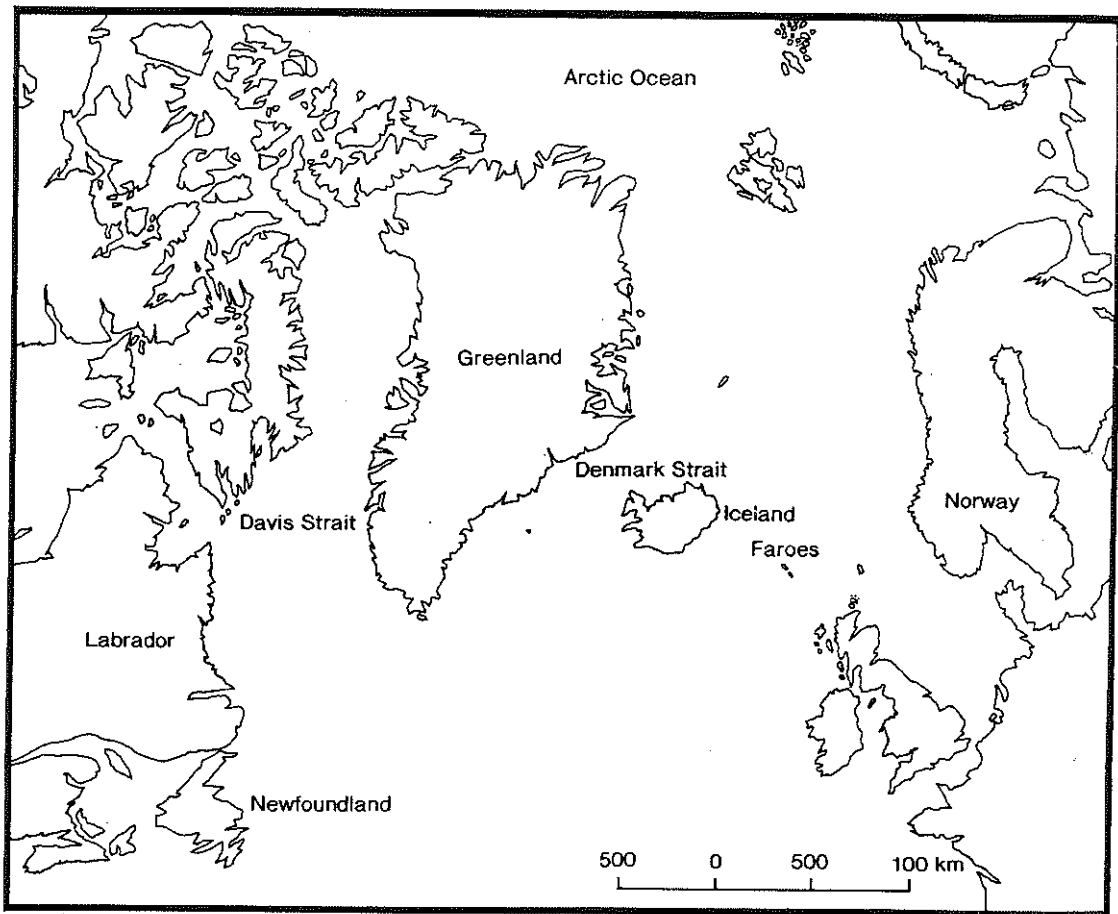


Figure 2 - The North Atlantic.

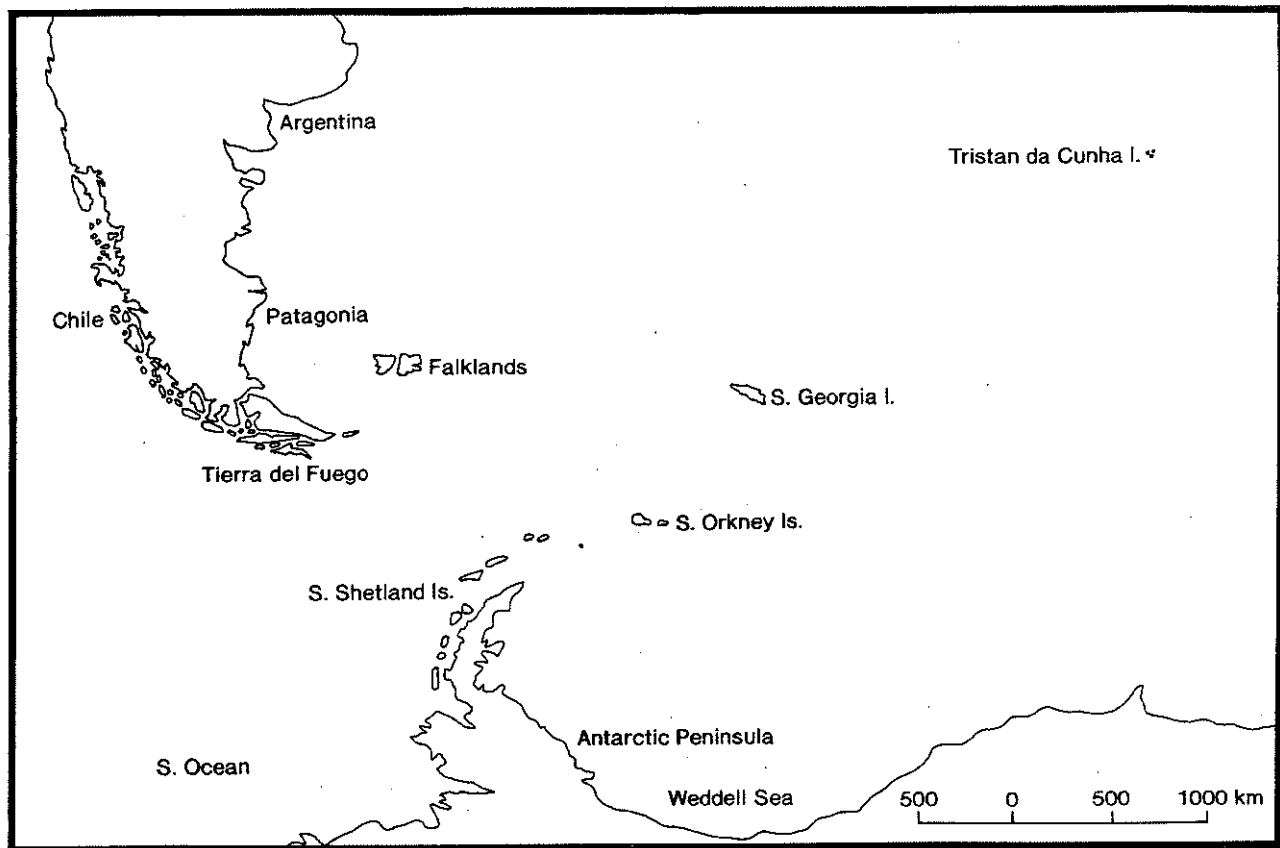


Figure 3 - The South Atlantic.