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# The land fauna of Ascension Island: new data from caves and lava flows, and a reconstruction of the prehistoric ecosystem

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**Abstract.** Terrestrial arthropods were investigated in 1990 and 1995 on Ascension, a young and extremely isolated volcanic island in the equatorial Atlantic. Three new genera (of Araneae, Oribatida and Psocoptera) were discovered and the number of apparently endemic species was increased from fourteen to about twenty-nine. Some 311 species of land animals (a few now extinct) are known to have established themselves on the island; in a few groups there may be significant numbers of unrecorded species. About ninety-five endemic and non-endemic species are considered to be native (including two marine turtles, twelve seabirds and two extinct landbirds); seventy-eight are of doubtful status; and at least 138 were probably introduced by humans. Natural colonists arrived mainly by air (drifting with the wind during migratory movements) but some evidently travelled on floating objects or attached to birds or other animals. Natural colonization was almost entirely from Africa.

Before the arrival of humans, Ascension had an early successional ecosystem. The fauna in the lava and cinder deserts of the lowlands—both on the surface and in subterranean cracks and caves—was dominated by taxonomically varied scavengers and mainly arachnid predators. The scattered angiosperms here and in the foothills supported some host-specific herbivores with associated predators; they were also exploited (especially after exceptional rains) by a number of Orthoptera, Hemiptera and Lepidoptera derived from migratory African

populations and perhaps reinforced at intervals by additional groups of colonists. The more extensive and largely cryptogamic vegetation on the central peak had a poor fauna probably composed mainly of micro-arthropods. Along coasts, on islets and in the extensive seabird colonies there were additional arthropod species and also a flightless rail and a night heron (both now extinct).

Invertebrate stocks that colonized Ascension underwent a variety of evolutionary changes including phyletic evolution leading to endemic status, adaptation to subterranean life (Araneae, Pseudoscorpiones, Collembola and Psocoptera), character release (phorid Diptera), and probably splitting of lineages (speciation) within the island (Isopoda, Collembola and gryllid Orthoptera). The relatively high diversity of Pseudoscorpiones (five species in five genera) and their 100% apparent endemism is notable.

The indigenous fauna of Ascension provides a view of an early stage in the processes of colonization, adaptive evolution and radiation which—over much longer periods—give rise to the richer and more distinctive faunas of older oceanic islands such as Ascension's nearest neighbour, St Helena, where a few invertebrate clades have undergone repetitive speciation and some adaptive radiation.

**Key words.** Ascension Island, St Helena, zoogeography, insect migration, colonization, island evolution, lava habitats, cave biology, arthropods.

## INTRODUCTION

*'I have heretofore asked the question concerning Mauritius henns and dodos, thatt seeing those could neither fly nor swymme, beeing cloven footed and withoutt wings on an island far from any other land, and none to bee seence elce where, how they shold come thither? Soe now againe concerning the Ascention birds allsoe, thatt can neither fly nor swymme. The island beeing aboutt 300 leagues from the coast of Guinnea and 160 leagues from the island of St Matheo, the nearest land to it, the question is, how they shold bee generated, whither created there from the beginning, or thatt the earth produceth them of its owne accord, as mice, serpents, flies, wormes, etts. insects, or whither the nature of the earth and*

*climate have alltred the spape and nature of some other foule into this, I leave it to the learned to dispute of.'*

Peter Mundy in June 1656 (Temple & Anstey, 1936)

The quotation from Peter Mundy highlights the particular biological significance of isolated oceanic islands. We can now generally assume that the ancestors of all their indigenous, terrestrial biota arrived over water. The composition of the fauna and flora provides evidence on the pattern of transoceanic movement, and the characteristics of island species throw light on evolutionary processes. Although Ascension cannot compete with older oceanic islands and archipelagos in terms of diversity or taxonomic

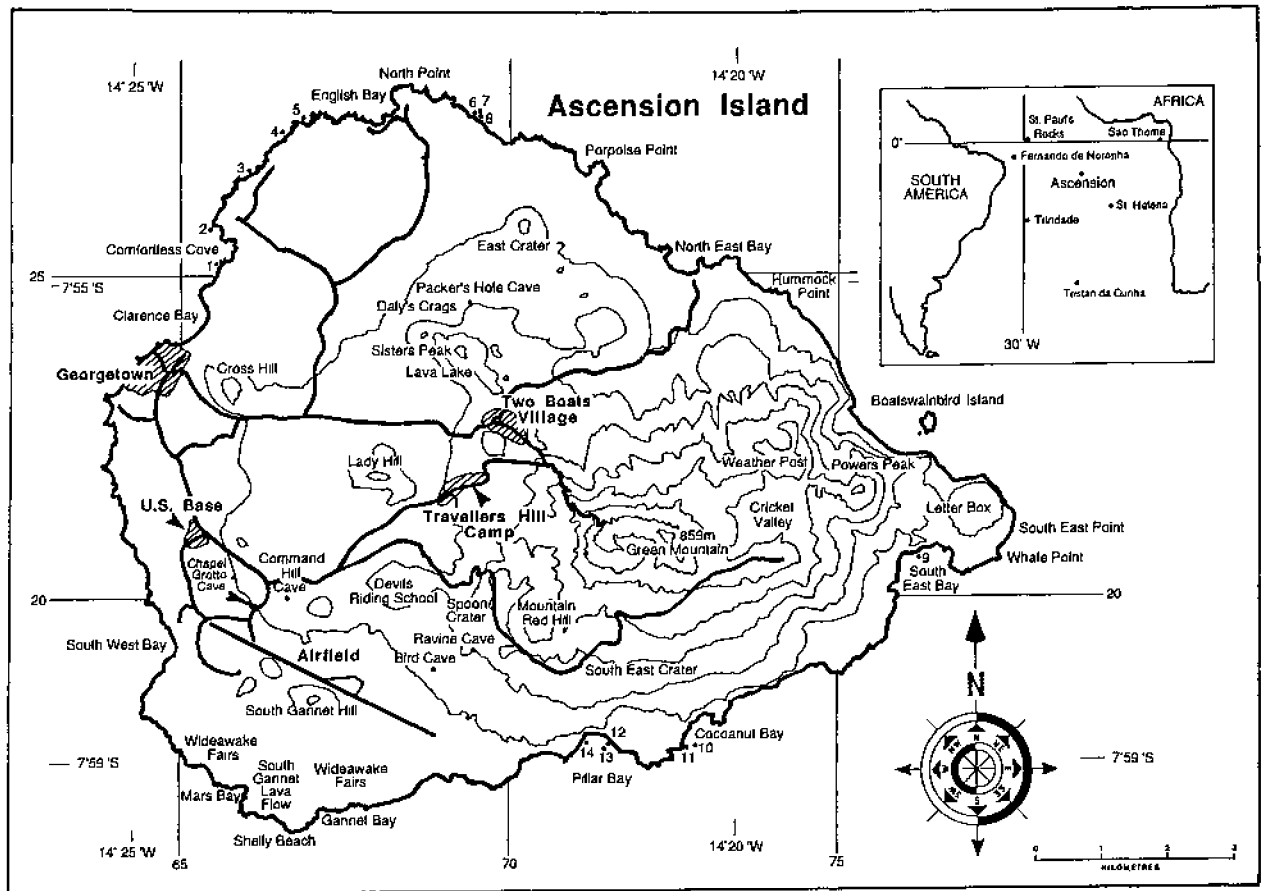


FIG. 1. Map of Ascension Island, South Atlantic Ocean, showing locations of collecting sites. Numbered grid lines (indicated at 5 km intervals) are those of the Universal Transverse Mercator Grid, zone 28; they should be prefixed with the letters ES. Contour interval 100 m.

distinctiveness in its endemic fauna, it can provide a snapshot of a relatively early stage in the process of arrival and diversification of land animals on what was—in the relatively recent past—a pile of almost sterile steaming rock emerging from the tropical Atlantic almost midway between the African and South American continents.

Ascension is an extremely isolated and relatively young oceanic island. Lying at  $7^{\circ}57'S$   $14^{\circ}22'W$  (Fig. 1), it is 1300 km from St Helena, 2232 km from Recife on the coast of Brazil and 1504 km SSW of Cape Palmas (Liberia). To the east, the coast of Gabon is just over 2600 km away and that of Angola and northern Namibia—another potential source for the biota—about 3000 km.

The island is situated about 300 km northwest of the plume of the Ascension hotspot (Brozina & White, 1990), some 100 km west of the Mid-Atlantic Ridge and immediately south of the Ascension Fracture Zone. The sea floor around the island is 5–6 million years old (Brozina, 1986) and the island cannot be older than this. The oldest dated subaerial rocks are estimated at 1.5 million years (Harris, Bell & Atkins 1982; Harris, 1986). Ascension is moving away from Africa at a rate of some 36 mm per year (Brozina, 1986) in conformity with spreading at the Mid-Atlantic Ridge, but cannot ever have been more than about

200 km closer to Africa than it is now. The island is geologically active and the last on-shore eruption may have been within the last millennium (Rosenbaum, 1992).

Ascension Island now has an area of  $c.97$  km<sup>2</sup>, but eustatic changes in sea level resulting from Pleistocene glaciations will have led to substantial fluctuations in this throughout its existence. The island has rugged volcanic terrain (Figs. 2–3). The relatively low and dry western part is dominated by scoria cones and basaltic lava flows, mantled in many places with fine pyroclastic deposits. The higher eastern end is moister with many domes of trachyte lava, culminating in Green Mountain, which has an altitude of 859 m. Just north of the eastern end of the main island lies Boatswainbird Island, with an area of about 5 ha; there are also a number of rocky stacks around the coast (Fig. 1). These sites, which are free of alien mammals, are now of crucial importance for breeding seabirds (Ashmole, Ashmole & Simmons, 1994).

Ascension has a tropical but oceanic climate, with little seasonal change. Monthly average maximum temperatures at sea level vary only between about 27 and 31°C, with the warmest weather in March–April and coolest around September (Mathieson, 1990; note that figures quoted in Ashmole *et al.*, 1994 from Duffey, 1964 appear to be in

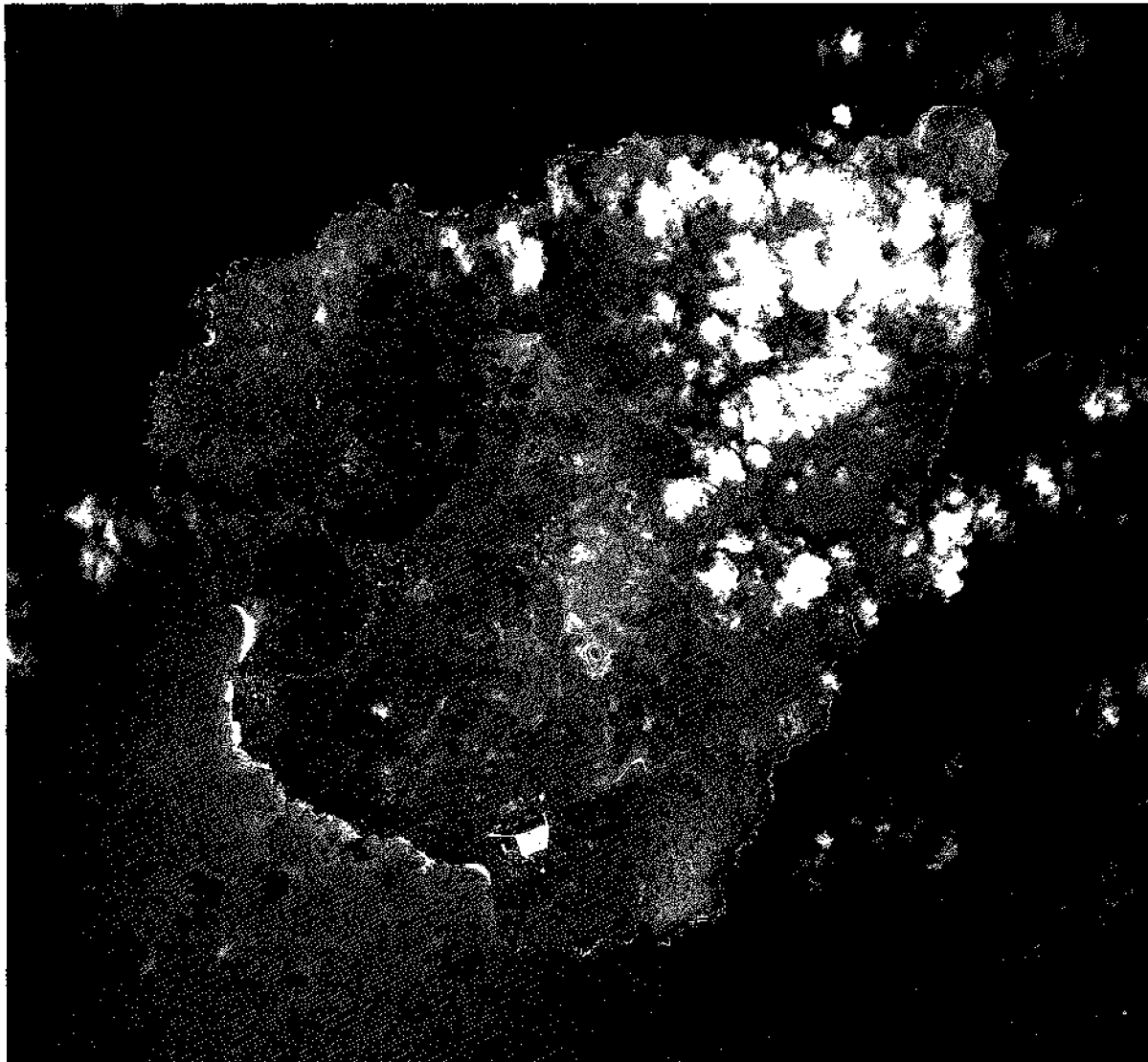


FIG. 2. Aerial photograph of Ascension Island, 1989. Crown Copyright.

error). The island lies in the path of the South-East Trade Winds, and southeast and easterly winds blow for more than half the time in every month (Duffey, 1964; Scullion, 1990). The trade wind inversion at a height of c. 1000–1500 m acts as a strong cap inhibiting vertical cloud development and thus ensures generally low rainfall (Riehl, 1979). Nevertheless, as the winds rise over the eastern end of the island they bring cool and misty conditions to the ridge of Green Mountain, and a mean annual rainfall (at an altitude of 660 m) of about 680 mm. At Two Boats—northwest of the mountain at an altitude of 290 m—rainfall is about half as great and on the western coast it averages only about 100–200 mm, leading to desert conditions in the lowlands.

At irregular intervals, however, there are torrential rains that promote the development of ephemeral vegetation in normally barren areas (Duffey, 1964; Bourne, 1984; Hall, 1989). The exceptional rains in 1963 (Packer, 1983) and in March 1984 were clearly associated with El Niño/Southern Oscillation (ENSO) phenomena, involving abnormal

southward displacements of the Intertropical Convergence Zone, which affected the tropical Atlantic at these times (Philander, 1986). Ascension is also affected by southern hemisphere 'easterly waves', disturbances apparently originating in central equatorial Africa and moving westwards across the tropical Atlantic (Hall, 1989).

Ascension Island was discovered by a Portuguese navigator in 1501; we use the word 'prehistoric' to refer to events prior to that date. The island was visited by ships irregularly during the next 300 years, before being occupied by Britain in 1815 (Packer, 1983). A history of human influences on the biota, and a summary of observations of the early naturalists, is provided by Duffey (1964). The history of the seabird colonies is discussed by Stonehouse (1962) and Ashmole *et al.* (1994).

The reaction of early entomologists to the Ascension fauna was mixed. Osbeck (1771) who visited the island in 1752, recorded without further comment: '*Dermestes elytris hirsutis cinereis*, in the sand; *Hippobosca nigra*, on the

*Pelecanus Aquilo* (*Fregata aquila*); *Musca vulgarissima*, and *Musca nivea*.' Webster (1834) commented on the insect life in disparaging terms, saying that '... the residents almost consider themselves as labouring under some of the plagues of Egypt in the swarms of flies by which they are annoyed.' 'Ants are beyond all number, mosquitoes plentiful as they are tormenting, scorpions, centipedes, large spiders and crickets, in ample quantity, and the only insect attractive on account of its beauty is the mountain butterfly.'

The coleopterist Wollaston (1861), in describing a collection from the island, warned naturalists 'from ever attempting to go there again for the purpose of collecting.' McLachlan (1878), in a short note commenting on insects destroying crops on the island, suggested that all the species concerned had probably been introduced with plants. Similarly, Waterhouse (1881), documenting a collection of myriapods and insects, implied that almost all the species also occurred elsewhere, and did not discuss which of them might be native to the island. Stüder (1889) commented on the contrast of the fauna with those of older islands, and said that it was very difficult to decide whether the insects were indigenous or had been introduced by man. Riley (1893) listed some specimens from Ascension but made no general comment.

Dahl (1892) started his account of Ascension by saying: 'One could scarcely imagine a less favourable place, not only for the establishment but also for the maintenance of animal life, as Ascension' (Dahl 1892, trans. G. H. Harper). However, Dahl continued less dismissively, commenting: 'I find the island by no means as uninteresting as Wollaston did. The little that does occur has thereby in many ways an enhanced interest.'

The only systematic investigation of the terrestrial ecology of Ascension was carried out by Duffey (1964): all future references to his work relate to that paper unless otherwise specified. Duffey visited almost all parts of the island, made a thorough survey of the vegetation and collected a wide variety of terrestrial invertebrates. Although he obtained several new endemic arthropods, he emphasized the predominance of widespread animal species, and suggested that most of these had arrived by accident with introduced plants.

In one of the few recent contributions to Ascension entomology, Robinson & Kirke (1990) gave an account of a collection of Lepidoptera made on the island in 1988, reviewing previous records for this order and adding some fourteen species. They concluded that there was little or no endemism among the Lepidoptera and that almost the whole fauna was derived from the Old World tropics.

The authors' interest in the invertebrates of Ascension arose from investigations of arthropod dispersal and of the fauna of lava and cave habitats on other volcanic Atlantic islands (Ashmole & Ashmole, 1987, 1988; Ashmole, Ashmole & Oromí, 1990; Oromí *et al.*, 1990) and of processes of faunal succession in such habitats (Ashmole *et al.*, 1992). Whereas that work had concerned archipelagos, Ascension offered the contrast of extreme isolation.

Volcanic activity produces unvegetated lava flows and deserts of scoria, with many cracks and often also lava tubes. These sterile habitats subsequently undergo a process of primary succession, but in dry climates plant productivity

in them may remain low for long periods. The communities of resident invertebrates living in them depend largely on organic material brought from elsewhere, by the wind (Edwards, 1987; Ashmole *et al.*, 1992) or—in the case of coastal regions and islands—also by the sea (Lindroth *et al.*, 1973; Ashmole *et al.*, 1990). These barren habitats are often those least disturbed by human activities and by the spread of introduced animals and plants. Indigenous species, many of them scarce and nocturnal, may survive unnoticed in such places.

Our main invertebrate work on Ascension was done between 9 March and 4 April 1990. Though the visit was made for ornithological reasons (Ashmole *et al.*, 1994) we were able to carry out systematic sampling of epigeal and hypogean communities in several parts of the island. After the original submission of the present paper we were able to visit Ascension again, from 10 May to 7 June 1995. On this occasion the primary aim was to assess the feasibility of eradication of alien mammals (Bell & Ashmole, 1995), but some time was spent attempting to fill gaps in the earlier invertebrate study. A few of the specimens from the recent visit have not yet been fully identified, but new data have been inserted in the paper wherever possible.

Techniques developed during our work on Atlantic islands permit efficient collecting both underground and on the surface in barren volcanic terrain. As we show below, our sampling in these latter habitats and the use of traps significantly altered the picture provided by Duffey's more general survey. Duffey did his collecting by hand, turning over stones and using a sweep net on vegetation; he concentrated on macro-invertebrates and did not collect on lava fields or in caves (Dr E. Duffey, *pers. comm.*). Our collecting demonstrated the presence of a number of new endemic arthropods and other probably indigenous species, and led us to reconsider the nature of the fauna as a whole.

Preliminary analysis suggested that many species recorded from the island were known to be anthropochorous; that is, readily transported by man, on ships, in cargoes, packing material and clothes, or with domestic animals or in other ways. It was noticeable, however, that the remaining fauna included a high proportion of species known to be adapted for long distance migration. It therefore seemed worthwhile to assess, for all terrestrial species established on the island, the probability that they were indigenous rather than introduced (intentionally or by mistake) by humans.

Having made these judgements about the process of colonisation, we attempt a reconstruction of the animal communities of Ascension Island in its pristine state, making use of information on the original vegetation of the island and the results of work on primary faunal succession on other volcanic islands. We then discuss the diversity of the indigenous fauna of Ascension and consider the evolutionary processes that have operated there and on the much older island of St Helena, Ascension's nearest neighbour in the tropical South Atlantic.

## METHODS AND STUDY SITES

Methods and equipment used in 1990 were those developed during our previous work (Ashmole *et al.*, 1992). The aim



FIG. 3. Sisters Peak from the northwest. In the middle distance are Daly's Crags, mantled with pyroclastic cinder deposits on which there are—especially towards the left—diffuse whitish patches of weathered guano left by seabirds that nested there in the past. The white 'flags' on the foreground lava are also old guano; they are always on the northwest face of the rocks, reflecting the birds' tendency to roost facing the South-East Trade Wind. Packer's Hole and Fumarole are just out of sight to the left, Lava Lake is over the ridge to the right.

was to sample a wide variety of subterranean and surface habitats, giving priority to those areas that seemed to be least altered from their pristine condition.

Caves on Ascension Island include lava tubes, spatter cones and cavities of more complex origin (Olson, 1977; Packer, 1983; James, 1985). At two of the cave sites (Command Hill and Packer's Hole), we used the same standard sampling technique (see below) in three distinct habitats: the dark zone of the cave (indicated by C in Table 1), the cave threshold, where there is still some light (indicated by T), and on the surface of the nearby lava flow or pyroclastic deposit (indicated by L). Extra traps were left in the dark zone for about 10 days. The standard technique was also used on several other lava flows that lacked accessible subterranean habitats. Most of the lava sites were in areas with old guano or phosphatic deposits (Fig. 3) left by seabird colonies exterminated in recent centuries (Ashmole, 1963; Olson, 1977; Ashmole *et al.*, 1994, Bourne *et al.*, manuscript). Less intensive sampling was carried out at a few more caves and crevices and at several additional surface sites: the extent of this sampling is indicated below for each site.

The standard sampling technique involved searching and hand collecting for three hours and leaving eight pairs of traps for four days. Each trap pair comprised one baited bottle and one pitfall trap; specifications and working methods were described in Ashmole *et al.* (1992). At the end of the trapping period traps of both types were closed with screw caps and brought back to the field laboratory

where the contents were examined and filtered and the animals sorted.

During the 1990 study a total of 304 traps were set and 24 person-hours of searching was undertaken. In three places we also set out water traps to check for the presence of 'biological fallout' (Ashmole & Ashmole, 1987) contributing nutrients to the scavenger communities inhabiting the barren lava.

During the 1995 visit we had four main objectives.

(1) Obtaining additional subfossil bird bones and collecting extra specimens of problematic invertebrate taxa discovered in 1990, by revisiting key sites.

(2) Collecting invertebrates on the endemic Ascension spurge *Euphorbia origanoides* L.

(3) Collecting invertebrates on Boatswainbird Island, an offshore guano island where only one significant invertebrate collection had previously been made (by Duffey) and where introduced species would be less likely to be present. In 1990 we were not granted permission to visit this island, but in 1995 NPA and two ornithologist colleagues were able to spend 24 h there and to undertake invertebrate sampling as well as making observations on the seabirds.

(4) Sampling non-cave subterranean habitats using a pipe-trap developed in 1994 for work on St Helena. This trap is derived from one used by Juberthie in sampling the 'MSS' or mesocavernous shallow stratum (Juberthie, Delay & Bouillon, 1980; Ashmole, 1994). The trap consists of a steel pipe with internal diameter 45 mm, length 2 m and with a closed and pointed lower end. The lower half of the



FIG. 4. Packer's Hole, looking down the steep entrance passage into the interior of the cave. The roof is mainly of trachyte, while the floor has cinders that trickle in from the entrance and through cracks. This is the type locality for the cavernicolous linyphiid spider *Catoneiria caeca* Millidge & Ashmole and one of the places where the liposcelid psocopteran *Trogloctes ashmoleorum* was found.

pipe has four longitudinal rows of 9 mm diameter holes to allow entry of animals. The pipe is driven into the substrate with a sledgehammer and eventually extracted with a car jack. Three trapping vials are lowered into the pipe when it is in position, borne at different levels on a flat steel strip of the type used in shelf supports. The vials contain the usual liquid and baits (Ashmole *et al.*, 1992).

Locations of the main 1990 sampling sites are shown in Fig. 1; essential details of the sites are given below.

**Command Hill.** UTM ES 666 200, 150 m a.s.l. This area consists of fairly weathered lava on a steep slope, with a few grasses and lichens. The cave (see Olson, 1977) is a lava tube running down the slope, with the entrance part way down; both ends are fully dark.

**Packer's Hole.** UTM ES 694 245, c.185 m a.s.l. This area is still unstable and was affected by some of the most recent volcanic activity on Ascension. The cave is a narrow, sharply inclined cleft, apparently formed by collapse; according to James (1985) it is 49 m long and 18 m deep (Fig. 4). The lava outside is mantled with cindery pyroclasts which trickle into the cave. There are a few lichens but virtually no other plants, but small accumulations of plant fragments form under many rocks. This site was also visited in 1995: four pairs of traps were set, with 2 h search.

**Chapel Grotto Cave.** UTM ES 657 203, c.100 m a.s.l. Eight pairs of traps for 5 days in dark zone only, 45 min search. This cave is one of many in the large area of pahoehoe-type lava near Southwest Bay. A vertical shaft gives access to a short lava tube, via a low (0.3 m) arch that traps warm air within, leading to high temperature and humidity. Bird bones were collected belonging to three individuals of the extinct rail and one of the extinct night heron (Bourne *et al.*, manuscript). This cave was also visited twice in 1995 to search for additional subfossil bird bones.

**Ravine Cave.** UTM ES 694 192, c.200 m a.s.l. Four pairs of traps for 5 days, 45 min search. This cave is not mentioned by James (1985). It is a short lava tube in the side of a ravine; erosion of the cliff has made several small entrances, so that no part of the cave is completely dark, but cracks doubtless give access to a fully dark and equable cave environment. This cave was also visited in 1995: four pairs of traps were set, with 30 min search.

**Bird Cave.** UTM ES 688 189, c.120 m a.s.l. Four pairs of traps for 2 days, and casual collecting. This cave is a complex of several small cavities associated with spectacular lava channels; none of the cavities is fully dark.

**Comfortless Crevices.** UTM ES 657 252, c.5 m a.s.l. Four pairs of traps set for 3 days, in deep crevices and spaces under overhangs in an extremely jagged basaltic flow within 30 m of the coast; saturated with old guano. None of the accessible places is fully dark.

**South Gannet Lava Flow.** This extremely rough flow of 'aa' lava originates at the east end of South Gannet Hill and reaches the sea between Gannet Bay and Mars Bay; it is the site of an abandoned seabird colony and is saturated with old guano; there are a few tiny clumps of grass. We set eight pairs of traps for 4 days at each of four stations forming a transect at right angles to the coast, and at one station on older rocks.

(a) Shore: UTM 665 164; traps among basaltic outcrops on Shelly Beach, close to sea level.

(b) Pools: UTM 665-6 165; these are the marl pools and coral pools described by Chace & Manning (1972) and Abele & Felgenhauer (1985); traps 50–100 m inland; 3 h of searching was carried out at this site, but not elsewhere on the flow.

(c) Inland: UTM 666 166; traps c.200 m inland, c.10 m a.s.l.

(d) Upper: UTM 667 175, traps c.40 m a.s.l., c.1 km inland and 300 m from the western edge of the flow; also water trap set for 4 days.

(e) Off-lava: UTM 664 177, c.30 m a.s.l.; a control site on old rocks with some plants, well inland and 50–100 m west of South Gannet flow.

**Wideawake Fairs (Runway and Mars Bay).** UTM ES 688 174, c.40 m a.s.l., four bottles set for 2 days; UTM ES 661 173, c.15 m a.s.l., four bottles set for 7 days. These traps were placed within active colonies of the Wideawake (Sooty Tern) *Sterna fuscata*, in order to sample fauna associated with the nesting seabirds.

**Porpoise Point.** UTM 709 263, c.15 m a.s.l. Eight pairs of traps set for 4 days. About 200 m inland, in a hollow bordered by more recent lava flows, with heavy accumulations of old guano and hardly any plants.

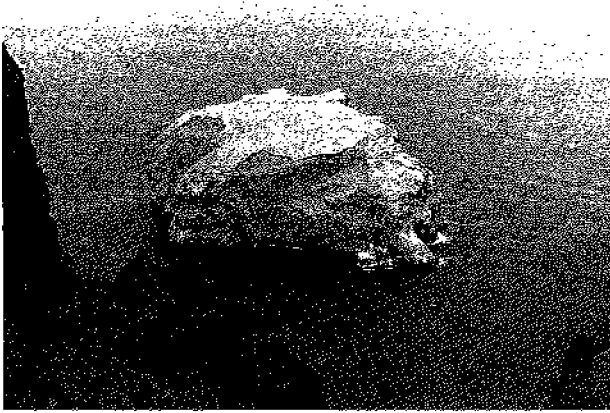


FIG. 5. Boatswainbird Island from near Powers Peak. The island is now the only breeding site for the Ascension frigatebird and is the type locality for both the pseudoscorpions shown in Fig. 8.

**Lava Lake** UTM 685-7 235, c.150-170 m a.s.l. Eight pairs of traps set for 4 days. A rugged area about 50 m by 200 m, with deep cracks; apparently recent lava (Packer, 1983), but older rock with a little vegetation and old guano is nearby.

**Letterbox Lava.** UTM ES 763 215, c.150 m a.s.l., and 766213, c.120 m a.s.l. Eight pairs of traps set for 4 days, in two groups, both in areas of apparently recent lava with hardly any vegetation, but the second with old guano deposits.

**Sisters Cinders.** UTM ES 698 242, c.180 m a.s.l. Four pairs of traps set for 2 days; chosen because the substrate was entirely of pyroclasts, mainly around 1 cm diameter, and with no large rocks; no vegetation, although there were areas with grass within c.100 m.

**English Bay Coast.** UTM ES 692 275, sea level. Four bottles set for 4 days, among basaltic rocks as close as possible to the shore.

Additional sites used in 1995 and referred to in the text are as follows.

**Boatswainbird Island** (Fig. 5). UTM ES 763 226, 104 m a.s.l. max. Eight pairs of traps set for one night; c.4 h searching.

**Lower Valley Crater, 1 km south of North East Bay.** UTM ES 724 242, 90 m a.s.l. This site was on a ridge of loose scoria. Pipe trap set for 14 days.

**South Gannet Hill.** UTM ES 670 180, 90 m a.s.l. This was an area of barren aa lava. Pipe trap set for 13 days.

**Daly's Crags.** UTM ES 685 248, 95 m a.s.l. This site has deep deposits of cinders similar to those at the 1990 'Sisters Cinders' site, nearby. Pipe trap set for 5 days.

## RESULTS

Results of the systematic collecting in 1990 are summarized in Table 1; further information on the species obtained in both 1990 and 1995 is included in the Appendix. Authorities for all scientific names of animals are given in the Appendix and not in the main text. These data show that the barren lava flows of Ascension have moderately diverse communities of predatory and scavenging arthropods. Caves and other subsurface habitats are also occupied by

arthropods, some of which show morphological adaptation to subterranean life. At the start of the 1990 study ten apparently endemic species of arthropods were known from Ascension Island; this number has now risen to three endemic genera and some twenty-five species. In a later section we attempt a reconstruction of the pristine island ecosystem; only the most notable new finds are mentioned here.

A new genus was established by Millidge & Ashmole (1994) for a minute, blind cave spider, *Catonetria caeca* (Linyphiidae: Linyphiinae), discovered in 1990 and so far known only from Packer's Hole Cave. Capture of an adult male and female in 1995 has led to some reassessment of the relationships of this species (Merrett & Ashmole, 1997) which is close to *Agyneta* Hull. Millidge & Ashmole (1994) suggested that the ancestors of *Catonetria* reached the island by ballooning; no sister species has yet been found on the surface.

Oribatid mites collected at several lava sites (Table 1) have been described by Luxton (1995) as a new genus and species, *Cordylobates fragilis*, tentatively placed in the family Ceratozetidae. The genus is close to *Humerobates* Sellnick and to *Baloghobates* Hammer. Gut contents of *C. fragilis* suggest that they feed on lichens and pollen.

Three endemic pseudoscorpions had been found by Duffey in 1958. The recent work led to discovery of two more apparently endemic species. No non-endemic pseudoscorpions have yet been found and the group thus has the highest percentage of apparent endemism of any arthropod order on Ascension; at present it also has the highest number of endemics, although Araneae may eventually prove to have more.

*Apocheiridium cavicola*, the most interesting of the new pseudoscorpions, is taxonomically isolated in its genus. It was discovered in a cave in 1990 and is morphologically adapted to subterranean life (Mahnert, 1993 and *pers. comm.*). Capture of another individual in 1995 in a pipe trap at c.90 m in a barren ridge of loose scoria indicates that the species is capable of living in the sub-surface cracks in unweathered volcanic substrates.

Isopods from Ascension collected by Duffey were studied by Ferrara & Taiti (1981), who concluded that all nine species 'were certainly introduced by man'. Our 1990 collections, however, together with new information on African woodlice, have led Taiti & Ferrara (1991) to reassess the situation. The new material included eight species, of which four were not previously recorded from Ascension; two of these were new to science. The isopod genus *Niambia* Budde-Lund (Platyarthridae) is represented on the island by two closely related species. Though they are akin to other members of the genus in southern Africa, they share derived cephalic characters not found in these, and Taiti & Ferrara (1991) suggest that the two Ascension species may have differentiated on the island.

Another isopod, *Elumoides coecus*, was discovered in 1990 in Chapel Grotto and Command Hill caves (Taiti & Ferrara, 1991). It is a member of a poorly known family largely confined to tropical Africa. The genus *Elumoides* has one species in Cameroon and one with a wide distribution from the Seychelles to Hawai'i and including the plateau of



TABLE 1. Arthropods collected on Ascension Island in 1990.

Explanation. For site names see 'Study Sites'. Under Habitat, c indicates deep cave zone; t threshold zone; l surface lava or cinders; initials under SG refer to stations on the South Gannet Lava flow (see text). l indicates a single specimen, X more than one specimen. Authorities for all scientific names are given in the Appendix. Asterisks indicate apparently endemic species.

Site	CH	PH	CG	RC	BC	CC	SG	WF	PP	LL	LB	SC	EB	O			
Habitat	c	t	l	c	t	t	t	s	p	i	u	o	l	l	l	l	l
<b>Scorpiones</b>																	
<b>Buthidae</b>																	
<i>Buthus hottentotta</i>																	l
<b>Araneae</b>																	
<b>Scytodidae</b>																	
<i>Scytodes</i> sp.		X	X						X		X						
<b>Loxoscelidae</b>																	
<i>Loxosceles</i> sp.																	l
<b>Pholcidae</b>																	
<i>Hedyspilus lawrencei</i>		l			l						X	X					
<i>Micropholcus chavanei</i>		l								X	X	X					
<i>Pholcus</i> sp.					l												
<b>Oonopidae</b>																	
* <i>Opopaea ?euphorbicola</i>										l	l						
? <i>Orchestina</i>	l																
<b>Oecobiidae</b>																	
<i>Oecobius</i> sp.			l														
<b>Theridiidae</b>																	
<i>Lactrodectus geometricus</i>						l											
<b>Linyphiidae</b>																	
* <i>Catonetria caeca</i>			X														
<b>Gnaphosidae</b>																	
<i>Trachyzelotes jaxartensis</i>		X						X	l			l					
<i>Zelotes inauratus</i>										X							
<b>Prodidomidae</b>																	
* <i>Prodidomus ?clarki</i>										X							
? <i>Zimirina</i> sp.							X										
? <i>Zimiris</i> sp.			l						l								
<b>Salticidae</b>																	
<i>Hasarius adansonii</i>	X		X					X	X	l	X		X				
<b>Ixodida</b>																	
<b>Ixodidae</b>																	
<i>Rhipicephalus</i> sp.							X										
<b>Argasidae</b>																	
<i>Ornithodoros denmarki</i>										l							
<b>Prostigmata</b>																	
<b>Bdellidae</b>																	
<i>Bdellodes</i> sp.								X									
<i>Spinibdella</i> sp.													X				
<b>Eupodidae</b>																	
* <i>sp. nov.</i>									X								
<b>Oribatida</b>																	
<b>Ceratozetidae</b>																	
* <i>Cordylobates fragilis</i>			X								X	l					
<b>Oribatulidae</b>																	
<i>Lucoppia</i> sp.										X							
<b>Haplozetidae</b>																	
<i>Incabates</i> sp.									X								
<b>Oppiidae</b>																	
<i>Lasiobelba</i> sp.			l														
<b>Pseudoscorpiones</b>																	
<b>Cheiridiidae</b>																	
* <i>Apocheiridium cavicola</i>					l												
<b>Isopoda</b>																	
<b>Philosciidae</b>																	
<i>Littorophiloscia tropicalis</i>							X	X									
<i>Atlantoscia floridana</i>																	X
<b>Platyarthridae</b>																	
* <i>Niambia duffeyi</i>									l			l					
* <i>Niambia longiantennata</i>		X	X	X				X	X	X		l				l	

TABLE 1. continued

Site Habitat	CH			PH			CG		RC	BC	CC	SG	WF PP LL LB SC EB O												
	c	t	l	c	t	l	c	t	t	t	s	p	i	u	o	l	l	l	l	l	l	l	l	l	
<b>Porcellionidae</b>																									
<i>Agnara madagascariensis</i>								X							1										
<i>Porcellionides pruinosus</i>		1																							
<b>Eubelidae</b>																									
<i>*Elumoides coecus</i>	1							X																	
<b>Armadillidae</b>																									
<i>Cubaris murina</i>																X		X							
<b>Decapoda</b>																									
<b>Gecarcinidae</b>																									
<i>Gecarcinus lagostoma</i>						1					1		X									X			
<b>Scolopendromorpha</b>																									
<b>Scolopendridae</b>																									
<i>Scolopendra morsitans</i>				X											X	X		1							
<b>Cryptopidae</b>																									
<i>Cryptops</i> sp.			1																						
<b>Geophilomorpha</b>																									
<b>Geophilidae</b>																									
<i>*Tuoba ashmoleorum</i>												1													
<b>Collembola</b>																									
<b>Entomobryidae</b>																									
<i>Cyphoderus</i> sp.								X																	
<i>Drepanura</i> sp.																			X						
<i>*Pseudosinella</i> sp.A	X	X		X	X				X																
<i>*Pseudosinella</i> sp.B			1			X						X	X	X	X	1	X	X	X	X					
<i>*Pseudosinella</i> sp.C												X	X												
<i>Seira</i> sp.A (?domestica)			X			X									X	1		1							
<i>Seira</i> sp.B				1																					
<b>Sminthuridae</b>																									
<i>Denisiella</i> sp.																									
<i>Sphaeridia</i> sp.																									
<b>Thysanura</b>																									
<b>Lepismatidae</b>																									
<i>Acrotelsa collaris</i>				X																					
<i>Ctenolepisma longicaudata</i>	1		X		X	X			X	1	X	X	X	X	X	1	X	X	X	X			1		1
<b>Orthoptera</b>																									
<b>Gryllidae</b>																									
<i>Grylloides sigillatus</i>		1	X		X	X					1				X	X		X	1	1					
<i>*Mogoplistinae</i> sp.A								X																	
<i>*Mogoplistinae</i> sp.B													X	X											
<i>*Mogoplistinae</i> sp.C												X	X												X
<b>Blattodea</b>																									
<b>Blattidae</b>																									
<i>Periplaneta americana</i>	X	X	X	1		1	X	X	1	X				1	X	X		X	X						
<b>Thysanoptera</b>																									
<b>Phlaeothripidae</b>																									
<i>Haplothrips gowdeyi</i>																									
<b>Psocoptera</b>																									
<b>Psyllipsocidae</b>																									
<i>Psocathropos lachlani</i>		X	1		1	X									1			X							
<i>Psyllipsocus ?ramburii</i>				X																					
<b>Trogiidae</b>																									
<i>Cerobasis</i> cf. <i>maya</i>			1													X									
<b>Liposcelidae</b>																									
<i>Liposcelis bostrychophila</i>														1										1	
<i>Liposcelis</i> sp.						1																			
<i>*Troglotractes ashmoleorum</i>	X	1		X				1						1											
<b>Ectopsocidae</b>																									1
<i>Ectopsocus strauchi</i>																									1
<b>Coleoptera</b>																									
<b>Staphylinidae</b>																									
<i>Atheta coriaria</i>												1													
<i>Belonuchus</i> cf. <i>formosus</i>											1														

TABLE 1. continued

Site	CH			PH			CG			RC	BC	CC	SG	WF			PP	LL	LB	SC	EB	O
Habitat	c	t	l	c	t	l	c	t	t	t	t	s	p	i	u	o	l	l	l	l	l	l
<b>Dermestidae</b>																						
<i>Dermestes ater</i>																	X					
<b>Anobiidae</b>																						
<i>Lasioderma serricorne</i>																		X				
<b>Ptinidae</b>																						
<i>Gibbium psylloides</i>			X							X						l				X		
<b>Nitidulidae</b>																						
<i>Urophorus humeralis</i>																			X			
<b>Tenebrionidae</b>																						
<i>Gonocephalum prolixum</i>			X														X	X				
<i>Clitobius ovatus</i>													l					X				
<i>Alphitobius</i> sp.																		l				
<i>Hemasodes batesi</i>																		X	X			
<i>Blapstinus metallicus</i>						l												X	X		l l	
<b>Anthrribidae</b>																						
<i>Araecerus fasciculatus</i>																				l		
<b>Hymenoptera</b>																						
<b>Evaniidae</b>																						
<i>Evania appendigaster</i>																					l	
<b>Bethylidae</b>																						
*? <i>Trachepyris</i> sp.nov.																					X	
<b>Vespidae</b>																						
<i>Polistes fuscatus</i>																	l		l	l	X	
<b>Formicidae</b>																						
<i>Cardiocondyla emeryi</i>																		X				
<i>Cardiocondyla mauritanica</i>						X											l			X	l X	
<i>Paratrechina longicornis</i>	X					X																
<i>Pheidole megacephala</i>						X																
<i>Solenopsis</i> cf. <i>globularia</i>						X					X			l	X	X						
<b>Lepidoptera</b>																						
<b>Noctuidae</b>																						
<i>Heliothis armigera</i>						l															X	
<b>Pyralidae</b>																						
<i>Herpetogramma phaeopteralis</i>																					l	
<b>Tineidae</b>																						
<i>Pheroeca</i> cf. <i>altuella</i>			l		X			X	X	X						l	l		l			
?Family																						
Indet.																			l	l		
<b>Diptera</b>																						
<b>Phoridae</b>																						
<i>Megaselia curtineura</i>	l	x		x						X	X	X	X	X	X	X	X	X	X	X	X	
<b>Milichiidae</b>																						
<i>Milichiella lacteipennis</i>			l																			
<b>Ephydriidae</b>																						
<i>Hecamede brasiliensis</i>													X									
<i>Atissa pygmaea</i>													X									
<b>Drosophilidae</b>																						
<i>Drosophila buzzatii</i>			X			l				l										X		
<i>Drosophila melanogaster</i> gp.																				l		
<i>Zaprionus vittiger</i> gp.						l																
<b>Muscidae</b>																						
<i>Musca domestica</i>																					l	
<i>Synthesiomyia nudiseta</i>														l				l		l		
<b>Sarcophagidae</b>																						
<i>Sarcophaga exuberansoides</i>			l														l			X		
<i>Sarcophaga</i> sp.																				l	l	

Henderson Island (Benton & Lehtinen, 1995), suggesting great powers of dispersal. *E. coecus* is only the third known member of the genus and differs from the other two in being eyeless and also in having pleopodal lungs, normally

an important taxonomic character; however, since it resembles its relatives closely in other characters, Taiti & Ferrara (1991) preferred not to erect a new genus for it. *E. coecus* is small, colourless and able to roll up into a ball;

its lack of eyes and its apparent absence from surface sites suggest that it is an obligate cavernicole.

Our collembolan collections from Ascension are still being studied, but the data already indicate a clear pattern of niche separation. In particular, collections from barren lava and caves (Table 1) included three species in the artificial genus *Pseudosinella* (Entomobryidae) which Dr K. Christiansen (pers. comm.) considers have probably evolved on the island from an ancestral *Lepidocyrtus*; they are treated more fully in the Appendix. *Pseudosinella* species A is the dominant collembolan in caves and other subterranean habitats; it is unpigmented and eyeless and shows some troglomorphy (morphological adaptation to cave life). *Pseudosinella* species B is dominant on the inland barren lava flows, while *Pseudosinella* species C is abundant near the shore on the South Gannet lava flow.

Crickets of the subfamily Mogoplistinae were previously known on Ascension only from a juvenile collected by Duffey. Our collections included three species (Table 1) which have been examined by Dr Daniel Otte, who suggests (pers. comm.) that more than one genus may be represented. Unfortunately the group is taxonomically difficult and the relationships of these forms cannot yet be worked out. However, the three species appear to show ecological segregation within the island. Mogoplistinae sp. A is small and distinctive; it was found in Ravine Cave in threshold conditions and—with the probably introduced *Gryllodes sigillatus*—at Lava Lake, which has very deep cracks; species A is probably a largely subterranean form. Mogoplistinae sp. B is much larger, pale and seems characteristic of low-lying lava flows; it was not found within 50 m of the shore. At the South Gannet Pools station this species overlapped with the slightly smaller and much darker Mogoplistinae sp. C, which was found only within 100 m of the shore, where it was very abundant. On Boatwainbird Island in 1995 we obtained both species B and C, but their distribution there was not worked out.

Psocopterans, previously unrecorded from Ascension, proved to be widely distributed and diverse in caves and lava flows: these detritivorous animals are evidently preadapted to life on a barren volcanic island. Two of the newly discovered species provide almost the only examples of apparent New World affinities in the Ascension arthropod fauna. One in the family Trogiidae which was found at two lava sites is very similar (perhaps identical) to *Cerobasis maya*, described recently from the Yucatan Peninsula, Mexico (Garcia Aldrete, 1991). The second, in the family Sphaeropsocidae, is represented by a single damaged specimen related to *Sphaeropsocopsis microps* Badonnel from natural edaphic habitats in Chile.

Another psocopteran—one of three species of Liposcelididae in our collections—is of particular interest, representing a new genus and species in the subfamily Liposcelidinae, which previously included only the genus *Liposcelis* (Lienhard, pers. comm.); the new species has several morphological characteristics that seem to represent adaptations to subterranean life. In 1990 it was found in several caves (Table 1), but one individual was obtained in a trap on lava, implying that individuals sometimes come

to the surface, probably at night. In 1995 the species was collected in a pipe trap set in barren lava rubble.

Capture of this psocopteran, the pseudoscorpion *Apocheiridium cavicola* and the troglomorphic collembolan *Pseudosinella* species A (as well as a few other animals) underground in raw volcanic landscapes in the lowlands of Ascension, demonstrates that the pipe traps provide an effective method for sampling subterranean animals that are normally accessible only where there are caves.

Further discussion of our results is deferred until after analysis of the fauna as a whole, which is based on the 1990 data and the new finds made in 1995, together with previously published information.

## NATURAL COLONIZATION AND HUMAN INTRODUCTION

Few islands are more remote from continental land than Ascension (Fig. 1 and data in the Introduction) and the distance from Africa would have been only slightly less at the time of formation of the island. Natural colonization of Ascension must therefore have involved rare and largely stochastic trans-oceanic dispersal of propagules. Hypotheses about such events are open to criticism by those who feel that biogeographic hypotheses based on dispersal are inherently unsatisfactory because they are hard to falsify. It may sometimes be necessary, however, to use circumstantial evidence relating to dispersal if we are to arrive at an understanding of the most likely causes of observed distributions (Carlquist, 1981). Fortunately, molecular approaches can now sometimes provide tests of alternative hypotheses, as in studies of Ascension Island green turtles (Bowen, Meylan & Avise, 1989) and Hawaiian crickets (Shaw, 1996).

Arrival of a propagule on an island is not synonymous with establishment: many immigrant species will meet unsuitable environmental conditions, or will lack appropriate food sources. Propagules may repeatedly reach islands as vagrants but fail to establish populations. Immigrants especially likely to fail include the following.

(1) Species (including some Lepidoptera) in which offspring of migrant individuals also have an inherent tendency to emigrate (Farrow, 1984 and *pers. comm.*).

(2) Monophagous herbivores whose foodplants may not be present on isolated islands.

(3) Species requiring continuous supplies of special resources such as carrion, nectar or fruit, which on small islands may occasionally fail.

(4) Parasites restricted to single host species or a group of closely related species that may not be represented on the island.

(5) Species with specialized habitat requirements.

Species adapted for long distance migration are typically exploiters of ephemeral resources (Southwood, 1962; Drake, Gatehouse & Farrow, 1995) and many are polyphagous. Even the latter, however, may fail to maintain permanent populations on islands with very low plant diversity. Presence of a population on Ascension Island at the present time (after introduction of a great variety of alien plants)

does not necessarily indicate that the species had a niche in the prehistoric ecosystem, even though the modern population may be derived from naturally colonizing, recent immigrants (cf. Ferguson, Milburn & Wright, 1991 for Bermuda).

Even if conditions and resources are suitable and sedentary genotypes available, the risk of extinction of a colonizing group by stochastic processes is high while the population comprises only tens of individuals or fewer (Schoener & Spiller, 1987; Diamond & Pimm, 1993), and remains so in species with high variability in population growth rates (Harrison, 1991).

Environmental variability may also lead to the loss of colonizing groups. For instance, Lindroth *et al.* (1973) recorded extinction (most convincingly in the fly *Heleomyza borealis* Boh.) among the early immigrants to Surtsey, Iceland, apparently caused by the unreliability of resources from year to year. Long term environmental fluctuations are also especially dangerous on islands (or habitat islands).

Whereas species on larger land masses may survive unfavourable periods at higher or lower latitude or altitude, or in wetter or drier areas, island populations are less likely to have access to 'climatic refuges' of this kind.

On a small volcanic island such as Ascension, there is a significant risk of elimination of whole communities if an interval during which colonization and succession can proceed is succeeded by massive eruptive volcanism (cf. Anak Krakatau, Thornton *et al.*, 1988). Although Thornton *et al.* point out that volcanism can also permit persistence of populations that might otherwise become extinct as a result of succession, this effect is unlikely to have been important on Ascension, where successional processes are slow.

It is likely, therefore, that the terrestrial biota of Ascension, before the arrival of humans, was kept in a highly dynamic state by the interaction of biological, stochastic, climatic and geological factors. During the existence of the island, many established populations may have become extinct; some of these may have subsequently recolonized the island and the cycle could have been repeated.

Our analysis focuses on the nature of the 'prehistoric' fauna of Ascension (i.e. that present just before the discovery of the island in 1501) which was uninfluenced by human activity. We realize that in other areas, such as Oceania, the start of human influence may not be such an obvious reference point. In the Appendix we make an explicit assessment—for each species known to be established on the island—of the likely origin of the Ascension population. The aim is to distinguish the indigenous (native, autochthonous) species, which colonized the island naturally or are endemic forms derived from such colonists, from the introduced (alien) species, which arrived with intentional or accidental human aid during the last 500 years (cf. Zimmerman, 1948; Lindroth, 1963; Holdgate, 1965; Peck, 1990). Although a substantial number of species have to be left in a 'doubtful' category and some of the other individual decisions will be incorrect, the overall picture is likely to be robust.

The most direct indication that a species is indigenous is provided by endemism: the taxonomic distinctness of an

island form from its nearest continental relatives is *prima facie* evidence that its ancestors colonized the island naturally. However, assessments based solely on endemism are unsatisfactory for several reasons.

(1) Island forms described as endemic sometimes prove to be similar to forms discovered subsequently elsewhere. This is a serious problem in poorly known taxa, or in regions where island faunas are better known than those of the adjacent continents. We therefore generally refer to species and genera known only from Ascension as 'apparent endemics'.

(2) Rapid evolutionary change (whether adaptive or caused by random genetic drift) might give rise to a distinct island form even though the population was introduced by humans in historic times (Baker & Moed, 1987).

(3) Conversely, species may be indigenous to an island without being endemic, either because of insufficient time since colonization for the evolution of obvious differences from the source population, or because immigrants from the source population reach the island so frequently that gene flow prevents evolutionary divergence (Ricklefs & Cox, 1972; Slatkin, 1987).

It is therefore necessary to apply less direct criteria, as well as endemism, in seeking to distinguish indigenous from introduced forms. In relation to Ascension, four main categories of animals must be suspected as having arrived with human aid.

(1) Species that are known to be frequently transported by humans, intentionally or accidentally. These include many vertebrates such as cats and rodents (Atkinson, 1985); external parasites of humans or their domestic animals, such as bed bugs, fleas and lice; species likely to colonize ships or to be included with ships' ballast (Lindroth, 1957); wood-boring insects likely to be imported with timber; and species that infest stored food or are easily transported in other types of cargo as 'travellers' on ships (Aitken, 1975, 1984).

(2) Animal species likely to have been imported with the thousands of plants brought to the island in the 19th century, mainly from the Cape of Good Hope and England (Duffey, 1964). These might include some herbivores and a variety of soil animals (Peck, 1990).

(3) Monophagous herbivores or other species with specialized diets, that are now able to survive on the island but whose special requirements would apparently not have been satisfied before the ecosystem was altered and alien plant species introduced by humans.

(4) Animals with distribution on the island restricted to the vicinity of ports or other likely arrival points for immigrants aided by humans (cf. Basilevsky, 1976 for St Helena).

A useful indication that an island species *might* be indigenous is provided by a demonstration that it can survive in habitats that have changed little under the influence of humans, for instance the barren lava flows and caves of Ascension. Such evidence should be used only as a starting point, however, since introduced species (e.g. *Periplaneta americana*) may also be able to live in these habitats.

Conjecture that a species is indigenous may also arise from the representation of it or close relatives on a number

of other isolated islands. The argument is strong if older islands have endemics and younger islands have undifferentiated forms of the same taxon, but weaker if the populations are non-endemic on all the islands concerned (because of the likelihood of human introduction to all of them).

A particular difficulty arises with cosmopolitan (or pantropical) species. Many species that are now more or less cosmopolitan have evidently been carried around by humans (e.g. Berland, 1926; Moore & Legner, 1974) but others may be similarly widespread because they are adapted for natural long-distance migration and eventually reach many oceanic islands without human aid (Thornton & Harrell, 1965; Ferguson *in* Ferguson *et al.*, 1991). Distinguishing the two types is not easy, but we are reluctant, for instance, to assume that widespread littoral flies are introduced, since the chance of 'rafting' or aerial dispersal seems substantial (see Appendix: Ephydriidae).

In general, we base our assessments of the probability that non-endemic species are natural colonists mainly on evidence about the migratory capabilities of the species or its relatives. Migratory behaviour in insects and other taxa is now understood as an adaptation to temporary habitats that vary in availability and quality both in space and time (Southwood, 1962; Drake *et al.*, 1995). Furthermore, species within major taxa often fall into more or less distinct sedentary or migratory groups.

Although migration is in no sense a passive or accidental process (Kennedy, 1961) the destination of wind-assisted migrants must always be subject to an element of unpredictability. This stochastic component is responsible for the occasional arrival of migrants on oceanic islands on the periphery of the normal 'migration arena' of the population; subsidiary populations founded in this way form spurs in the 'population trajectory' (Drake *et al.*, 1995) that persist for widely varying periods. If they avoid extinction they may eventually become sedentary, endemic species and thus cease to be components of the original 'migration system'.

## MODES OF NATURAL IMMIGRATION

Natural immigration of terrestrial animals to Ascension could occur in three ways: (1) flying, or drifting in air currents; (2) swimming, floating or rafting on flotsam, while drifting in ocean currents; or (3) travelling on another animal, either accidentally or as an evolved mechanism for migration (phoresy). These modes are discussed below in general terms, but issues relating to particular taxa are considered in the Appendix.

### Immigration by air

Most analysts have concluded that aerial immigration is the principal means of arrival of terrestrial arthropods on oceanic islands (e.g. Zimmerman, 1948; Holdgate, 1965; Peck, 1994a). Information on the occurrence of arthropods in the air above the open ocean has been collected by many workers (references in Peck, 1994a) and although these data have rarely been adequately analysed they suggest that it is

mainly groups adapted for aerial migration that colonize remote islands and archipelagos.

Documentation of immigration itself is difficult, though a serious attempt was made by Gressitt (1964) on Campbell Island, using large nets on the windward shore. Direct observations of non-resident conspicuous insects on isolated islands can sometimes provide relevant evidence (e.g. Lindroth *et al.*, 1973; Fox, 1978), especially if the occurrences coincide with weather systems generating airflows that could have brought the insects from a source area. A more systematic approach was used by Farrow (1984), working on Willis Island in the Coral Sea, who used long-term light-trapping and meteorological analysis to provide direct evidence for trans-oceanic immigration of a wide variety of insects, many of which have close relatives in the Ascension fauna.

Drake & Farrow (1988) provide a general review of the influence of meteorological features on insect migration. Immigration to Ascension by air must always have been dependent on weather patterns in the Equatorial and South Atlantic. No systematic observations of arthropod migration in this area have been made, but Johnson & Bowden (1973) and Bowden & Johnson (1976) carefully assessed the likelihood of trans-Atlantic transport of insects. They concluded that the complete absence of winds blowing right across the Atlantic from west to east within 25 degrees north or south of the equator, made it impossible for insects to cross these regions from the New to the Old World at any time of year. These studies imply that animals are very unlikely to reach Ascension by air from the west.

Transport from the east is much more likely. The Intertropical Convergence Zone (Monsoon Trough) in the Atlantic never lies south of 5°S (Barry & Chorley, 1992), so Ascension Island is always within the zone of the South-East Trade Winds. Johnson & Bowden (1973) suggested that westward-moving tropical disturbances could carry African insects out to sea and into the trade winds, which have velocities of up to more than 40 km/h. A more recent meteorological analysis by Hall (1989) suggests that such disturbances, originating in central equatorial Africa, form southern hemisphere 'easterly waves' that move westwards across the tropical Atlantic, bringing exceptional weather to Ascension; these can involve easterly winds of at least 50 km/h at heights of 3–5 km.

Although it is not clear which potential immigrants might utilize the high level easterly winds, it seems probable that most aerial immigrants to Ascension have come from the west coast of southern Africa, a distance of nearly 3000 km. 'Ballooning' spiders or small insects might make the crossing in about 3 days, provided that atmospheric conditions enabled them to maintain altitude both by day and night. Large insects flying actively and predominantly downwind might reach Ascension Island in as little as 2 days, a period known to be within the flight capacity of locusts and also some noctuid moths (Gregg *et al.*, 1994).

The map provided by Bowden & Johnson (1976), plotting records of insects in the tropical Atlantic, indicates many sightings of Orthoptera more than half way to Ascension from the coast of Africa south of the Equator, as well as a

wide variety of insects further north. Additional records are provided by Walker (1931) and Clagg (1966).

A preliminary analysis by J. Bowden (Bowden & Johnson, 1976, p.111) suggested that the arrival of several species of Lepidoptera on Ascension was closely associated with the movement of frontal systems from south western Africa over the Atlantic. The specimens concerned were collected in late 1974 and sent to Rothamstead Experimental Station; they have now been identified. We feel, however, that it is unwise to take the matter further, since it now appears that some of the species may have had populations already established on the island.

The most dramatic—though circumstantial—example of the arrival of insects on Ascension by air occurred on 22 May 1976; it was not obviously related to exceptional weather, with only 5.8 mm rainfall in the month concerned (Mathieson, 1990). Ghauri (1983) reported that huge swarms of the cosmopolitan leafhopper *Balclutha saltuella* (Kirschbaum) (= *B. pauxilla* Lindberg) descended on the island. The insects were first detected just before dawn between 05.00 and 06.00; they were attracted to lights but dispersed somewhat as it became fully light; residents spent much time sweeping up the insects from inside the houses. Specimens for identification were recovered from household fixtures 8 months later.

Ghauri was convinced that the insects did not originate on Ascension Island, citing the lack of suitable habitat for this grass-feeding species. We are not quite so sure, since large areas on Ascension become covered with grass (mainly *Enneapogon cenchroides* (= *mollis*) C.E. Hubbard) after exceptional rains, and in 1963, after such rains, a plague of an unidentified 'tiny pale green grass fly' is known to have occurred (J. Packer, *pers. comm.*); furthermore, we collected *B. saltuella* on the island in 1995, after rain. However, the suddenness of the appearance of *Balclutha* in 1976 and the fact that rainfall in the previous year was below the average for the period 1962–89 (Mathieson, 1990) gives support to the immigration hypothesis.

Ghauri argued that the insects had probably travelled for about two days with southeasterly winds from grasslands in Angola more than 3000 km away. Adaptive long distance migration of cicadellid leafhoppers in other areas is well documented (Taylor & Reling, 1986) and it is not implausible that *B. saltuella* should have made the transoceanic flight to Ascension. Intriguingly, this species has recently been added to the British fauna after discovery of an individual in the Isles of Scilly, another place that is sometimes reached by aerially migrating species from warmer continental areas (Ashmole & Ashmole, 1995).

There is also a possibility that some immigrant species may have reached Ascension from West Africa, only about 1500 km north of the island, under the influence of exceptional weather systems, possibly associated with ENSO events (Philander, 1986). The relevance of these is indicated by the fact that one of the few records of vagrant dragonflies on Ascension occurred during such a disturbance. A single dragonfly was seen at the Georgetown Power House on 3 March 1963 (letter dated 8 March 1963 from F. E. Duncan to Arthur Loveridge). The weather during March 1963 was

unsettled and on 29–30 nearly 11 inches (28 cm) of rain fell in Georgetown (John Packer, *pers. comm.*).

In considering the probability of aerial immigration by the various members of the Ascension fauna we tried to determine which of the species were known to undertake long-distance aerial migration, or belonged to higher taxa in which such movement had been documented. Relevant evidence comes from direct observation, tracking by radar and from capture of specimens at high altitudes in the air (aircraft or kites) or from tall structures or ships at sea. It is noteworthy that even wingless species may be adapted for aerial migration: ballooning behaviour of spiders is well known, but behavioural adaptations for aerial dispersal have now been shown to exist in a variety of other small, wingless arthropods such as tetranychid mites (Margolies, 1987).

### Immigration by sea

Peck (1990, 1991) analysed the arthropod fauna of the Galápagos and concluded that rafting might be the most important mode of natural colonization for terrestrial arthropods, and especially for eyeless species whose continental ancestors were also eyeless. In a later paper (Peck, 1994a) he emphasized the role of aerial dispersal in the fauna in general but pointed out that direct flotation on the sea surface—as well as rafting—could be relevant for some taxa. In a study much more extensive than that by Ashmole & Ashmole (1988) off Tenerife, Peck (1994b) used a neuston (or pleuston) net to collect arthropods from the sea surface; like us, he was unable to determine how many of these were alive. As Peck pointed out, some of the animals were doubtless originally airborne and then fell to the sea surface, but others may have been washed out to sea by heavy rains, or drifted out of littoral habitats. We are doubtful whether flotation without the aid of 'rafts' plays a significant role in transoceanic colonization of islands by arthropods.

Many coastal species, however, have high population densities and are often found on debris that has been washed up and may later be refloated (Lindroth *et al.*, 1973). Halophilic arthropods such as some mites, isopods, collembolans and mogoplistine crickets are especially likely to survive long periods on flotsam (as eggs, young or adults), and so are larvae of wood-boring animals (Heatwole & Levins (1972); even vertebrates are known to be occasionally transported in this way (e.g. Cheke, 1975). Of potentially great importance, but difficult to study on account of its rarity, is the transport of groups of land animals and plants on clumps of vegetation or 'floating islands' (Zimmermann, 1948; Holzapfel & Harrell, 1968; Taylor *et al.*, 1979).

Flotsam reaching Ascension is likely to arrive on currents from the southeast or east (Scullion, 1990), so the most likely immigration route is from the west coast of southern Africa. Data presented by Guppy (1917) suggest that the passage from the continent would be likely to take about 3 months.

With respect to both aerial and seaborne immigration it should be remembered that Pleistocene climatic fluctuations will have resulted in variation in winds and currents in the

South Atlantic: many of the modern populations may have been founded by propagules arriving under conditions somewhat different from those pertaining now.

#### Immigration on another animal

External parasites of birds such as Phthiraptera (= Mallophaga) and Hippoboscidae must sometimes arrive in new areas as a consequence of living on their hosts. Some other taxa, especially among Pseudoscorpiones and Acari, have evolved phoresy (on birds or insects) as a means of dispersal; it seems likely that this mode of arrival has been important on Ascension, at least for the Pseudoscorpiones. In some other groups it is less clear whether transport on other animals is accidental or adaptive: for instance, snails have been found nipped on the legs of bees and on the plumage and feet of birds (Rees, 1965).

#### ASSESSMENT OF STATUS OF SPECIES ESTABLISHED ON ASCENSION

In the Appendix we consider the origin of the Ascension populations of each of the terrestrial species considered to be (or have been) established on the island and place each of them in one of four categories, the second and third of which involve subjective judgements on the available evidence. The categories are as follows.

(1) 'Apparently endemic' species, which are thought to have evolved on the island from natural immigrant ancestors; this category is normally abbreviated to 'endemic'.

(2) 'Indigenous non-endemic' species, which were probably members of the prehistoric terrestrial community but are not taxonomically differentiated; normally abbreviated to 'indigenous'.

(3) 'Introduced' species, which were probably brought to the island by humans, either accidentally or on purpose.

(4) 'Doubtful' species, for which natural and human-assisted arrival seem roughly equally probable, or natural immigration seems likely but establishment may have been impossible before the introduction of alien plants; or for which adequate identification is not available.

The approach is systematic, following the sequence used by Kaestner (1980) for non-hexapod arthropods and the ordinal sequence of Gullan & Cranston (1994) for the hexapods. Within the orders of hexapods the sequence of families is that of Borror, De Long & Triplehorn (1981) and within these, genera are arranged alphabetically. Mention of the presence of a species on St Helena, where no authority is quoted, is based on the paper on the relevant group in the series resulting from the Belgian expeditions to that island in 1965–67, published in *La faune terrestre de l'Isle de Sainte-Hélène, Ann. Mus. Roy. Afr. Centr., Sér. In-8° Sci. Zool.* 181 (1970), 192 (1972), 215 (1976) and 220 (1977). Records attributed to Duffey are from his 1964 paper.

Table 2 provides a numerical summary of all species recorded from Ascension, grouped at ordinal or higher level, based on the individual assessments detailed in the Appendix.

Out of a total known fauna of 311 species, 138 are

considered to be probably introduced by humans and many more are possibly so. Since there are twenty-nine endemic species and sixty-six more considered as indigenous, this implies that Ascension Island—at the time of its discovery by humans—had breeding populations of between ninety-five and 173 animal species. However, some other native species, especially of nematodes, mites and chewing bird lice (Phthiraptera) are probably still to be discovered. The native fauna included two marine turtles, twelve marine birds (one endemic), two land birds (both endemic and extinct) and one additional non-endemic land bird that may have been established on the island in the past. The remainder of the known terrestrial fauna consisted of 78–156 species of invertebrates. These may have included a generically endemic ocnerostrilid oligochaete and perhaps a few gastropod molluscs, but the vast majority were arthropods. The latter included twenty-five apparently endemic species, three of them representing endemic genera (in Araneae, Oribatida and Psocoptera).

In the prehistoric arthropod fauna of Ascension the large numbers of endemic species were apparently in the orders Pseudoscorpiones and Araneae, Isopoda, Collembola and Orthoptera. Overall species richness, however, was probably easily highest in the orders Araneae and Lepidoptera, followed by Diptera, Orthoptera, Collembola, Psocoptera, Pseudoscorpiones, Isopoda and Hemiptera; Acari were probably also diverse. Coleoptera—now the second most diverse order (after Araneae)—were probably poorly represented in the past; other invertebrate orders had less than five species.

Since its discovery in 1501, 138–216 additional animal species, brought to the island by humans, are known to have established breeding populations. We expect that a number of other species in this category remain to be found on the island, and others will arrive in future.

#### THE PREHISTORIC ECOSYSTEM: A SPECULATIVE RECONSTRUCTION

The formation of the volcanic island of Ascension some one and a half million years ago produced a pile of lava and ash inhospitable to most forms of life. The way in which animal communities develop on such terrain in the period following volcanic activity has been studied especially by Lindroth *et al.* (1973), Howarth (1979), Edwards *et al.* (1986), Thornton *et al.* (1988 and related papers) and Ashmole *et al.* (1992).

Some of these studies have shown that in areas surrounded by older terrestrial communities, the early colonists of both surface and subterranean habitats consist of scavengers and predators that depend for nourishment mainly on the input of organic matter from other areas where vegetation is already established. On Ascension, the lack of nearby vegetated land must have severely restricted the input of wind-drifted biological material from terrestrial sources. Nutrient input could occur, however, in several other ways (Lindroth *et al.*, 1973; Heatwole, Done & Cameron, 1981; Ashmole *et al.*, 1990): (1) chemolithotrophic bacterial activity; (2) input of marine bacteria and other organic material from the 'sea-salt aerosol' (Wilson, 1959;



TABLE 2. Summary of terrestrial animals recorded from Ascension Island.

*Notes.* Under 'Endemic' numbers with queries refer to species not yet studied in detail but probably distinct; numbers in parentheses indicate new species discovered by us (included in the preceding figure). The column headed 'Indigenous' relates to probably indigenous species, additional to the endemics; vagrant birds, dragonflies and hawkmoths are omitted. The column headed 'Doubtful' is used both for species in which the origin of the Ascension population is particularly uncertain, and for most populations whose specific identity is not yet known. The column headed 'Introduced' relates to species certainly or probably introduced by humans, either intentionally or by accident; species that were introduced but have subsequently died out or been exterminated are omitted, as are non-feral farm and domestic animals.

TAXON	Endemic	Indigenous	Doubtful	Introduced	Total
Anura	0	0	0	1	1
Chelonia	0	2	0	0	2
Squamata	0	0	0	2	2
Aves	1 + 2ext.	11	1	5	20
Mammalia	0	0	0	5	5
Tricladida	0	0	0	1	1
Gastropoda	0	1	3	6	10
Oligochaeta	1?	0	0	5	6
Scorpiones	0	0	0	2	2
Araneae	4 (1)	3	23	13	43
Ixodida	0	1	0	1	2
Prostigmata	1?(1)	2	0	0	3
Oribatida	1?(1)	1	2	0	4
Pseudoscorpiones	5 (2)	0	0	0	5
Amphipoda	0	0	1	2	3
Isopoda	3 (2)	1	1	8	13
Decapoda	0	1	0	0	1
Polydesmida	0	0	0	1	1
Julida	0	0	0	2	2
Scolopendromorpha	0	0	1	2	3
Lithobiomorpha	0	0	0	1	1
Geophilomorpha	1 (1)	0	1	1	3
Collembola	3(3)	2	5	2	12
Thysanura	0	0	0	3	3
Orthoptera	3?(2)	4	1	1	9
Phasmatodea	0	0	0	1	1
Dermaptera	0	0	0	1	1
Isoptera	0	0	0	1	1
Blattodea	0	0	1	4	5
Embioptera	0	0	0	2	2
Thysanoptera	0	1	0	0	1
Homoptera	0	2	2	5	9
Heteroptera	0	3	1	2	6
Psocoptera	1 (1)	3	4	0	8
Phthiraptera	0	1	0	0	1
Coleoptera	0	3	6	29	38
Neuroptera	0	1	0	0	1
Hymenoptera	1?(1)	0	2	13	16
Lepidoptera	2	11	14	8	35
Siphonaptera	0	1	0	0	1
Diptera	0	11	9	8	28
<b>Total</b>	<b>29</b>	<b>66</b>	<b>78</b>	<b>138</b>	<b>311</b>

Blanchard, 1983), assisted by sea breezes (Drake & Farrow, 1988); (3) transfer of organic material, by wind or movement of animals, from the productive intertidal zone towards the interior; (4) input of marine biomass by nesting seabirds; (5) input of biomass in the form of carrion and flotsam deposited on the beaches and utilized by terrestrial animals.

We suspect that the last three factors were most important in supporting the earliest animal communities on Ascension.

Subsequent development of ecosystems on volcanic

terrain involves a process of faunal succession linked to vegetational succession, with increasing dependence of the animal communities on local primary production. On Ascension, the arid climate of the lowlands limited the development of vegetation cover even after some plant species arrived, but scattered plants became established in the desert and more complex but still depauperate plant communities developed on Green Mountain. The nature of the vegetation just before interference by man has been

discussed by Duffey (1964) and Cronk (1980) on the basis of accounts by early travellers such as Osbeck (1771), who visited the island in 1752, Stüder (1889) and Dahl (1892); our descriptions of the vegetation in various regions of the island are based on all these sources.

We provide below an overview of the various animal communities of Ascension Island shortly before the arrival of humans. This summary is necessarily speculative. Although for simplicity we use direct statements such as 'species X was present' and eschew the word 'probably', the discussion must be read as informed opinion rather than demonstrable fact. In the Appendix we have attempted to identify species that—on the basis of their known biology—can plausibly be considered to have colonized the island naturally, and those that are more likely to be introduced; the latter group are not mentioned here, but some doubtful cases are included with qualification.

The assignment of apparently indigenous species to the various habitats is based on our own systematic collections (summarized in Table 1) and the collection of Lepidoptera made by Kirke (Robinson & Kirke, 1990), supplemented by information in Duffey's (1964) account. The reconstruction is most tenuous in respect to the high mountain zone, where the original vegetation has been almost entirely destroyed, and in the foothill zone where the main indigenous shrub has disappeared and introduced plants are dominant. The seabirds are not considered here because their original populations are discussed in detail elsewhere (Ashmole *et al.*, 1994; Bourne *et al.*, in prep.).

### Coastal communities

The sandy beaches of Ascension were breeding places for the marine turtles *Chelonia mydas* and *Eretmochelys imbricata*, which were probably much more numerous than at present. Along the coastal margins of the lava fields almost the only plants were *Portulaca oleracea* L., *Ipomoea pes-caprae* L. and perhaps also *Commicarpus helenae* (= *Boerhaavia verticillata*).

The animal communities within about 100 m of the shore were similar to those present now. Scavengers included the landcrab *Gecarcinus lagostoma* and the halophilic collembolan *Pseudosinella* species C and the abundant mogoplistine cricket species C, along with the isopod *Littorophiloscia tropicalis* and two tenebrionid beetles, *Clitobius ovatus* and—in sandy places—a species of *Phaleria*. Diptera included a number of typical seashore flies. The canaceid *Canace* sp. and the syrphid *Eristalis aeneus* bred in decaying plant material, and adults of the latter fed on nectar of *Ipomoea*. Seashore carrion was utilized by the ephydrid *Hecamede brasiliensis* and the chloropid *Cadrema pallida*, as well as the generalist phorid *Megaselia curtineura*. A calliphorid *Chrysomya* sp. and one or two species of *Sarcophaga* may also have been present.

Herbivores were scarce in this zone, but *Ipomoea pes-caprae*, which has little or no chemical protection (Wilson, 1977), was utilized patchily by the polyphagous species mentioned below in relation to the inland lava flows (especially orthopterans and the butterfly *Hypolimnas*

*missippus*) and perhaps also by the pterophorid moth *Trichoptilus wahlbergi*.

The most conspicuous terrestrial predator here was the endemic and now extinct night heron *Nycticorax* sp.; both here and further inland it may have preyed extensively on the landcrab, as *Nycticorax violacea* (L.) is thought to prey on its relative *Gecarcinus planatus* Stimpson on Socorro Island, Mexico (J. Llinas, in Jiménez *et al.*, 1994). Arthropod predators included the geophilid centipede *Tuoba ashmoleorum* in soft damp substrates, and bdellid mites of the genus *Bdellodes* which preyed on small arthropods or their eggs on the surface. The staphilinids *Atheta coriaria* and *Belonuchus formosus* may have been present, and the spiders may have included the prodidomine gnaphosid *Zimirina* sp. and perhaps also *Trachyzelotes jaxartensis*.

### Communities of inland lava and cinders

Under the normal dry conditions, the lava fields and cinder cones away from the coast and below about 330 m were barren apart from occasional tussocks of the grass *Aristida adscensionis* (L.), which is widespread in the tropics; in places with accumulations of fine ash there were cushions of the endemic *Euphorbia origanoides* L. In dry watercourses there were occasional clumps of the sedge *Cyperus appendiculatus* Brongniart (which is restricted to South Atlantic islands) and also of the grass *Digitaria* sp. aff. *adscendens* H.B.K. and a few individuals of the endemic rubiaceous shrub *Oldenlandia adscensionis* (DC.) Cronk.

The scavenger community in this zone was somewhat different from that on the coast: the halophilic collembolan, cricket and isopod species were replaced respectively by *Pseudosinella* species B (and perhaps also a species of *Drepanura* and the sminthuridids *Denisiella* and *Sphaeridia*), mogoplistine species B, and one or both of the isopods *Niambia longiantennata* and *N. duffeyi*. The tineid moth *Phereoeca altuella* lived in cracks on these lava flows as well as in cave thresholds, feeding on dry remains of insects; the phorid was again present, and perhaps also the milichiid *Milichiella lacteipennis*.

Herbivores were normally scarce in this zone, but an apparently endemic new species of eupodoid mite was present in some areas, perhaps feeding on algae, and the generically endemic oribatid *Cordylobates fragilis* fed on lichen and pollen. Also feeding on lichens was the apparently endemic tineid *Eudarcia* sp. The lygaeid bug *Nysius ericae* utilized *Portulaca oleracea* and perhaps *Euphorbia origanoides*, and the latter species may also have been eaten by the rhopalid *Liorhyssus hyalinus* and a species of aphid. *Cyperus appendiculatus* was eaten by the moth *Cosmopterix attenuatella*.

After the occasional torrential rains the increased crop of grass and other vegetation was exploited by several grass-feeding Hemiptera including the delphacid *Toya thomasseti* and perhaps sometimes the cicadellid *Balclutha saltuella* and an orthotyline mirid, as well as a variety of polyphagous herbivores, which in recent centuries have sometimes reached plague abundance. Some of these species were present in the desert even under the normal dry conditions: the acridids *Schistocerca gregaria* and *Locusta migratoria*,

the gryllid *Gryllus bimaculatus* and the tettigoniid *Ruspolia differens*. Beetles and moths may also have made use of the ephemeral vegetation, but are treated later in the context of the more permanent habitats higher up.

The predator community in this zone was dominated by spiders. Likely species include a species of *Scytodes*, the endemic *Opopaea euphorbicola*, *Zelotes inauratus*, *Zimiris* sp., the endemic *Prodidomus clarki* and *P. duffeyi*. *Araneus theisi* and one or more theridiids may also have been present. Another predator in the desert was the pseudoscorpion *Allowithius ascensionis*. In cinder fields small arthropods were preyed on by a bdellid mite *Spinibdella* sp., and a scolopendromorph *Cryptops* sp. may also have been present. Predatory insects on the scattered plants included the heteropteran *Tropiconabis capsiformis* and perhaps also a lacewing *Chrysopa* sp. and an unidentified syrphid, both thought by Dahl (1892) to be preying on aphids.

### Communities of the foothills

On the lower slopes of the mountain, between about 330 and 600 m (the semi-desert of Duffey), the dominant plant in the open was *Portulaca oleracea*; there were also scattered grasses (*Aristida adscensionis* and in the upper part the tiny endemics *Sporobolus durus* Brongniart and *S. caespitosus* Kunth.), together with *Cyperus appendiculatus* and *Euphorbia origanoides* (Stüder, 1889; Krümmel, 1892). The endemic fern *Pteris adscensionis* Swartz was present among the rocks and the shrub *Oldenlandia adscensionis* probably increased in density with altitude.

Scavengers in this zone doubtless included a number of species already mentioned, but with greater abundance of species utilizing plant litter. The isopods *Niambia* spp. and the psocopterans *Cerobasis* cf. *maya* and *Ectopsocus strauschi* were present.

There is no evidence on the herbivores associated with *Oldenlandia adscensionis*, but the hemipterans already mentioned were present in this zone, together with the larvae of the nymphalid *Hypolimnas misippus* on *Ipomoea pes-caprae* and *Portulaca oleracea*. The thysanopteran *Haplothrips gowdeyi*, the anthicid *Omonadus floralis* and the gastropod *Vallania pulchella* were present here and perhaps in the adjacent zones. Other herbivores that may have been present are coccinellid beetles in the genera *Cheilomenes* and *Exochomus*, an aphid and one or more additional gastropods. The foothills were also an important habitat of the landcrab *Gecarcinus lagostoma*, which in this zone was mainly herbivorous, like *G. planatus* on Socorro Island (Jiménez *et al.*, 1994).

This region provided permanent refuges for the polyphagous orthopterans and lepidopterans that were abundant in the lowland deserts after rain. Noctuids were well represented, the most likely species being: *Mythimna loreyi* feeding on grasses; *Spodoptera exigua* and *S. littoralis*; *Trichoplusia ni* and *Thysanoplusia orichalcea*. Pyralids included *Herpetogramma licarsisalis* and probably also *Hellula undalis* and *Spodalea recurvalis*.

Predators in the foothills included the scolopendromorph *Cryptops* sp. and possibly the geophilomorph *Mecistocephalus insularis*, spiders included the lycosid

*Pardosa inopina*, a tetragnathid *Dyschiriognatha* sp., several gnaphosids, and perhaps *Araneus theisi* and one or more clubionids. Parasitoids were not well represented in this or any other habitat, but the bethylid ?*Trachepeyris* sp. was present, and perhaps also an ichneumonid campoplegine.

### Communities of the high mountain

In the misty region close to the ridge of Green Mountain (above 600 m on the windward side and rather higher in the north and west) the original vegetation was dominated by ferns, of which six were endemic. However, the endemic grass *Sporobolus caespitosus* Kunth. was also present, and a few of the angiosperms mentioned in relation to the foothills penetrated this zone. There were also more than thirty species of mosses (including an unknown number of endemics), two species of lycopods, about ten liverworts and large numbers of lichens including many endemics. The invasion of this vegetation by introduced plants largely vitiates assessment of the original animal community there. We would expect scavenging, herbivorous and predatory mites to have been present; other scavengers and herbivores doubtless included collembolans and psocopterans, and perhaps the tineid moth *Erechthias* sp. feeding on dead plant material and the syrphid *Eristalis tenax* breeding in wet places. There may have been a few host-specific herbivores, but none have been recorded. Predators doubtless included mites and a few spiders, such as the linyphiids *Lepthyphantes* sp. and *Bathyphantes* sp.

### Communities in seabird colonies

Seabird colonies on islets and in the desert lowlands of the main island had accumulations of guano but negligible vegetation. Decaying animal matter and guano was exploited by two mogoplistine crickets, the tenebrionid beetle *Clitobius ovatus*, the milichiid fly *Leptometopa latipes*, the chloropid *Siphunculina striolata* and perhaps one or two flesh flies *Sarcophaga* sp. Other scavengers that may have been present were *Dermestes ater* or another dermestid beetle, the tineid moth *Tinea subalbida* feeding on feathers and dry remains of insects, a pyralid moth noted by Duffey on Boatswainbird Island and the isopod *Cubaris murina*.

Predators in these colonies included the endemic Ascension frigatebird *Fregata aquila* (Fig. 6) and the extinct night heron *Nycticorax* sp., both of which took young birds, and the extinct flightless rail *Atlantisia elpenor* (Fig. 7) which fed mainly on invertebrates associated with the seabirds; both heron and rail also acted as general scavengers. Predatory arthropods in the colonies included the endemic pseudoscorpions *Stenowithius duffeyi* and—at least on islets—*Neocheiridium* sp. and *Garypus titanius*; the latter is the largest known member of this order (Fig. 8). There were also two species of gnaphosid spiders (a probable drassodine and a probable *Nodocion* sp.), one or more clubionids and perhaps also an oecobiid *Oecobius* sp. and a salticid *Plexippus paykulli*. Some other spiders mentioned as occurring in the desert were doubtless also present in the colonies.

The landcrab *Gecarcinus lagostomus* also played a



FIG. 6. Two juvenile Ascension frigatebirds, *Fregata aquila* Linn., the only extant bird species endemic to Ascension Island. The lower individual is in the act of swallowing a hatchling sooty tern, *Sterna fuscata* Linn.

predatory role in mainland bird colonies; although it is an omnivore rather than simply a predator, it may have caused significant losses of eggs and young of seabirds. Olson (1981) suggested that the almost complete absence of populations of procellariiform birds (apart from the crevice-nesting *Oceanodroma castro*) from Ascension might be due to the presence of *Gecarcinus*, to which young petrels would be extremely vulnerable since they are typically left unattended for long periods.

External bird parasites certain to have been part of the original fauna are the argasid tick *Ornithodoros denmarki*, a number of feather lice including *Saemundssonina ?remota*, the hippoboscid fly *Olfersia aenescens* and the pulicid flea *Xenopsylla aff. gratioiosa*. A bethylid parasitoid of invertebrates was also present.

#### Subterranean communities

The subterranean fauna is found not only in caves, but also distributed throughout the network of smaller spaces that underlies recent volcanic terrain, forming the 'MSS' or

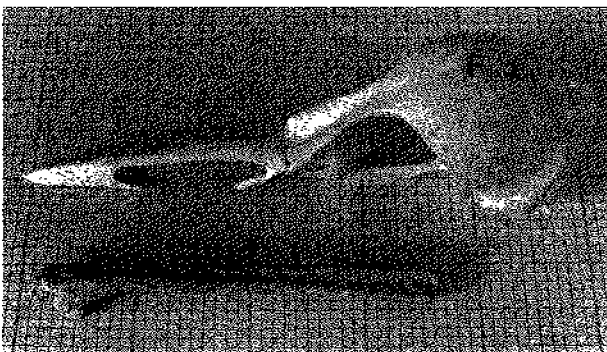


FIG. 7. The first specimens of *Atlantisia elpenor* Olson, the extinct flightless Ascension rail: skull and tarso-metatarsus found respectively in Packer's Fumarole (near Packer's Hole) and in old guano on the South Gannet Lava Flow, during the British Ornithologists' Union Centenary Expedition, 1957–59.



FIG. 8. Endemic pseudoscorpions from Boatswainbird Island. The large specimen is *Garypus titanius* Beier, the largest known pseudoscorpion; the small specimen is *Stenowithius duffeyi* Beier. Scale bar shows units of 0.5 mm.

mesocavernous shallow stratum (Juberthie, Delay & Bouillon, 1980; Medina & Oromí, 1990; Ashmole, 1994). Scavengers in these habitats included the troglomorphic collembolan *Pseudosinella* species A, the cricket *Mogoplistes* species A, and two species of psocopterans: the liposcelidid *Troglotroctes ashmoleorum* and a species of *Sphaeropsocopsis*; these may have been accompanied by another collembolan *Seira* sp., one or more psyllipsocids and—in lowland caves—the blind white isopod *Elumoides coecus*. *Gecarcinus lagostoma* was also present. Predators included several arachnids adapted to subterranean life: the pseudoscorpion *Apocheiridium cavicola*, the linyphiid spider *Catonetria caeca* and probably also a pholcid with reduced eyes. Other spiders that may have been present include an oonopid *Orchestina* sp., one or more pholcids and the gnaphosid *Trachyzelotes jaxartensis*.

#### Stygobionts

Although this paper is concerned with terrestrial animals it should be mentioned that some stygobionts (groundwater organisms) have been recorded from Ascension. Populations of two endemic caridean shrimps are present at the site that we called South Gannet Pools (Chace & Manning, 1972; Abele & Felgenhauer, 1985). The atyid *Typhlatya rogersi* Chace & Manning was the first member of its genus found in salt water; it is preyed on by *Procaris ascensionis* Chace & Manning, which represents a new family (Procarididae). Biernbaum (1996) found three endemic amphipods in these anchialine pools and suggested that speciation was in process in one genus. Stock & Vonk (1989) made more general studies of groundwater fauna on the island, and Vonk & Stock (1991) recently described a new blind marine interstitial isopod *Caecostenetroides ascensionis* (Gnathostenetroididae) from a beach near Hummock Point. Though Chace & Manning were inclined to think that

*Typhlatya* had colonized the island since it became subaerial, both they and Vonk & Stock mentioned the possibility that populations of shallow-water crustaceans might have persisted on islands and seamounts in the area since the opening of the Atlantic.

## DIVERSITY AND EVOLUTION ON ASCENSION AND ST HELENA

Ascension shares with other young and remote islands a tendency for the indigenous fauna and flora to have both low species richness ('impoverishment') and disproportionate representation of taxa that are easily dispersed ('disharmony'). Such 'waif-biotas' are established on oceanic islands by long-distance dispersal.

Considering the arthropods alone (and ignoring the feather lice that come with birds and are anyhow unstudied on Ascension), Table 2 shows twenty-five endemics and a total of 151 species in the endemic, indigenous and doubtful categories. For comparison, the Tristan group—even more isolated in the South Atlantic—has about 120 arthropods in roughly comparable categories (Holdgate, 1965). An analysis of this kind has not yet been done for St Helena, but it has more than 350 endemic species (and about seventy endemic genera) in a total arthropod fauna (including obvious introductions) of nearly 1000 species. However, as argued below, many of the St Helena species have been formed by speciation events on the island.

Disharmony in the native Ascension fauna is exemplified by the strong representation of dispersive taxa such as Araneae, Lepidoptera, Orthoptera, Pseudoscorpiones and Psocoptera, and by the probable prehistoric absence of a number of widespread taxa with limited powers of dispersal, for instance vertebrates other than birds and turtles, Dermoptera, Isoptera and Formicidae. Whereas Araneae and Coleoptera have comparable numbers of species in the fauna today, there may have been only half a dozen species of Coleoptera on Ascension in the past, but more than twenty species of Araneae.

Some groups missing from the Ascension fauna have high dispersal ability and may have reached the island but been unable to establish themselves due to habitat deficiency or the absence of specific food plants or hosts for parasites (cf. Farrow, 1984). These include many families of Diptera and Hymenoptera, as well as Odonata and the hawkmoths (Sphingidae). The latter, for instance, are strong flyers that are often collected at sea and have colonized other oceanic islands including Hawai'i, Norfolk Island (Holloway, 1977), Henderson Island (Benton, 1995) and St Helena (Melliss, 1875); they were also recorded as immigrants to Willis Island in the Coral Sea (Farrow, 1984). Sphingids have doubtless reached Ascension on various occasions (a single individual has been collected) but at least in the past would not have found suitable larval food plants or adequate sources of nectar.

If it had been undisturbed by humans, the natural fauna of Ascension would presumably have gradually increased in richness. As Wilson (1969) pointed out, island biogeography theory suggests that islands will continue to accumulate species over long periods, even disregarding speciation,

which is discussed below. This is partly through the gradual arrival of taxa preadapted to the peculiar physical conditions of the local environment, which will have lower average risk of extinction than initial colonists (the latter arrive quickly because of high dispersal ability). At the same time, adaptive evolution within the colonizing populations will reduce their risk of extinction and thus contribute to an increase in the number of species present. On a volcanic island, processes of succession will also play a major part (Lindroth *et al.*, 1973; Thornton & New, 1988; Ashmole *et al.*, 1992). As plants colonize and complex vegetation develops, herbivorous immigrants are more likely to have their requirements fulfilled, and their establishment in turn provides scope for development of associated communities of specialized predators and parasites.

Ascension Island is a relatively young and extremely isolated island, and the lack of maturity of its fauna is easily demonstrated in many groups (see Appendix). Coleoptera, for instance, have some thirty-eight species in thirty-three genera, but probably less than ten species are indigenous and none are endemic. That this is not a long-term equilibrium is shown by comparison with St Helena, which lies in a comparable geographical situation, is similar in size, but is very much older (minimum 14 million years versus minimum 1.5 million for Ascension). On St Helena there are 256 species of beetles placed in 137 genera. If only endemic species are considered, we find 157 species in fifty-one genera, or 3.1 species per genus (Basilewsky, 1985).

One relevant factor in the contrast between the two islands is that congeneric species may accumulate on an old island by repeated colonization from a single continental stock. If the first colonization is followed by genetic divergence between the mainland parental stock and the island population and this gives rise to reproductive isolation, a subsequent colonization by the same stock can lead to sympatry of two congeneric species on the island (Mayr, 1942; Holloway, 1977; Williamson, 1981). The same kind of process can occur between the islands in an archipelago, the marine channels between the islands providing spatial isolation leading to allopatric speciation (Lack, 1947; Carson, 1970; Harper, 1987).

The latter effect is relevant if isolated single islands such as Ascension and St Helena had companions in the past. Two old seamounts west of Ascension were once high islands (Brozena, 1986) but expected rates of submergence of islands formed at a mid-ocean ridge indicate that even the closer one probably ceased to be an island before the emergence of Ascension. Grattan seamount, 250 km southeast of Ascension and submerged by only 72 m, was presumably just subaerial in the past, at least during the last glacial maximum when sea level was more than 100 m lower than at present. However, Grattan is presumably younger than Ascension and is unlikely to have played a significant part in the colonization of the latter by animals and plants, although seabirds and turtles doubtless made use of it for breeding. Near St Helena is Bonaparte Seamount (minimum depth 105 m) 110 km to the west, which has probably been subaerial in the past, at least during Pleistocene glaciations. It is younger than St Helena but the possibility of faunal

interchange between the two islands during its periods of emergence must be borne in mind.

It has long been realized, however, that among invertebrates, divergence and speciation often occurs within islands as well as between them (e.g. Carson, 1970; Basilewsky, 1985). New evidence on cavernicolous species also supports the regular occurrence of speciation within single islands (e.g. Howarth, 1988, 1991; Peck, 1990; Oromí *et al.* 1991). Comparison of the faunas of Ascension Island and St Helena shows the overwhelming effect of the multiplicative process of repetitive speciation (Stanley, 1979). Given enough time, it seems that a few groups which have the capacity to speciate within the confines of a single island, do so repeatedly and thus come to dominate the fauna in numerical terms. On ancient St Helena this process is relatively far advanced in several groups, while on youthful Ascension it has barely begun.

The contrast in diversity between the two islands is not evenly spread taxonomically. Even on St Helena repetitive speciation within clades has been the exception rather than the norm, though the numerical effect on the composition of the fauna has been great. The groups in which the process has obviously operated are charopid and subulinid Gastropoda, cicadellid and mirid Hemiptera, anthribid, curculionid and carabid Coleoptera and tineid Lepidoptera. Comparable cases in Hawaiian crickets has recently been analysed using both acoustic and molecular methods (Otte, 1994; Shaw, 1996).

In some groups on St Helena true adaptive radiation has taken place, with clades of endemic species apparently generated by adaptation to different climatic zones or by host plant specialisation (cf. Johnson *et al.*, 1996). For example, the Miridae of the subfamily Phylini have nine species, several of which are associated with particular endemic plants. They are currently placed in eight endemic genera but perhaps originate from a single colonization event. Ascension, in contrast, has only one mirid of unknown status; adaptive radiation involving different host plants would hardly have been possible here because of the very low diversity of vascular plants (about twenty-five indigenous species, half of them ferns).

High diversity in some other groups on St Helena may be the result of speciation with little or no adaptive specialization, perhaps as a result of exceptionally low mobility in a topographically complex landscape (Gittenberger, 1991; Cameron, Cook & Hallows, 1996). The bembidiine carabids of St Helena provide an example: many modern species were apparently sympatric at a fine level (some are probably now extinct) but there does not seem to have been strong niche differentiation (Wollaston, 1877; Basilewsky, 1972).

In many other families and genera on St Helena, for instance among the spiders, diversity is relatively low, colonizing stocks having given rise to only one or a few species. Endemism, however, is very high (except among putatively introduced species) and is often at the generic rather than the specific level. In the case of St Helena's plants, generic endemism has been convincingly interpreted in terms of an island relict hypothesis suggesting that taxonomic isolation of the St Helena forms is a result of

ancient colonization followed by extinction of the ancestral stock on nearby continents (Cronk, 1987). There are many obvious parallels among the St Helena arthropods, one being the carabid beetle *Aplothorax burchellii*, which is the sole species in a very distinct endemic genus that must represent an ancient relict stock (Basilewsky, 1972).

In some groups of island animals, however, generic endemism may simply reflect long-continuing phyletic change. The pseudoscorpions provide a possible example. This is a group that on a worldwide basis shows relatively low diversity but high dispersal ability, mainly by phoresy. Ascension Island, in its short life, has acquired at least five apparently endemic species in different non-endemic genera. On St Helena eight species are known but three of these are probably introduced from Europe. The remainder comprise four species in three endemic genera and one endemic species in a widespread genus. Endemism is thus mainly at the specific level on Ascension and at the generic level on St Helena, but radiation is minimal even on St Helena, with only one presumed speciation event.

On Ascension evidence of phyletic change is relatively scarce. Some 69–83% of the indigenous fauna (the figure depending on how many 'doubtful' species are really indigenous) comprise non-endemic species that seem little changed from their ancestral stocks. In the case of species with high dispersal ability such as some Lepidoptera, periodic arrival of new immigrants may inhibit differentiation (Slatkin, 1987; Roderick, 1996). In other cases, colonization may have been relatively recent and divergence between island and mainland stocks may have started without being recognized in the taxonomy. For example, the Ascension population of the migratory locust *Locusta migratoria* has been shown to be both genetically dwarfed and to have genitalia distinct from the mainland stock, even though interbreeding is still possible (see Appendix).

High intraspecific variability is another evolutionary phenomenon much discussed in relation to island populations (van Valen, 1965; Williamson, 1981). The phenomenon of ecological release—the enlargement of a niche in the absence of competing species—would be predicted to be strongest on young islands with a low average number of species per genus. We have not studied our Ascension material from this point of view, but Disney (1991) found an exceptional degree of morphological variability in our samples of the phorid fly *Megaselia curtineura* (which evidently colonized the island from tropical Africa). The intriguing implication is that the sole indigenous representative on Ascension of a normally species-rich group may be experiencing ecological release and that the morphological variation is a reflection of this; further study of the population is desirable.

A more puzzling case is that of the endemic pseudoscorpion *Stenowitzius duffeyi* in which our specimens show a high degree of variability—including asymmetries—in trichobothrial pattern, a feature that is normally used in characterizing genera (V. Mahnert, *pers. comm.*). The species seems to be restricted to Boatswainbird Island and the population may be inbred, but this would not be expected to increase variability.

More clearly adaptive change has already occurred on Ascension in cases where selective pressures are presumably strong, as in the evolution of true cavernicoles. These are species that can complete their life cycles in subterranean habitats (Chapman, 1993) and may show morphological adaptation to subterranean life (trogomorphy; Christiansen, 1962). Examples are provided by the blind, white linyphiid spider *Catonetria caeca* and the troglomorphic liposcelidid psocopteran *Trogloctes ashmoleorum* (both considered as generic endemics), together with the pseudoscorpion *Apocheiridium cavicola* and isopod *Elumoides coecus* (both cave adapted and so different from other members of their genera that their affinities are unclear) and the collembollan *Pseudosinella* species A (a hypogean form that may have been derived on the island from an epigeal ancestor); details are provided in the Appendix.

These cases suggest that adaptation to subterranean life may be one of the first evolutionary processes occurring when arthropods reach young volcanic islands. Recently formed volcanic terrain in hot, dry climates is inhospitable to most arthropods (Ashmole *et al.*, 1992) but subterranean spaces provide escape from severe conditions on the surface. Scavengers and predators may be able to establish populations even if there is little vegetation on the surface. Some may be 'lavicoles', remaining below the surface by day but emerging at night to forage on the surface (Martín, Oromí & Izquierdo, 1987; Ashmole *et al.*, 1992), while others may live entirely underground and become morphologically adapted to subterranean life.

On the Canary Islands, the latter group have been found in subterranean spaces away from caves only in areas where there is soil at the surface (Medina & Oromí, 1990). However, the use of pipe traps on Ascension in 1995 (see Methods) has shown that troglomorphic species (at least *Apocheiridium cavicola*, *Pseudosinella* species A and the new liposcelidid psocopteran *Trogloctes ashmoleorum*) can live in dry, lowland, volcanic habitats with scoria or lava rubble at the surface and hardly any vegetation.

This raises the possibility that on young volcanic islands some populations may become established in subterranean habitats directly from aerially dispersing propagules arriving from the continent, rather than indirectly from resident epigeal populations by parapatric speciation in the way suggested as normal for cave animals on islands (Howarth, 1987; Peck, 1990; Oromí *et al.*, 1991; Ashmole, 1994). In such cases the search for epigeal sister species will be vain. Once established underground, selection for efficient functioning there could lead to rapid evolution of the features that characterize obligate cavernicoles (Christiansen, 1962; Wilkens & Hüppop, 1986; Howarth, 1993).

In a few arthropod taxa on Ascension, however, the process of divergence and speciation within the island may have begun. Of particular interest are the platyarthrid isopods *Niambia duffeyi* and *N. longiantennata*, the three mogoplistine cricket species and the three collembolan *Pseudosinella* species. In both the mogoplistines and the *Pseudosinella*, one species has colonized the subterranean environment and two species show habitat segregation on the surface between inland and coastal habitats. Ashmole

*et al.* (1992) have argued that typically lavicolous species may be derived from halophiles. Since mogoplistines are flightless and often halophilic and the colonists presumably arrived by sea, it is possible that the inland lava form (species B) originally lived on the coast but was displaced inland by the subsequent arrival of species C, in a manner comparable to that implied for species undergoing the taxon cycle (Wilson, 1961; Howden, 1985). Alternatively, a single colonization event may have been followed by speciation within Ascension.

More detailed work on these taxa is needed, but they already provide a glimpse of an early stage of adaptive radiation within a single small island. Recent studies on within-island speciation on Hawai'i, as well as the preliminary work carried out on St Helena, show how such processes can proceed in the long term, leading to the development of island ecosystems which—though based on a small number of colonizing stocks—eventually come to rival the complexity of those on continents (Basilewsky, 1985; Howarth & Mull, 1992; Otte, 1994).

Some losses occur, however, as volcanic islands come to geological and biological maturity. Ashmole *et al.* (1992) showed how physical and ecological changes lead to gradual elimination of lavicoles from epigeal volcanic habitats. Similarly, recent work on the Canary Islands and St Helena (Hoch & Asche, 1993; Ashmole & Ashmole, manuscript) indicates that few true cavernicoles (as opposed to soil animals) survive after millions of years during which subterranean cavities collapse or become gradually filled with silt.

## CONCLUSION

Ascension Island is one of the most isolated of oceanic islands and is also geologically young. Older islands with many distinctive endemic forms have naturally attracted more attention, but we suggest that study of Ascension Island can provide a picture of a much earlier stage in the development of an isolated biota, and thus illumine the processes of colonization and evolution that have given rise to the mature (though now devastated) ecosystems of older islands such as St Helena.

It follows that in future management of Ascension Island, priority should be given to conservation of the indigenous terrestrial biota, comprising the severely endangered native plants, the depleted seabird community and the populations of indigenous—and in some cases endemic—arthropods that we have shown to be present. The ecology of Ascension has undergone extensive change in historical times, mainly through introduction of alien plants and both herbivorous and predatory animals. Although many of the losses of plant and animal species are irreversible, a strategy should now be designed to prevent further damage to the special biological features of the island, by protecting the remaining relatively undisturbed habitats such as barren lava flows and caves, together with areas bearing remnants of the indigenous flora. Such action should be combined with a programme of ecological restoration, aimed principally at the populations of marine turtles and seabirds (Ashmole *et al.*, 1994).

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## APPENDIX

### ANURA

**Pipidae.** The African clawed toad *Xenopus laevis* (Daudin) is found in the dewpond on Green Mountain and in some water tanks, but is clearly introduced (Loveridge, 1959; Duffey, 1964).

### CHELONIA

**Cheloniidae.** *Chelonia mydas* (L.) (Green turtle) breeds on the sandy beaches of the island (Mortimer & Carr, 1987). Indigenous.

*Eretmochelys imbricata* (L.) (Hawksbill) apparently breeds in small numbers (Packer, 1983). Indigenous.

### SQUAMATA

**Iguanidae.** *Liolaemus wiegmanni* (Duméril & Bibron) is common in the arid lowlands (Loveridge, 1959); it is native to South America and is presumably introduced.

**Gekkonidae.** *Hemidactylus mercatorius* Gray (*H. mabouia* (Jonnés)) is found in many buildings (Loveridge, 1960). This species occurs in east, south and southwest Africa, and also in West Africa where its distribution is spotty, apparently due to introduction at ports (Loveridge, 1947). We follow Loveridge in considering the species as introduced.

### AVES

When humans first visited Ascension it was a breeding station for vast numbers of seabirds, most of them widely distributed in tropical oceans, but including one endemic species. The colonies on the main island were drastically reduced as a result of predation by introduced rats and cats, as well as by direct human activities (Stonehouse, 1962; Ashmole, 1963). Two landbird species were resident on the island in the past but are now extinct, and one more may have been present. Five introduced landbird species are now established. Unsuccessful introductions of birds have been numerous and are summarized by Duffey (1964). Vagrant landbirds reach the island fairly frequently (Bourne, 1990); the lack of evidence for the presence of other indigenous landbirds thus probably reflects the restricted habitat availability on Ascension in the past, or the difficulty experienced by vagrant birds in establishing and maintaining populations, rather than their inability to reach it.

**Procellariidae.** *Puffinus lherminieri* Lesson (Audubon's shearwater) is shown by subfossil evidence to have occurred on Ascension in the past and an individual was caught on Boatswainbird Island in 1959 (Ashmole *et al.*, 1994); although breeding has not been confirmed we treat the species as indigenous.

**Hydrobatidae.** *Oceanodroma castro* (Harcourt) (Madeiran storm petrel). Indigenous.

**Phaethontidae.** *Phaethon aethereus* L. (red-billed tropic bird). Indigenous.

*Phaethon lepturus* Daudin (white-tailed tropic bird). Indigenous.

**Sulidae.** *Sula dactylatra* Lesson (masked or blue-faced booby). Indigenous.

*Sula leucogaster* Boddaert (brown booby). Indigenous.

*Sula sula* L. (red-footed booby). Indigenous.

**Fregatidae.** *Fregata aquila*. (Ascension frigate bird). Endemic.

**Ardeidae.** *Nycticorax* n.sp. Bourne *et al.* (manuscript) conclude that an endemic, small species of night heron was established before the arrival of humans but was quickly exterminated. One skeleton was discovered in a cave by Olson (1977) and another by us in a different cave. Night herons are represented on a number of oceanic islands including the Mascarenes and the Falklands. Endemic, extinct.

**Phasianidae.** *Francolinus afer* (Latham) (red-necked spurfowl). Introduced, probably from Namibia (Blair, 1989).

**Rallidae.** *Atlantisia elpenor* Olson (Ascension rail). This endemic and flightless species was seen alive by the traveller Peter Mundy in 1656 (Temple & Anstey, 1936) and subfossil bones have been found on the island (Ashmole, 1963; Olson, 1973; Bourne *et al.*, manuscript). The species seems to have been exterminated before the time of the first human settlement in 1815, presumably as a result of predation by rats and by sailors. Endemic, extinct.

*Gallinula alleni* (Thomson) (Allen's gallinule). This species has occurred as a vagrant on the island within historic times and Olson (1977) recorded a single bone possibly referable to it. The find was in a cave and suggests the possibility of an established population in the past. Doubtful.

**Laridae.** *Anous minutus* (Boie) (Black or white-capped noddy). Indigenous.

- Anous stolidus* L. (brown or common noddy). Indigenous.  
*Gygis alba* Sparrman (white tern). Indigenous.  
*Sterna fuscata* L. (sooty tern or wideawake). Indigenous.  
**Fringillidae.** *Serinus flaviventris* (Swainson) (yellow canary). Introduced.  
**Estrildidae.** *Estrilda astrild* (L.) (common waxbill). Introduced.  
**Ploceidae.** *Passer domesticus* (L.) (house sparrow). Introduced in 1986; a small breeding colony is established in Georgetown (Nash, Hughes & Walmsley, 1991).  
**Sturnidae.** *Acridotheres tristis* (L.) (common mynah). Introduced.

#### MAMMALIA

No mammals are native to Ascension, but five species have established free-living populations after being introduced by humans (there are also domestic pigs and sheep). Goats *Capra hircus* L. were introduced prior to 1700 and numbered about 600 in 1828 (Stonehouse, 1960), but were exterminated soon after the end of World War II. Duffey mentions that unsuccessful attempts were made late in the 19th century to establish hedgehogs *Erinaceus europaeus* L. to combat garden pests.

*Equus asinus* L. Donkeys escaped from domestication in the 1830s (Hart-Davies, 1972) and now have a feral population of around 100.

*Oryctolagus cuniculus* (L.). Rabbits were introduced about 1830; they are now relatively scarce.

*Rattus rattus* (L.). The black rat was probably accidentally introduced about 1700; it is now found mainly on Green Mountain (Davis, 1966).

*Mus musculus* L. The house mouse was probably accidentally introduced in the first half of the 18th century; it is now widespread.

*Felis* sp. Domestic cats were introduced in 1815 and quickly established a feral population.

#### TRICLADIDA

**Rhynchodemidae.** *Microplana* sp. This terrestrial flatworm was recorded by Duffey. Introduced.

#### GASTROPODA

Duffey found nine or ten species of snails on the island, of which only one was previously recorded. Most of the species have probably been introduced with plants. However, land snails—especially those of minute adult size—have reached many oceanic islands naturally (Vagvolgyi, 1975). A few species may be indigenous on Ascension, transport by birds being the most likely mode of colonization (Rees, 1965).

**Vertiginidae.** *Vertigo pygmaea* (Drap.) is a holarctic species common in Europe; it is also present in St Helena. Introduced.

**Pupillidae.** *Lauria* sp. was recorded by Duffey. Members of this genus are widespread in Europe, but there are also endemic species on the Canary Islands and Madeira (M.B. Seddon, *in litt.*). *L. cylindracea* (da Costa) was found on St Helena as early as 1832; it is of extremely small size and is a species mentioned by Rees (1965) as having exceptionally sticky mucus, with the implication that it might be transported by birds, as has been demonstrated for *Vitrina pellucida* (Müller). Further investigation of the Ascension population of *Lauria* is needed. Doubtful.

**Chondrinidae.** *Granopupa granum* (Drap.) occurs around the Mediterranean, in northwest Africa and the Canary Islands (M.B. Seddon, *in litt.*). It is not likely to be transported with plants and its extremely small size renders dispersal by birds or in air currents more plausible than for larger species (Vagvolgyi, 1975). Doubtful.

**Valloniidae.** *Vallonia pulchella* (Müller) is a widespread holarctic species with a range including northwest Africa and the Macaronesian islands and south to the Cape Verde archipelago; a very similar species, *V. excentrica* Sterki, occurs on St Helena and has been confused with *V. pulchella* in the past. *V. pulchella* is of minute size and is capable of self-fertilisation (M.B. Seddon, *in litt.*). Probably indigenous.

**Helicodiscidae.** *Helicodiscus singleyanus* (Pilsbry) (recorded by Duffey as *Vitrea scintilla* (Lowe)) is a poorly understood species occurring in eastern and central U.S.A., but also in a few widely separated localities in Europe and in Madeira and northwest Morocco. Further study of the Ascension population is needed. Doubtful.

**Zonitidae.** *Oxychilus* (*Oxychilus*) *cellarius* (O.F. Müller) is common in caves and buildings in Europe and the Middle East, and has been spread by man. Introduced.

**Subulinidae.** *Opeas* (*Opeas*) *hannensis* (Rang) (= *goodallii* Miller, = *punitum* (Pfeiffer)) originates from the New World tropics, is widely spread by man and now occurs on the Cape Verdes and St Helena as well as Ascension. Introduced.

*Opeas* sp. was recorded separately by Duffey, so a second species of the genus may be present, but is likely also to be introduced.

*Subulina striatella* (Rang) is a tropical West African species that has been widely transported with plants. Introduced.

**Bradybaenidae.** *Bradybaena similis* (Férussac) is a widespread species that is a pest of coffee and has been spread with it by man; it is the only gastropod recorded from Ascension in the last century, but is doubtless introduced.

#### OLIGOCHAETA

**Lumbricidae.** *Allolobophora* sp. was recorded by Duffey and by Sims (1964); it is evidently introduced from Europe.

*Bimastus eiseni* (Levinsen) was recorded by Duffey and is evidently introduced from Europe.

**Megascolecidae.** *Pheretima morrisi* (Beddard) was recorded by Duffey, Sims (1964) and Gates (1969); the genus is native to southeast Asia and Malaysia. Introduced.

*Pheretima californica* Kinberg was collected by J. Packer and identified by Gates (1969). This species is thought to originate from China. Introduced.

*Pheretima hawayana* (Rosa) was collected by J. Packer and identified by Gates (1969). This species is thought to originate from China. Introduced.

**Ocnoderilidae.** Two juvenile worms collected by John Packer on Green Mountain in 1962 have been studied by Gates (1969). The specimens were soft and could not be studied in detail, but had unusual calciferous glands. Gates commented that 'No other ocnoderile is known to have glands of the kind indicated above. Although reference to any known genus is impossible, the worms obviously were ocnoderile.' Ascension Island thus possesses an apparently endemic genus of these earthworms, which occur in both South America and Africa; some of them are specialized for shore life. Study of additional specimens is badly needed. Endemic.

#### SCORPIONES

**Buthididae.** *Isometrus maculatus* (Degeer) was recorded by Duffey; it is now ubiquitous in warm regions and is presumably introduced.

*Buthus hottentota* (Fabr.). A specimen was obtained by us in Georgetown; it is native to West Africa and is likely to have been imported with fruit. Introduced.

#### ARANEAE

Spiders that undertake ballooning flights have high dispersal ability; it thus seems likely that they were well represented in the prehistoric fauna. It is not easy, however, to distinguish native and introduced species, since it is clear that many species have been carried around the warm regions of the world by humans: these are mainly those typically found in or on buildings (Berland, 1926; Bristowe, 1939).

**Dysderidae.** *Dysdera crocata* C.L. Koch was recorded by Duffey; it is widely distributed and seems to have been dispersed by humans (Bristowe, 1939), but the genus has radiated on other Atlantic islands (Wunderlich, 1991). Doubtful.

**Oonopidae.** The family is represented by four species on Ascension, and it is noteworthy that there are endemic species in Hawai'i, St Helena and many other islands, suggesting great powers of dispersal in this group.

*Opopaea euphorbicola* Strand was described from Ascension (Strand, 1909). Duffey suggested that this species might not be truly endemic, but our specimens from barren lava sites appear distinct from other members of the genus known from the same region (J. Murphy, *in litt.*). Endemic.

?*Orchestina* sp. We obtained a subadult in the dark zone of Command Hill Cave. Doubtful.

*Oonops* sp. Recorded by Duffey. Doubtful.

?*Gamasomorpha* Recorded by Duffey. Doubtful.

**Scytodidae.** A species close to *Scytodes tenerifensis* Wunderlich was obtained by us in 1990 at several lava sites (Table 1) and in 1995 in a pipe trap at Lower Valley Crater. Bristowe (1931a) comments on the apparent absence of aerial dispersal in this group, and notes that specimens on Lang Eiland, Krakatau were found only in the volcanologists' huts. Nonetheless, the genus shows endemism in Macaronesia (Wunderlich, 1991) and is represented on St Paul's Rocks, an extremely isolated group of islets in the central equatorial Atlantic (Edwards & Lubbock, 1983). We suspect that these spiders may disperse by rafting (perhaps as egg sacs) and consider the Ascension species as probably indigenous.

**Loxoscelidae.** *Loxosceles rufescens* (Dufour), found by Duffey and by us, is synanthropic and widespread elsewhere. Introduced.

**Pholcidae.** Six species of pholcids have been found on Ascension and some penetrate the old lava, as on other islands where we have worked. Many pholcids are synanthropic, and the apparent absence of endemic species on St Helena might suggest that they have limited natural dispersal ability. However, they occasionally reach high altitudes in the air (Glick, 1939) and many endemic species are present in the Macaronesian archipelagos (Wunderlich, 1991) so natural colonization of oceanic islands evidently sometimes occurs.

*Artema mauriciana* Walck., recorded by Bristowe (1931b) and by Duffey, is widespread in warm regions. Introduced.

*Hedypsilus lawrencei* de Lessert (described from the Belgian Congo), was recorded by Duffey and found by us in several lava and cave-threshold sites (Table 1). Doubtful.

*Modisimus* sp. was recorded by Duffey. Doubtful.

*Micropholeus chavanei* Millot, found by Duffey and by us, was originally described from Madagascar. Introduced.

*Smeringopus elongatus* Vinson, recorded by Duffey, is one of the tropical cosmopolitan species noted by Berland (1926). Introduced.

Pholcid indet., found by us in Ravine Cave in 1990. The sole specimen, which is in poor condition, appears to have reduced eyes. Doubtful.

**Theridiidae.** Theridiids are good natural dispersers (Bristowe, 1931a, 1939) and have endemic and non-endemic forms on many islands, but some are synanthropic and likely to be dispersed with human belongings (Berland, 1926).

*Theridion tepidariorum* C.L. Koch, cosmopolitan in warm regions and clearly synanthropic (Berland, 1926). Introduced.

*Theridion rufipes* Lucas, recorded by Duffey, is almost cosmopolitan and synanthropic. Introduced.

*Teutana grossa* (C.L. Koch), recorded by Duffey, is almost cosmopolitan and synanthropic. Introduced.

*Latrodectus geometricus* C.L. Koch, found by Duffey and by us, is widespread in warm regions. Doubtful.

**Linyphiidae.** *Lepthyphantes* sp. and *Bathyphantes* sp., recorded by Duffey. These genera are well represented in aerial catches of spiders, and also on Krakatau and Hawai'i (Bristowe, 1931a, 1939), and both have apparently endemic species on St Helena. For the moment we consider them as of doubtful status.

*Catanetria caeca* Millidge & Ashmole, discovered in 1990 in Packer's Hole Cave and found there again in 1995, is endemic and troglitic; it is a minute, blind and white spider which represents a new genus in the subfamily Linyphiinae (Millidge & Ashmole, 1994; Merrett & Ashmole, 1997). Generic endemic.

**Araneidae.** *Araneus theisi* (Walck.), recorded by Duffey, is one of the spiders identified by Berland (1926) as a synanthropic tropical cosmopolitan species. However, araneids are good colonists, dispersing by air as spiderlings. Doubtful.

**Tetragnathidae.** *Dyschiriognatha argyrostilba* (O.P.C.), recorded by Duffey, is the African representative of a widespread genus with oceanic distribution. In view of the subsequent description of an endemic species of this genus on St Helena the identity of the Ascension species perhaps needs checking. Indigenous.

**Agelenidae.** *Tegenaria domestica* (Clerck), found by Dahl (1892) in holes in the rocks around 500 m on Green Mountain, is a cosmopolitan species known to travel with man (Berland, 1926; Bristowe, 1939). Introduced.

**Gnaphosidae.** This family (including Prodidominae) is well represented on Ascension and it seems likely that some species have arrived naturally, probably by ballooning. However, several species are not yet fully identified.

Drassodinae indet. At least one unidentified species, probably of this subfamily, was found on Boatswainbird Island by Duffey and by us. Doubtful.

?*Nodocion* sp. A female and immature obtained on Boatswainbird Island in 1995 may be referable to this genus (J. Murphy, *in litt.*). Doubtful.

*Prodidomus clarki* Cooke was collected by Duffey and described by Cooke (1964). Endemic.

*Prodidomus duffeyi* Cooke was collected by Duffey and described by Cooke (1964). Endemic.

*Pterochroa funerea* (Dalmas) was recorded by Duffey (as *Pterotricha lugubris*). This species has been considered endemic to St Helena and is one of only two animal species now apparently endemic jointly to St Helena and Ascension; since transportation by ship between these islands is possible, we consider the species as of doubtful origin on Ascension.

*Trachyzelotes jaxartensis* (Kroneberg) (recorded by Duffey as *Camillina acanthognathus* Purcell) and found by us in both lava and cave sites (Table 1), is probably the same as *Prosthesima ascensionis* Strand, 1909, described on the basis of a subadult male. Platnick & Murphy (1984) consider that it is originally native to the Mediterranean, but this is an area from which introduction to Ascension is somewhat unlikely. Doubtful.

*Urozelotes rusticus* (L. Koch), recorded by Duffey and found by us on Boatswainbird Island, is a widespread synanthropic species (Platnick & Murphy, 1984). Introduced.

*Zelotes inauratus* (O.P.C.), found by us on partly vegetated lava near the South Gannet lava flow. The species is apparently native to the Mediterranean region. Doubtful.

?*Zimirina* sp. Found by us on the shore, suggesting halophily and the possibility of colonisation by rafting. Doubtful.

?*Zimiris* sp. Found by us on South Gannet lava flow. Doubtful.

**Clubionidae.** Clubionids disperse by air and there are endemic species on St Helena, so indigenous species may well be present on Ascension; however, none have yet been fully identified.

*Clubiona* spp. Dahl (1892) reported the presence of this genus and Duffey found two species, one of them (recorded as *Clubiona* sp. aff. *vachoni*) from Boatswainbird Island. Doubtful.

**Corinnidae.** *Corinna* sp. was recorded by Duffey without details. In 1995 we obtained a corinnid near Spoon Crater which may be the same species; it has an epigyne similar to *Brachyphaea* but has not yet been studied in detail. Doubtful.

**Oecobiidae.** *Oecobius annulipes* Lucas, recorded by Duffey, is a cosmopolitan and synanthropic species that has been found on board ship (Berland, 1926; Bristowe, 1939). However, the genus is diverse on the Macaronesian islands in the North Atlantic (Wunderlich, 1991) so the identity of the Ascension population should perhaps be checked; our only specimen was immature. Oecobiids have been trapped in both airborne and shipborne nets (Crosby & Bishop, 1936; Holzappel & Harrell, 1968) so aerial dispersal evidently sometimes occurs. Doubtful.

**Lycosidae.** *Pardosa inopina* (O.P.C.), found by Duffey, may be the same as the *Lycosa* recorded by Banks (in Riley, 1893); the species is widespread in Africa. Lycosids are regular aeronauts and have successfully colonised other oceanic islands: several genera are represented by endemic species on St Helena, and lycosids have undergone a minor adaptive radiation in Hawai'i (Howarth & Mull, 1992). Indigenous.

**Selenopidae.** Duffey recorded *Anyphops stantoni* (Pocock) (as *Selenops nemorensis* Kauri). Benoit (1977), who detected the synonymy, suggested that the species was introduced to St Helena shortly before 1940. Introduced.

**Salticidae.** Salticids are evidently excellent natural dispersers, having been collected at high altitudes in the air (Crosby & Bishop, 1936) and being well represented among early colonists of Krakatau

(Bristowe, 1931a) and with several endemic species on Hawai'i (Howarth & Mull, 1992) and St Helena. However, they are also sometimes transported by humans and the only three fully identified species known from Ascension were mentioned by Berland (1926) in his discussion of widespread synanthropic spiders that he considered to have been distributed by man.

*Dendryphantus* sp. was recorded by Dahl. This genus is represented among aerial dispersers (Bristowe, 1939), but Dahl's specimen was found in a building on Green Mountain. Introduced.

*Hasarius adansonii* (Aud.), recorded by Banks (in Riley, 1893) and Duffey, was found by us to be abundant on barren lava (Table 1). Introduced.

*Menemerus bivittatus* (Dufour) was recorded by Duffey. Introduced.

*Plexippus paykulli* (Aud.) was found by Duffey (and by us in 1995) on Boatswainbird Island as well as on Ascension itself. Doubtful.

#### ACARI

It is probable that a good many species of Acari remain to be discovered on Ascension, especially in the more vegetated and higher areas. We found that a number of species were present in barren lava sites. Some of these doubtless arrived as passengers on introduced mammals, indigenous or introduced birds, or naturally arriving flies or other arthropods (cf. Lindroth *et al.*, 1973). However, Acari also disperse in large numbers freely in the air (Glick, 1939) and some may have reached Ascension in this way from Africa. Furthermore, many species are halophilic and Lindroth *et al.* (1973) have shown that some—especially among the Oribatida—can survive several days exposure to sea water; they might therefore reach islands by rafting, as also suggested by Benton & Lehtinen (1995).

#### IXODIDA

**Ixodidae.** *Rhipicephalus* sp. Eight larvae were obtained by us at Comfortless Crevices. Professor James Keirans, who identified them, comments (*in litt.*) that they are the only *Rhipicephalus* larvae with bulging eyes that he has seen outside Africa; the species presumably reached Ascension with introduced mammals such as donkeys.

**Argasidae.** *Ornithodoros denmarki* Kohls, Sonenshine & Clifford. A single female was found by us in a Sooty Tern colony on the main island. Indigenous.

#### PROSTIGMATA

**Bdellidae.** We collected two species, both in barren areas (Table 1). Bdellids are predators of small arthropods and their eggs, and are plausible natural colonists.

*Bdellodes Oudemans* (sp. indet.). Indigenous.

*Spinibdella* Thor. (sp. indet.). Indigenous.

**Eupodidae.** Mites found by us at the inland station on the South Gannet Flow represent a new species that will be described by Dr Anne S. Baker. She has provisionally placed them in the Eupodidae but comments (*in litt.*) that they appear to have one or two characters of the Penthaleidae. Both these families are cosmopolitan and are plant feeders. This mite is presumably indigenous and represents a new apparent endemic for Ascension.

#### ORIBATIDA

**Ceratozetidae.** *Cordylobates fragilis* Luxton. Specimens collected by us at several lava sites (Table 1) have been described by Luxton (1995) as a new genus and species which he places tentatively in the family Ceratozetidae. The genus is close to *Humerobates* Sellnick and to *Baloghobates* Hammer. The guts of some of the specimens contained masses of amorphous material that could be lichen, but pollen is also apparently included in the diet. Generic endemic.

**Oribatulidae.** *Lucoppia* sp. was collected by us at the South Gannet Flow Off-lava station. *Lucoppia* is a large and widespread genus. Doubtful.

**Haplozetidae.** *Incabates* sp. was collected by us in guano-saturated lava at the South Gannet lava flow; this is a widespread genus, and the species seems likely to have been transported to Ascension by seabirds, from another breeding station. Indigenous.

**Opipiidae.** *Lasiobelba* sp., found by us in the threshold of Packer's Hole cave; this is a large and widespread genus. Doubtful.

#### PSEUDOSCORPIONES

Three apparently endemic pseudoscorpions were found by Duffey and described by Beier (1960); we discovered one more in 1990 and another in 1995 (Mahnert, 1993 and *in litt.*). It is possible that one or more of the species will eventually be found elsewhere, but there seems little doubt that all five are indigenous on Ascension. None of the genera concerned have been found on St Helena, but this may reflect a lack of investigation of the fauna of seabird colonies there. Pseudoscorpions are well known for phoresy and any of the species (or their ancestors) might have reached Ascension attached to birds. However, Heatwole & Levins (1972) found live pseudoscorpions on flotsam, so the possibility of transoceanic rafting to the island cannot be excluded.

**Garypidae.** *Garypus titanus* Beier is an endemic species discovered by Duffey in the seabird colony on Boatswainbird Island. *G. titanus* (Fig. 8) is the largest known pseudoscorpion and is apparently confined to this 5 ha island. In 1995 individuals were seen hunting at night in the open on the guano surface of the summit plateau.

**Cheiridiidae.** *Apocheiridium cavicola* Mahnert, 1993. In 1990 we obtained a single male of this new cheiridiid in the semi-dark Ravine Cave. In 1995 a female was caught in a pipe trap at c.90 m in a barren ridge of loose scoria beside Lower Valley Crater (1 km south of North East Bay); this is on the opposite side of the island from Ravine Cave. The implication is that the species is capable of living in the sub-surface cracks in unweathered volcanic substrates. *A. cavicola* is morphologically adapted to subterranean life and is so different from all other species of the genus that its affinities are not clear (Mahnert, 1993 and *in litt.*); most of its congeners live under the bark of trees, but a cavernicolous species was recently described by Muchmore (1992) from Texas. Mahnert (*in litt.*) notes that phoresy on birds has been recorded in this genus, and he considers that although *A. cavicola* is a troglomorphic cavernicole, its ancestors may have travelled to Ascension with birds, subsequently becoming adapted to cave life. Endemic.

*Neocheiridium* sp. Our 1995 collection on Boatswainbird Island included a single specimen in poor condition of a probably undescribed species similar to members of the genus from the Neotropics and Africa (Mahnert, *in litt.*). Although it has not yet been studied in detail we are treating it as an apparent endemic.

**Cheliferidae.** *Stenowitzius duffeyi* Beier (Fig. 8) was discovered by Duffey on Boatswainbird Island and found to be common there in 1995. The specimens show an unusually high degree of variability, as already discussed. Endemic.

*Allowithius ascensionis* Beier. Duffey found this species on the coast opposite Boatswainbird Island (note that the reference to '*Allochernes ascensionis*' in Beier, 1960, p.38 is evidently a *lapsus calami*). Endemic.

#### AMPHIPODA

**Talitridae.** *Platorchestia platensis* (Krøyer). Stock & Biernbaum (1994) document the presence at high altitudes of a morphologically and ecologically aberrant form, of which the exact taxonomic status is doubtful. A 'tropical form' of *P. platensis* is widespread near the coast in tropical and warm-temperate localities on both sides of the Atlantic, though not on St Helena. The Ascension material occurs at higher altitudes and is morphologically distinct, raising the possibility that *P. platensis* might be indigenous. However, introduction with plants is also possible. Doubtful.

*Talitriator insularis* Stock & Biernbaum, 1994. This new species was described on the basis of material collected on Ascension by several workers including Duffey (who recorded it as an undescribed species in the *T. eastwoodae* species complex); it also occurs on St Helena. The other members of the genus are endemic to South Africa, and Stock & Biernbaum consider that *T. insularis* is either a St Helena endemic accidentally introduced to Ascension, or an undescribed South African species introduced to both islands. Introduced.

*Talitroides alluaudi* (Chevreux). This 'tramp' species, found on



Green Mountain (Stock & Biernbaum, 1994) also occurs on St Helena and has doubtless been introduced to both islands with plants.

#### ISOPODA

**Philosciidae.** *Atlantoscia floridana* (Van Name), found by Duffey, and by us in a casual collection in Cricket Valley, is a primarily South American species with a range including St Helena, Florida and Trindade Island; it includes parthenogenetic populations (Johnson, 1986). We agree with Taiti & Ferrara (1991) in considering it as probably introduced to Ascension.

*Littorophiloscia tropicalis* Taiti & Ferrara, found by us at the South Gannet Pools and Shore sites, is a halophilic species with pantropical distribution: Taiti & Ferrara (1991) consider that it probably colonised Ascension by dispersal on driftwood. Indigenous.

**Platyarthridae.** *Niambia duffeyi* Ferrara & Taiti, 1981, was described on the basis of two males collected by Duffey; it was represented in our samples by only two females, from widely separated lava localities. Endemic.

*Niambia longiantennata* Taiti & Ferrara, 1991, discovered by us, proves to be more widely distributed on Ascension than *N. duffeyi*. We found it to be the most numerous isopod on unvegetated lava flows both near the coast and some distance inland (Table 1); it also occurred in Packer's Hole cave. Endemic.

**Trachelipidae.** *Pagana dimorpha* (Dollfus), found in several localities by Duffey, is native to islands of the western the Indian Ocean. Introduced.

**Porcellionidae.** *Agnava madagascariensis* Budde-Lund, found by us in Command Hill Cave and one vegetated lava site, is also known from West Africa and the Indian Ocean. We follow Taiti & Ferrara (1991) in considering it as introduced to Ascension.

*Porcellio scaber* Latr., found by Duffey in several localities, is a Mediterranean and western European species. Introduced.

*Porcellionides pruinus* (Brandt), recorded by Duffey (as *Metoponorthus* sp.) and also found by us, has similar distribution to the last species. Introduced.

**Eubelidae.** *Elumoides coecus* Taiti & Ferrara, 1991, found in Chapel Grotto and Command Hill caves, is discussed in the Results section. Taiti & Ferrara (1991) felt unable to reach a conclusion about its origins; we treat it as an apparent endemic to Ascension.

**Armadillidiidae.** *Armadillidium vulgare* (Latr.), found by Duffey, is native to western Europe and the Mediterranean. Introduced.

**Armadillidae.** *Cubaris murina* Brandt is a pantropical species found by Duffey and by us in the breeding colonies of *Sterna fuscata*; we also collected it in the very barren lava of Lava Lake (which has traces of old guano). Its association with occupied and abandoned seabird colonies and its apparent absence from more vegetated areas suggests that a propagule may have been carried to the island by a seabird; a degree of salt tolerance is indicated by the representation of the genus among live animals found on flotsam by Heatwole & Levins (1972). However, in view of the failure to find the species on Boatswainbird Island and the scepticism of Taiti & Ferrara (1991) we treat the species as of doubtful origin.

*Pseudodiploexochus tabularis* (Barnard), found by Duffey, was previously known from near Cape Town. It was probably introduced to Ascension with plants.

*Venezillo parvus* (Budde-Lund) (= *Sphaerillo parvus*), found by Duffey, occurs in many islands in the Indian Ocean. It was probably introduced with plants.

#### DECAPODA

**Gecarcinidae.** The landcrab *Gecarcinus lagostoma* M. Edw. is a clearly indigenous crustacean, though not terrestrial in its larval stages. Oviposition on beaches was observed by residents on the island in late January 1987. Landward movements of landcrabs less than 10 mm across have also been noted, for instance in late March 1963 (John Packer, pers. comm.).

#### POLYDESMIDA

**Paradoxsomatidae.** *Orthomorpha ?gracilis* C.L. Koch (? = *Oxidus gracilis*) was recorded by Duffey; *Oxidus gracilis* is a synanthropic species that also occurs on St Helena. Introduced.

#### JULIDA

**Julidae.** Duffey recorded a *Cylindroiulus* species and a *Glyphiulus* species which were both probably introduced with plants.

#### SCOLOPENDROMORPHA

**Scolopendridae.** *Scolopendra morsitans* L. is a pantropical and Mediterranean species found by us and by previous workers; it is presumably introduced.

**Cryptopidae.** *Cryptops hortensis* Leach, recorded by Duffey, is a holarctic species which is presumably introduced.

*Cryptops* sp. A specimen that we obtained, which is damaged, has been determined by J.G.E. Lewis as a species close to both *C. audax* Attems from Cape Province and *C. typhloporus* from Natal and Zululand. Introduction with plants from southern Africa is possible, but so is natural colonisation by rafting, especially since an apparently endemic species of *Cryptops* (as well as *C. hortensis*) is present on St Helena. Doubtful.

#### LITHOBIOMORPHA

**Lithobiidae.** Duffey recorded *Lithobius ?forficatus* L., which is probably introduced.

#### GEOPHILOMORPHA

**Schendylidae.** Duffey recorded *?Schendylurus* sp., which is probably introduced.

**Geophilidae.** *Mecistocephalus insularis* (Lucas) *sensu* Attems, recorded by Duffey, is widespread in tropical Africa and on a number of islands, including Sao Thomé and Fernando Poo (Bioko) in the Gulf of Guinea. Natural colonization seems possible, but it is hard to exclude arrival in soil with introduced plants. Doubtful.

*Tuoba* (= *Nesogeophilus*). We obtained a single specimen referable to this widespread genus, which is mainly littoral outside Europe (Lewis, 1996). It was collected at South Gannet Shore station at Shelly Beach, a remote area little affected by human activities on the island, but one where driftwood and other flotsam accumulates; natural colonisation by rafting thus seems probable. Endemic.

#### COLLEMBOLA

Initial work on our collections was done by Dr Arne Fjellberg and some of the forms have now been studied in detail by Christiansen (in press). In assessing the likelihood of natural immigration by Collembola it should be noted that workers on aerial dispersal have sometimes collected them high in the air: early records are summarized by Freeman (1952). Furthermore, Lindroth *et al.* (1973) found that two species of seashore inhabiting Collembola were among the early colonists of Surtsey and suggested that they had arrived on flotsam. Collembola may therefore have reached Ascension by air and by sea.

**Entomobryidae.** *Drepanura* sp. We collected four juveniles at Lava Lake. Doubtful.

*Entomobrya* sp. was recorded by Duffey in damp humus and under rotting wood on Green Mountain. Doubtful.

*Lepidocyrtus* sp. was recorded by Duffey with the previous species. Doubtful.

*Pseudosinella* spp. The genus *Pseudosinella* is an artificial one (K. Christiansen, *in litt.*) and the *Lepidocyrtus* just mentioned might be ancestral to the three *Pseudosinella* species that we collected on barren lava and in caves. We treat the species provisionally as apparent endemics.

*Pseudosinella* species A is the dominant collembolan in samples from caves and pipe traps (see Methods); it is unpigmented and eyeless and shows some morphological adaptation to subterranean life, having a claw structure unique in the genus. Whereas a regular troglomorphic feature in this genus is enlargement of one of the basal unguis teeth, this species has enlarged the median tooth instead, in a manner analogous to the adaptation shown in some cave species of *Sinella* in the Western United States (K. Christiansen, *in litt.*).

*Pseudosinella* species B is dominant on the inland barren lava flows (Table 1); it is pale grey, with 6 + 6 ocelli.

*Pseudosinella* species C is abundant near the shore on the South Gannet lava flow; it has 6 + 6 ocelli, is dark blue and—most unusually—lacks a basal spine on the mucro.

*Seira* (*domestica*), found by us, largely replaces *Pseudosinella* species B on more vegetated lava. Introduced.

*Seira* sp. In a sample from the dark zone of Packer's Hole Cave *Pseudosinella* species A was accompanied by a single individual of a clearly distinct species of *Seira* which has not been studied. Doubtful.

**Tomoceridae.** *Tomocerus* sp. was recorded by Duffey from a damp habitat on the mountain. Doubtful.

**Cyphoderidae.** *Cyphoderus* sp. In our collections this replaced the troglitic *Pseudosinella* in Chapel Grotto Cave, a specially warm and humid site close to human activities; A. Fjellberg (*in litt.*) considers that it is probably introduced.

**Sminthurididae.** *Denisiella* sp. A few individuals were collected by us in a remote site encrusted with old guano. We suspect that the species arrived either on seabirds or by air. Indigenous.

*Sphaeridia* sp. was collected at two lava sites with old guano. Members of this genus are probably well adapted for long distance dispersal, either as desiccated eggs or even as juvenile or adult instars (A. Fjellberg, *in litt.*). Indigenous.

#### THYSANURA

**Lepismatidae.** Three species of lepismatids are present on Ascension, none of them endemic. Many Thysanura seem to have been carried around the world by commerce, but none of the species concerned were among those recorded by Aitken (1984) in ships' cargoes. Glick (1939) obtained lepismatids in his samples taken in nets mounted on aircraft, some of them at heights of several thousand feet, so overseas aerial dispersal is conceivable in the group. However, the apparent absence of thysanurans from Boatswainbird Island suggests that all species are introduced.

*Ctenolepisma ciliata* (Dufour) was recorded by Duffey but not found by us. Introduced.

*Ctenolepisma longicaudata* Escherich, which is widespread in the Old World and also occurs on St Helena, was recorded by Duffey and found by us to be an abundant member of the invertebrate community on barren lava flows all over the island (Table 1). Introduced.

*Aerotelsa collaris* (Fabr.) was recorded by Duffey and by us, though less abundantly than *C. longicaudata*. Introduced.

#### ODONATA

No permanent bodies of freshwater were present on Ascension before human occupation and although a small pond is now present at the peak of Green Mountain, no dragonflies have established themselves. However, the almost cosmopolitan and habitually nomadic libellulid *Pantala flavescens* (Fabr.) has been collected in Georgetown and other dragonflies have occasionally been seen (Packer, 1983). We do not include dragonflies in our tabulation of the fauna, as they appear to be analogous to vagrant birds, which sometimes reach the island but fail to breed.

#### ORTHOPTERA

**Acrididae.** More than a century ago Stüder (1889) suggested possible natural aerial colonisation of Ascension by the two migrant locusts found on the island; we agree with this idea. Both species may have reached Ascension several times, but in each case there are indications that the island populations are distinct from those in Africa.

*Schistocerca gregaria* (Forskål), the desert locust, has been recorded from Ascension by Stüder (1889) and Duffey, was seen (but not captured) during our 1990 visit and was abundant in 1995. The species is widespread in northern Africa (*S. g. gregaria*) but also occurs in southern Africa (*S. g. flaviventris*) including Namibia and perhaps southwestern Angola (Waloff & Pedgley, 1986). The genus has its centre of diversity in the New World and *S. gregaria* may be relatively recently derived from *S. cancellata* of South America (Grunshaw *et al.*, 1990). The Ascension population is fully compatible with *S. g. gregaria* but its cuticular chemistry is somewhat distinct and it shows some phenotypic similarity to *S. cancellata* in its solitariform facies (Grunshaw *et al.*, 1990). Movements of *S. g. gregaria* sometimes involve continuous flight for several days, and in October 1988 large numbers crossed the Atlantic from east to

west, covering a distance of some 5,000 km (Ritchie & Pedgley, 1989); this form migrates in both the solitary and gregarious phase and undertakes regular, seasonal downwind displacements. The migratory status of *S. g. flaviventris* is less well understood. It seems possible for the founders of the Ascension population to have reached the island from either western or southwestern Africa with the assistance of tropical meteorological disturbances of the kind discussed by Johnson & Bowden (1973) and Hall (1989); being polyphagous and adapted to arid conditions, the pristine Ascension Island probably offered an adequate habitat. Indigenous.

*Locusta migratoria migratorioides* (Reiche & Fairmaire), the tropical migratory locust, has been recorded from Ascension (under various names) by Waterhouse (1881), Stüder (1889), Dahl (1892), Riley (1893) and Duffey; during our 1995 visit it was abundant in the areas covered by the grass *Enneapogon cenchroides*, for instance near Mars Bay. Dr Nick Jago (*pers. comm.*) informs us that specimens he obtained from the island at the time of the Falklands war (when both *Schistocerca* and *Locusta* were considered a potential hazard to aircraft) were unusually small for the species but that the aedeagus of males was exceptionally large. Breeding tests showed that the Ascension population was fully compatible with *L. m. migratorioides* from Mali. Intriguingly, the small size of the Ascension form persisted through five generations, implying that it had a genetic rather than environmental basis. *L. m. migratorioides* has a wide distribution that includes many remote islands in the Indian and Pacific oceans. The key breeding area in Africa is considered to be the floodplain grasslands of the Middle Niger in Mali, but the range extends into south and southwest Africa. This locust migrates more extensively in the solitary than the gregarious phase (Farrow, 1990) so its wanderings are not so well documented as those of *Schistocerca gregaria*; it could have reached Ascension from southwestern Africa, but perhaps more probably from West Africa in disturbed weather bringing winds from the northeast; its morphological distinctiveness implies a relatively ancient colonisation. This locust requires Gramineae or Cyperaceae to complete its life cycle (Uvarov, 1966, 1977): both groups were present in the prehistoric vegetation on Ascension. Indigenous.

**Tettigoniidae.** *Ruspolia differens* (Serville) was recorded by Duffey (as *Homorocoryphus nitidulus vicinus* Walker). The larval 'Conocephalidae' recorded from Ascension by Riley (1893) probably relate to this species. Although it has been recorded as a traveller on ships (Aitken, 1984) it was also mentioned by Ragge (1972) as being the only African orthopteran apart from locusts and *Gryllus bimaculatus* (see below) capable of long-distance flights. It has landed on ships more than 1200 km from the African mainland, and occurs (with *G. bimaculatus*) on a series of other oceanic Atlantic islands, including St Helena. Indigenous.

**Gryllidae.** Crickets form an important element in the fauna of Ascension, as on other volcanic islands in warm regions (Howarth, 1979; Ashmole & Ashmole, 1987; New & Thornton, 1988).

*Gryllus bimaculatus* Degeer has been recorded from the island by Stüder, Riley and Duffey and was found by us in 1995. The species is widespread in tropical and subtropical countries of the Old World and there are records of swarms undertaking long distance overseas dispersal flights (Gangwere, Morales Martin & Morales Agacino, 1972). Crickets from one such swarm landed on a ship more than 900 km off the coast of West Africa (Ragge, 1972). Ragge suggested that by movements of this kind the species might have colonized the islands of Madeira, the Canary Islands, Cape Verde Islands and even perhaps St Helena; he did not mention Ascension, but the same argument clearly applies, and although the species has sometimes been found in cargoes (Aitken, 1984) we are confident that it is indigenous.

*Gryllodes sigillatus* (Walker) (= *Gryllodes poeyi* Saussure) was recorded by Dahl (1892) and by Duffey, and was also found in the stomach of a lizard *Liolaemus wiegmannii* collected by Loveridge (1959). The record by Riley (1893) of *Gryllomorpha aptera* Herr.-Schäf. (a synonym of *G. dalmatina* Ooskay) may also refer to *G.*

*sigillatus*, in which the female is apterous. We found *G. sigillatus* to be widely distributed on the island, mainly in places with some vegetation (Table 1). The species is widespread in tropical and subtropical regions, including West Africa. It has been intercepted in various cargoes (Gangwere *et al.*, 1972; Aitken, 1984). Introduced.

*Trigonidium (Metioche) fuscicornis* (Stal) was described from Ascension by Stal (1861). Dr Daniel Otte informs us (*in litt.*) that this group is in great need of revision. We consider the record as doubtful, pending re-examination of the type specimen.

Subfamily Mogoplistinae. Duffey obtained a juvenile mogoplistine on Boatswainbird Island. Our collections included three species, which are discussed in the results section and which may represent two colonising stocks. Mogoplistines do not fly and are often found in salty environments on the shore (Ragge, 1965; Borrer *et al.*, 1981; Ashmole *et al.*, 1992) and thus seem good candidates for long distance dispersal by rafting; they were not recorded by Aitken (1984) as travellers on ships. We suggest that mogoplistines colonized the island naturally and provisionally consider all three species as endemic.

#### PHASMATODEA

**Phasmidae.** *Bacteria trophinus* Westwood, recorded by Waterhouse (1881), was considered to have come from Natal; it is not clear that it is established. Introduced.

#### DERMAPTERA

**Carcinophoridae.** *Euborellia annulipes* (Lucas) was recorded by Duffey (as *Anisolabis annulipes*), but our sampling indicated that it has not established itself on the barren lava flows. The species is cosmopolitan and is regularly reported as a traveller on ships (Aitken, 1984). Introduced.

#### ISOPTERA

**Kalotermitidae.** *Cryptotermes brevis* Walker was recorded by Duffey in buildings in Georgetown. Introduced.

#### BLATTODEA

**Euthyrhaphidae.** *Euthyrhapha pacifica* (Coquebert), recorded by Duffey, is a pantropical species that is probably introduced.

**Pycnoscelidae.** *Pycnoscelus surinamensis* (L.), found by Duffey on Ascension and also occurring on St Helena, is the only member of its genus with a range extending beyond the Oriental region. The species has been found on ships (Aitken, 1984) and some populations are parthenogenetic. Introduced.

**Oxyhaloidae.** *Leucophaea maderae* (Fabr.) was recorded by Riley (1893) (as *Panchlora maderae*). This species also occurs on St Helena and is the only member of this Afrotropical genus that has extended its range to become circumtropical. It has been found in a cargo of African maize meal (Aitken, 1984). Introduced.

**Blattidae.** *Periplaneta americana* (L.) is widespread on Ascension in almost completely unvegetated lava habitats, both above and below ground (Table 1), as well as in buildings and elsewhere on the island. Introduced.

**Blattellidae.** *Iscnoptera* sp. was recorded by Duffey. Doubtful.

#### EMBIOPTERA

**Oligotomidae.** This family is endemic to Asia and Australia, but several species have become widely distributed by commerce (Ross, 1970).

*Oligotoma saundersii* Westwood was recorded by Waterhouse (1881), who quoted the collector, Mr. Conry, as stating that it was 'doing much mischief in Ascension', but did not amplify. Dahl (1892) found *O. saundersii* in gossamer tubes under *Euphorbia* bushes and under stones. Duffey also recorded this species. Introduced.

*Oligotoma* sp. aff. *ceylonica* Enderlein was recorded by Duffey. Introduced.

#### THYSANOPTERA

**Phlaeothripidae.** *Haplothrips gowdeyi* (Franklin) is the only thrips recorded from Ascension: a single specimen was caught by us in a water trap. This species is found on flowers and foliage of a variety of plants, but especially on grasses (zur Strassen, 1976). It is now almost cosmopolitan in warm regions but probably originated in Africa (Johnson & Bowden, 1973). *H. gowdeyi* is a well known

migrant in the upper air (R. A. Farrow, *in litt.*) and we consider it as probably indigenous to Ascension.

#### HOMOPTERA

**Cicadellidae.** *Balclutha saltuella* (Kirschbaum) was found by us in 1995 on the endemic *Euphorbia organoides* on South Gannet Hill. Ghauri (1983) gave an account of the apparent aerial arrival of a swarm of this species on the island in May 1976 (see section on Modes of Natural Immigration). Indigenous.

*Exitianus* sp. A single damaged specimen was obtained in 1995 in grass near Mars Bay. This is a widespread grass-feeding group. Doubtful.

**Delphacidae.** *Toya thomasseti* (Muir) was found by Duffey on grass. A plague of a 'tiny pale green grass fly' that occurred in 1963 after exceptional rains (J. Packer, *in litt.*) probably relates either to this species or to *Balclutha saltuella*. *T. thomasseti* is an African species that also occurs on the Mascarene Islands and St Helena. Delphacids are known for aerial dispersal (Glick, 1939; Peck, 1994a), have reached the Tristan group (Holdgate, 1965) and have undergone radiations in Hawai'i and the Galápagos (Zimmerman, 1948; Peck, 1991). Indigenous.

**Aphididae.** Dahl (1892) recorded an unnamed aphid on *Euphorbia organoides* and commented that it provided prey for larvae of a chrysopid and perhaps also of a syrphid. Neither Duffey in 1958 nor we in 1995 were able to find aphids on *E. organoides* in spite of intensive searching. Doubtful.

**Margarodidae.** *Icerya purchasi* Maskell. The cottony cushion scale was mentioned by Cronk (1980) as a serious pest of the introduced *Casuarina equisetifolia* L. trees and of many other plants on the island including *Euphorbia organoides*. Cronk stated that *I. purchasi* had caused considerable mortality of the latter species, but expressed the hope that it might be controlled by the predatory coccinellid beetle, *Rodolia cardinalis* (Mulsant) (see Coleoptera section). Introduced.

**Orthezidae.** *Orthezia insignis* Browne was found on the island by Dr Simon Fowler (pers. comm.); we subsequently collected it from *Lantana*. Introduced.

**Coccidae.** *Coccus viridis* (Green). This tropicopolitan and polyphagous species, which can damage citrus and coffee, was found on the island by S. Fowler (pers. comm.); it is not known from St Helena. Introduced.

*Parasaissetia nigra* (Nietner) was recorded by Duffey; this is a cosmopolitan and polyphagous species, which has been recorded elsewhere as feeding on guava; it may well have been introduced with this shrub.

**Diaspididae.** *Lepidosaphes beckii* (Newman), a major pest of citrus, was collected on Ascension by S. Fowler (pers. comm.). Introduced.

#### HETEROPTERA

**Pentatomidae.** *Mecidea longula* Stal. A specimen collected by C.M. StG Kirke in 1988 was identified by W.R. Dolling (*in litt.*) as the 'true' *M. longula*, a species with an Antillean distribution that does not include the U.S.A. In 1995 we obtained three more specimens in grass near Mars Bay, so the species now seems to be established on the island. Members of the genus can reach high densities in grassland and have been intercepted in shipments of grass seed. It is likely that *M. longula* was introduced at a time when construction workers from the Caribbean were employed on Ascension.

**Nabidae.** *Tropiconabis capsiformis* Germar, recorded by Duffey, is a predatory, cosmopolitan species in a group well known as aerial dispersers and colonists and represented in samples collected at the sea surface (Peck, 1994b). The species occurs on most of the isolated Pacific islands and has endemic relatives—several of them flightless—on many oceanic islands including the Tristan group, St Helena and Hawai'i (Schmitz, 1976c). *T. capsiformis* presumably colonized Ascension naturally but has not differentiated into an endemic form. Indigenous.

**Cimicidae.** *Cimex lectularius* L. was recorded by Wollaston (1861). Introduced.

**Miridae.** Duffey recorded an unidentified mirid and in 1995 we

collected a subadult female in the tribe Orthotylini and in or near *Orthotylinus*. Miridae have undergone radiations on several island groups including St Helena and Hawai'i. Furthermore, in Leston's (1957) analysis of 'spread potential' of Heteroptera based on colonisation of oceanic archipelagos, this family had the highest value. Numerous mirids were found by Peck (1994b) on the sea surface in a convergence zone in the Galápagos. Doubtful.

**Lygaeidae.** *Nysius ericae* (Schilling). According to Schmitz (1976b), Ascension Island records of *Nysius thymi* (Wolff) by Duffey, Dahl (1892) and Loveridge (1959) actually refer to this species, which has a wide distribution including West Africa and St Helena. Members of the genus are effective colonists, with endemics on many oceanic islands (including St Helena) and a major adaptive radiation on Hawai'i (Howarth & Mull, 1992). They are also well known as long distance migrants, with many records of trapping from aircraft or ships; one of the latter is from the tropical Atlantic southwest of the Cape Verde Islands (Scudder, 1968). Furthermore, *N. ericae* has been recorded on flotsam (Schmitz, 1976b). Indigenous.

**Rhopalidae.** *Liorhyssus hyalinus* (Fabr.), found on *Euphorbia originoides* by Dahl and by Duffey, is a moderately polyphagous cosmopolitan species known as a migrant (Southwood & Leston, 1959); its apparent absence from St Helena occasioned some surprise (Schmitz, 1976a). Indigenous.

#### PSOCOPTERA

Although there were no previous records of psocopterans on Ascension, our trapping demonstrated that they are widely distributed and diverse in caves and lava flows: these detritivorous animals are evidently preadapted to life on a barren volcanic island. Our material is being studied by Dr. Charles Lienhard, who has kindly commented on the species (1996 and *in litt.*). Psocopterans seem not to be halophilic and have not been observed on floating objects, but they are effective aerial dispersers and even apterous forms such as *Liposcelis* species have been captured in nets mounted on aircraft and on ships (Thornton, 1964; Thornton & Harrell, 1965). They also have endemic species on many remote islands, including Hawai'i and Norfolk Island. However, Psocoptera (especially *Liposcelis* spp.) also sometimes travel in stored products on ships (Aitken, 1984).

**Trogiidae.** Specimens found at two lava sites are very similar (perhaps identical) to *Cerobasis maya* Garcia Aldrete, described recently on the basis of a single individual from the Yucatán Peninsula, Mexico (Garcia Aldrete, 1991). This micropterous species probably reached the island naturally, but the region of origin is still obscure. Indigenous.

**Psyllipsocidae.** *Psocathropos lachlani* Ribaga (= *P. microps* Enderlein) was found both in cave thresholds and on lava flows (Table 1 and 1995 data). Although both this and the next species are essentially cosmopolitan and are often found in human dwellings, they also occur in natural caves and seem preadapted to cave life; natural arrival on the island cannot be excluded. Doubtful.

*Psyllipsocus ramburii* (Sélys-Longchamps). One female and three nymphs were found in Packer's Hole Cave and one female in Ravine Cave. Doubtful.

**Sphaeropsocidae.** *Sphaeropsocopsis* cf. *microps* Badonnel. A single damaged specimen was obtained in 1995 in a pipe trap at Lower Valley Crater, near Northeast Bay. Lienhard comments that precise identification is impossible because the wings are lost, but that the specimen has only three ommatidia in each eye, a character shown in this genus by only one described species, *S. microps* from natural edaphic habitats in Chile. Further material is clearly needed, but this species and the trogiid just discussed provide almost the only examples of apparent New World affinities in the Ascension arthropod fauna. Indigenous.

**Liposcelididae.** *Liposcelis bostrychophila* Badonnel, found at two surface sites, is a parthenogenetic and apterous cosmopolitan species, probably of African origin, which has also been found on St Helena. It commonly occurs in food stores, houses and on ships, and may have been brought to the island by humans; however, natural arrival by air cannot be excluded. Doubtful.

*Liposcelis* sp. A single male from a different species group was found at a lava site; females are required for identification. Doubtful.

**Trogloctes ashmolearum** Lienhard. This new genus and species has been described by Lienhard (1996). Though completely apterous and close to *Liposcelis*, the new species differs from that genus in many ways, including relatively long legs. This character, together with reduced pigmentation, reduction of the eyes to only three ommatidia and probably relatively long antennae (no specimens have the antennae intact) could be interpreted as adaptations to cave life. In 1990 specimens were obtained in several cave sites and one female at South Gannet Flow Upper station (Table 1), but in 1995 many individuals were caught in the pipe trap inserted into lava rubble on the slopes of South Gannet Hill. It thus appears that the species is widely distributed in the subterranean environment on the island; its ancestors presumably arrived by air. Generic endemic.

**Ectopsocidae.** *Ectopsocus strauchi* Enderlein. A single specimen was obtained in a water trap. This is a fully winged species known from many Atlantic islands and from Morocco; it lives on vegetation and is likely to have arrived naturally by aerial dispersal, since members of this family are often caught in the air and at sea. Indigenous.

#### PHTHIRAPTERA (including MALLOPHAGA)

**Phlipopteridae.** *Saemundssonina tremota* Timmermann was recorded by Duffey. This feather louse is clearly indigenous. Other species of Phthiraptera will doubtless be found on the seabirds (cf. Holdgate, 1965 for the Tristan group and Peck, 1991 for the Galápagos).

#### COLEOPTERA

**Histeridae.** *Saprinus* sp. aff. *chalcites* Illig. was found by Duffey. Members of the genus prey mainly on larvae of Diptera in carrion or dung (Crowson, 1981). They are strong flyers, but are sometimes transported in cargoes (Aitken 1975). Introduced.

**Staphylinidae.** Some members of this family have been widely dispersed by humans, but staphylinids are also abundant in the 'aerial plankton' and evidently reach oceanic islands in this way (Glick, 1939; Crowson, 1981). It is thus difficult to assess the origins of the Ascension populations.

*Atheta coriaria* (Kraatz), found by us at Comfortless Crevices, originates from the tropics, probably Africa or Asia, and also occurs on St Helena. It is one of only nine staphylinids considered by Moore & Legner (1974) to be cosmopolitan and is the only one of these that is not found most commonly in accumulated manure of domestic animals, although it does typically occur in decaying matter. It has been recorded in cargoes on ships (Aitken, 1975). Doubtful.

*Belonuchus formosus* (Gravenhorst) (= *B. rufipennis* (Fabr.)), or a closely related species, was found by us at Comfortless Crevices. *B. formosus* is widespread in the New World but has been introduced to southern Europe and elsewhere. A species of *Belonuchus* was well represented in a catch at the sea surface in a convergence zone in the Galápagos, indicating that aerial migration occurs (Peck, 1994b). Doubtful.

*Philonthus longicornis* (Stephens) was the only beetle found on the mountain by Bewicke (recorded as *P. scybalarius* by Wollaston, 1861). It is one of the manure-inhabiting cosmopolitan species listed by Moore & Legner (1974), who consider that it has been dispersed by man with domestic animals. Introduced.

**Scarabaeidae.** *Ataenius heinekeni* (Woll.), recorded by Wollaston (as *Oxyomus heinekeni*) is a New World dung beetle also recorded from St Helena and Madeira. Introduced.

*Ataenius picinus* Harold was recorded by Duffey. Introduced. Confirmation is perhaps needed that two species of this genus are really present on Ascension.

**Dermeestidae.** The Ascension dermeestid fauna consists of widespread species that are frequently transported in cargoes of organic material on ships (Aitken, 1975). However, a live dermeestid larva was collected in the air at over 5000 feet by Glick (1939), so aerial dispersal evidently occurs. Furthermore, dermeestids have undergone

a radiation in Hawai'i (Howarth & Mull, 1992) and *Dermestes ater* Degeer has been found in seabird colonies on almost all the remote uninhabited islands of the Hawaiian Leeward Chain (Bryan, 1926) suggesting effective natural dispersal. Osbeck (1771) mentioned the presence on Ascension of '*Dermestes elytris hirsutis cinereis* in the sand'. The name *Dermestes* was used very broadly at that time (P. Hammond, pers. comm.) and the species concerned seems unidentifiable, but it is noteworthy that a beetle was present on the island at this early date.

*Attagenus fasciatus* (Thunberg) was recorded by Wollaston (1861) (as *A. gloriosae* Fabr.). Introduced.

*Dermestes ater* Degeer (= *D. cadaverinus* Fabr. = *D. felinus* Fabr.) was recorded by Wollaston (1861) and by Waterhouse (1881). Doubtful.

*Dermestes frischii* Kugelann was recorded by Waterhouse (1881) (as *D. vulpinus* Fabr.) and by Duffey. Introduced.

*Dermestes marmoratus* Say, a species native to North America, was recorded by Duffey, but only on Boatswainbird Island. Introduced.

**Anobiidae.** *Lasioderma ferrugineum* (Woll.) was described from Ascension by Wollaston (1861) (as *Xyletinus ferrugineus*), but with the comment that it might be an accidental importation; it has subsequently been found elsewhere. Introduced.

*Lasioderma serricornis* (Fabr.) is a cosmopolitan species found by us. Introduced.

*Stegobium paniceum* L., recorded by Duffey, is a cosmopolitan and anthropophilous species that is often found in ships' cargoes (Aitken, 1975). Introduced.

**Ptinidae.** *Gibbium aequinoctiale* Boieldieu has in the past been confused with *G. psyllodes* (Czenpinski) (Bellés & Halstead, 1985). Dr Bellés has confirmed that our specimens are referable to *G. aequinoctiale*, which is cosmopolitan in warm parts of the world. Duffey's record of *G. psyllodes* probably also refers to *G. aequinoctiale*, which is commonly found in cargoes. Introduced.

**Cleridae.** *Necrobia rufipes* (De Geer), recorded by Wollaston and by Duffey, is widespread in the tropics and elsewhere; it feeds on animal products, but also on copra, and is very common in cargoes (Aitken, 1975). Introduced.

**Nitidulidae.** *Urophorus humeralis* (Fabr.) (= *Carpophilus humeralis*) was found by us in 1990 in a barren inland lava flow; in 1995 we collected it in a cave and in a pipe trap, both in an area covered with deep cinders. This is a species of palaeotropical origin associated with fermenting fruits, sap of trees and similar substances; closely related species exploit decaying roots (J. Jelinek, in litt.). *U. humeralis* might be attracted to baited ground from a distance and is not likely to have been living underground. The species can be a pest in stored products and has been widely distributed in these. Introduced.

**Corylophidae.** *Orthoperus atomus* Gyll., recorded by Waterhouse (1881) (as *O. punctum* Marsham) is a minute beetle typically found in decaying vegetable matter. Although members of the group have been caught in nets on ships, *O. atomus* is also somewhat synanthropic. Introduced.

**Coccinellidae.** Coccinellids are well known as aerial migrants, but introduction with plants is clearly also possible.

*Cheilomenes lunata* (Fabr.) (= *Cydonia lunata*) was recorded by Duffey and by Loveridge (1959) from the stomach of a lizard *Liolaemus wiegmanni* that he collected. It has a range including Africa, the Indian Ocean and St Helena. Doubtful.

*Exochomus troberti* Mulsant. Males recently collected on the island and dissected by R.G. Booth prove to be of this African species (P. Hammond, pers. comm.). Duffey's record of *E. flavipes* Thunb. may also refer to *E. troberti*. Natural colonization of Ascension seems a possibility. Doubtful.

*Oenopia cuneata* (Thunb.) was found by Duffey but recorded as *Cheilomenes picticollis* Gorham (R.G. Booth, pers. comm.); this is a South African species and is presumably introduced.

*Rodolia cardinalis* (Mulsant) was introduced in December 1976 to control the cottony cushion scale *Icerya purchasi* (Cronk, 1980).

**Mycetophagidae.** *Typhaea stercorea* (L.). In 1995 we obtained one female in a trap in Packer's Hole Cave and three others nearby in a pipe trap at Sisters Cinders. The name *T. stercorea* has been applied to two species which occur in Africa and in which the females are not distinguishable (P. Hammond, pers. comm.). These beetles are mould feeders associated with decaying plant material and have been widely distributed by humans. Doubtful.

**Tenebrionidae.** *Alphitobius laevigatus* (Fabr.) (= *A. mauritanicus* (Fabr.)) was recorded by Wollaston (1861) and Duffey, and found by us on Boatswainbird Island. This is a cosmopolitan species. Introduced.

*Alphitobius diaperinus* (Panzer), recorded by Wollaston (1861), has similarly wide distribution and is often found in cargoes. Introduced.

*Blapstinus metallicus* (Fabr.), found by us at several lava sites, occurs in eastern North America. Introduced.

*Clitobius ovatus* Erichson, found by us at South Gannet Pools and in the Wideawake fairs, is a detritivorous halophilic species often living on sandy shores, for which transport by rafting is plausible. It occurs in the Canary and Cape Verde archipelagos and on the coast of western Africa from Morocco to Namibia; Ascension is thus a logical element in the range, although the species has not yet been found on St Helena. Indigenous.

*Gnathocerus cornutus* (Fabr.), recorded by Wollaston (1861), is a cosmopolitan species that has been recorded in ships' cargoes, especially of cereal products (Aitken, 1975). Introduced.

*Gonocephalum prolixum* (Erichson) (*sensu* Ferrer, 1995), which was found by us at several lava sites with vegetation, is widespread in sub-Saharan Africa (J. Ferrer, in litt.). It feeds on a variety of organic material, including stored agricultural products. Introduced.

*Hemasodes batesi* Waterhouse, found by us at two lava sites with vegetation, is an opportunist species originating in Amazonia. Introduced.

*Phaleria* sp. was recorded by Dahl (1892) on dead flying fish. Members of this genus are typical of sandy shores and very resistant to salt and exposure; three individuals were obtained by Peck (1994b) from the sea surface between islands in the Galápagos. The genus is represented on all the Macaronesian archipelagos, including the Cape Verdes (Oromí, 1982), but has not yet been found on St Helena. Indigenous.

*Tribolium castaneum* (Herbst), recorded by Duffey, is a cosmopolitan species that is often recorded in vegetable material in ships' cargoes. Introduced.

**Anthicidae.** *Omonadus floralis* (L.) (= *Anthicus floralis*), recorded by Waterhouse, is a cosmopolitan species. Members of this group are well known for aerial dispersal (Glick, 1939) and *O. floralis* has reached remote islands such as Willis Island in the Coral Sea (R.A. Farrow, in litt.). Indigenous.

**Anthribidae.** *Araecerus fasciculatus* (Degeer), recorded by Duffey, is a cosmopolitan species which is known to travel in cargoes from Africa, especially in cocoa and coffee (Aitken, 1975). It is notable as the only non-endemic anthribid among the twenty eight species found on St Helena. Introduced.

**Curculionidae.** *Pantomorus (Asynonychus) cervinus* (Boheman), recorded by Duffey, is a polyphagous and parthenogenetic species originating from South America but now widely distributed in the tropics and subtropics, including St Helena. Introduced.

*Allopetarothrum elumbe* (Boheman) was recorded from Ascension by Wollaston (1861) (as *Pentarthrum cylindricum*) and was apparently found in a decayed wooden box. The species has pantropical distribution (G. Kuschel, in Wibmer & O'Brien, 1986, p.360). Members of the Cossoninae have halophilic tendencies and are considered by Crowson (1981) as the classic example of a group of beetles capable of overseas dispersal by drifting in logs; they have undergone a major radiation in St Helena. Doubtful.

*Phlyctinus callosus* Boheman was recorded by Waterhouse and by Duffey; it originates from western South Africa, where it is a pest on vines, and also occurs on St Helena. Introduced.

*Naupaetus longimanus* Fabr. Pascoe (1879) described this species from Ascension as *Siderodactylus ornatus*, but it was synonymized by Waterhouse (1881) with *N. longimanus* from Brazil; it was also recorded from the island by Riley (1893). Dahl (1892) suggested that the species could have reached Ascension with imported plants. Introduced.

**Scolytidae.** *Hypothenemus eruditus* Westw. (= *Cryphalus aspericollis* Woll.) is a widely distributed Palearctic species. Wollaston mentioned that his specimen of this minute beetle was identical to his Madeiran and Canaries specimens. Introduced.

#### NEUROPTERA

**Chrysopidae.** Dahl (1892) found a species of *Chrysopa* abundant on the endemic *Euphorbia origanoides*, where the larvae preyed on aphids, and noted that it was not the European *C. vulgaris* Schneider as stated by Waterhouse (1881); this lacewing does not seem to have been found in the present century. There are endemic species of chrysopids on other oceanic islands including St Helena, Norfolk Island and Hawai'i, and species of *Chrysopa* have been caught at high altitudes in the air (Glick, 1939) and in nets on ships at sea (Holzapfel & Harrell, 1968). Indigenous (possibly endemic).

#### HYMENOPTERA

Very few Hymenoptera (apart from probably introduced ants—see below) have been recorded from Ascension. Some parasitoids may have been overlooked, but we are sure that there is a genuine paucity of Hymenoptera on the island.

**Ichneumonidae.** Duffey recorded the campoplegine '*Horogenes*', which may actually be referable to *Casinaria* or *Diadegma*; these genera are parasitic on larvae of Lepidoptera. *Diadegma* has been recorded as a traveller on ships, but Ichneumonidae are also well represented among aerially dispersing insects. Doubtful.

**Evanilidae.** *Evania appendigaster* L. was recorded by Waterhouse (1881) (as *E. laevigata*) and found by Duffey and by us. It presumably reached the island with the help of man, along with the cockroach *Periplaneta americana*, which it parasitizes. Introduced.

**Chrysididae.** *Chrysis angolensis* Radoszkowski, collected at Two Boats village in 1995, is probably a parasite of the eumenid *Pachodynerus erynnis* (see below) or of a mud-nest building wasp that has not yet been collected. Introduced.

**Bethylidae.** Bethylidae species A. In a water trap in a colony of *Sterna fuscata* we obtained two male epyrines probably representing an undescribed species of *Trachepyris* Kieffer, but possibly belonging to a related genus (Q. Argaman, *in litt.*). Bethylids have undergone a radiation in Hawai'i (Howarth & Mull, 1992) and have been caught at high altitudes in the air (Glick, 1939). Endemic.

Bethylidae species B. Specimens obtained in 1995 on Boatswainbird Island appear to represent a different species of bethylid, but have not yet been studied. Doubtful.

**Formicidae.** We found ants abundantly in a number of places, but they were absent (or present in very low numbers) at the most barren lava sites (Table 1). It should be noted, however, that *Pheidole* have been found in the desert in association with the endemic *Euphorbia origanoides* (Dahl, 1892; cf. Stüder, 1889). Ants are capable of rafting over short distances (Heatwole & Levins, 1972) and males and females have been caught in aerial nets carried by boats between islands in the Galápagos (Peck, 1994a); Peck considers that colonization of islands by this means is a likely event. However, ants have typically not achieved natural colonization of very isolated islands; Hawai'i and St Helena, for instance, seem to have entirely introduced ant faunas. Xavier Espadaler, who identified the ants that we collected, considers that all are pantropical tramp species almost certainly introduced by humans; the same can probably be said of the other species recorded from the island.

*Cardiocondyla emeryi* Forel was recorded by Duffey and by us. Introduced.

*Cardiocondyla mauritanica* Forel was found by us. Introduced.

*Cataglyphis* sp. was recorded by Dahl as new to the island, but has not been found subsequently. Introduced.

*Monomorium subopacum* (Smith) was recorded by Duffey (as *M. salomonis* L.: Bolton, 1987). Introduced.

*Paratrechina longicornis* (Latr.) was recorded by Duffey and by us. Introduced.

*Pheidole megacephala* Fabr. was found by us and tentatively recorded by Duffey. We think that Dahl's (1892) record of *Pheidole pusilla* probably refers to the same species. It should be noted that *P. megacephala* is thought to have played a large part in extermination of native insects in Hawai'i (Zimmerman, 1948) and may have had similar effects on Ascension. Introduced.

*Plagiolipsis* sp. ?*alluaudi* Emery was recorded by Duffey. Introduced.

*Solenopsis* cf. *globularia* F. Smith was found by us in several places including Boatswainbird Island. This may be the same as the *S. globularia steinheilli* Forel recorded by Duffey, since this genus badly needs revision (X. Espadaler, *in litt.*). Introduced.

*Tapinoma* sp. was recorded by Dahl. Introduced.

**Vespidae.** *Polistes (Fuscopolistes) fuscatus fuscatus* (Fabr.). We collected a number of specimens referable to this form; the species was also recorded by Duffey; it is of American origin and although it is known as a migrant (Johnson, 1969) it seems almost certain to be introduced.

**Eumenidae.** *Pachodynerus erynnis* (Lepeletier) was collected by us in 1995 and is probably now common on the island. It is native in the southeast of the United States and was probably introduced to the island recently along with imported equipment for the American base.

#### LEPIDOPTERA

Knowledge of the Lepidoptera of Ascension was increased by the recent work of Robinson & Kirke (1990) who provided data from sampling by Kirke in 1988 and also a review of earlier records; the present account generally follows their nomenclature.

While investigating the biology of species recorded from Ascension Island we were impressed by the high proportion of the Lepidoptera (and also Orthoptera) that proved to be polyphagous species known as migrant pests in Africa and elsewhere. This tendency conforms with the data of Fox (1978) who noted that the species of Lepidoptera reaching New Zealand with exceptional weather systems are all migratory within Australia and are invariably polyphagous pests. Similarly, in a study of the Lepidoptera of Bermuda, which is over 1000 km from the North American coast, Ferguson, Hilburn & Wright (1991) pointed out that although previous authors had assumed that most pest species were introduced by man, the more plausible hypothesis was that they had arrived naturally by overseas migration. Out of the 113 most obviously migratory Lepidoptera of eastern North America, seventy-seven are recorded from Bermuda. Whereas migratory species comprise only about 5% of the mainland fauna, the figure for Bermuda is around 50% and reaches 85% in the Noctuidae.

With respect to Ascension Island, it is possible that some polyphagous pest species have been brought in by humans with introduced plants or in some other way (as emphasized, for instance, by Robinson & Kirke). It is notable, however, that such species are not commonly intercepted in cargoes (Aitken, 1984). We suggest that the Ascension Lepidoptera fauna—like that of Bermuda—has arisen primarily by natural transoceanic aerial migration. As on Bermuda, however, some naturally immigrant species may have become established on Ascension only following changes in the habitat caused by humans.

**Tineidae.** Dahl (1892) found two unidentified species drowned in a tank, and Robinson & Kirke (1990) recorded several species. It is notable that tineoids have undergone a radiation on St Helena (Wollaston, 1879) and are represented on many oceanic islands; we suggest that they represent a significant element in the native fauna of Ascension.

*Erechthias minuscula* (Walsingham) was collected by Kirke on Green Mountain; this pantropical species is a pest of stored foodstuffs, particularly tubers. Introduced.

*Erechthias* sp. This undescribed species was collected by Duffey in September 1958, on Green Mountain (E. Duffey, *in litt.*), but was not listed in his paper. Robinson & Kirke (1990), who found

the specimens in the British Museum (Nat. Hist.), considered that the Ascension population might represent an unnamed endemic taxon. Probably endemic.

*Eudarcia* sp. Robinson & Kirke (1990) recorded this undescribed species after receiving specimens collected after spraying of prickly pear with herbicide. They pointed out that other members of the genus are lichen feeders and suggested that the species might be indigenous to Ascension. All specimens were female and the population may be parthenogenetic (G.S. Robinson, *in litt.*). Endemic.

*Pheroeoca allutella* (Rebel): one specimen of this pantropical species was obtained by Kirke on Green Mountain; we obtained cased larvae in a number of lava and threshold sites that are apparently also referable to this species (K. Bland, *in litt.*). Robinson & Kirke point out that *Pheroeoca* larvae are the 'wall bagworms' common in many parts of the tropics, which feed on the dry remains of dead insects and other arthropods. Indigenous.

*Tinea subalbidella* Stainton was collected by Duffey in August 1958; it was not listed by Duffey but Robinson & Kirke (1990) found the specimens in the British Museum (Nat. Hist.). It has a diet that includes feathers and dead insects and can be a pest of stored products (Robinson, 1989); it is widely distributed in warm parts of the Old World including West Africa. Although Robinson considered it as probably introduced to Ascension, we feel that aerial immigration from Africa is also possible, and therefore treat its status as doubtful.

**Cosmopterygidae.** *Cosmopteryx attenuatella* (Walker), collected by Kirke on Green Mountain, is a pantropical species whose larva is a leaf miner on sedges *Cyperus* spp. Members of the family are effective dispersers; *C. attenuatella* occurs on Bermuda (Ferguson *et al.*, 1991) and the group has reached Hawai'i on several occasions (Zimmerman, 1948); it seems likely that *C. attenuatella* is indigenous on Ascension, originally exploiting *Cyperus appendiculatus* Brongniart.

**Gelechiidae.** *Phthorimaea operculella* (Zeller), the potato tuber moth, was collected by Kirke near Traveller's Hill; it is a widely distributed tropical and subtropical species whose larva feeds on Solanaceae; it is often a pest on crops, and has been intercepted in ships' cargoes (Aitken, 1984). Introduced.

**Tortricidae.** *Crocidosema plebejana* Zeller, collected by Kirke near Traveller's Hill, is cosmopolitan in warm regions, and has been recorded on remote islands, for instance Norfolk Island (Holloway, 1977) and some of those in the Hawaiian Leeward chain (Bryan, 1926) indicating considerable dispersal ability; however, Ferguson *et al.* (1991) consider it as introduced to Bermuda. The species feeds on Malvaceae and other plants. Doubtful.

*Cryptophlebia leucotreta* (Meyrick) is an Afrotropical species collected by Kirke at Traveller's Hill and Green Mountain. It is a pest of citrus and other crops, and there is one record from a ship's cargo (Aitken, 1984). Introduced.

**Pyralidae (including Crambinae).** *Cactoblastis cactorum* (Berg) was collected by Kirke; it was deliberately introduced to Ascension in 1974 in the hope of limiting the spread of *Opuntia* (Packer, 1983).

*Hellula undalis* (Fabr.) was collected by Waterhouse and Duffey. It is an Old World tropical migrant, known also from St Helena (Wollaston, 1879) and is a pest of crucifers. Doubtful.

*Herpetogramma licarsisalis* (Walker) (= *H. phaeopteralis* {Guenée}), collected by us, Duffey and Kirke, and also included in the collection sent to Bowden, is a widespread tropical species that occurs on many isolated islands. It is recorded by Fox (1978) as an immigrant to New Zealand and by Farrow (1984) as a putative immigrant to Willis Island. The species is a pasture pest in Australia and congeners are reported to eat ferns (Ferguson *et al.*, 1991). Indigenous.

*Spoladea recurvalis* (Fabr.) (= *Hymenia fascialis* Cramer) was collected by Waterhouse, Duffey and Kirke, and also included in the collection received by Bowden. This species is a pantropical polyphagous migrant pest that breeds well on *Portulaca oleracea* on Bermuda, where it is considered native (Ferguson *et al.*, 1991);

it also occurs on remote Henderson Island in the Pacific, where there is also an endemic congener (Benton, 1995) and is abundant on St Helena (Wollaston, 1879). Indigenous.

*Hypargyria metalliferella* Ragonot, collected by Duffey and Kirke, is an Old World tropical species originally recorded from Ghana. Doubtful.

*Pyralis manihotalis* Guenée, recorded by Duffey, occurs from Africa to the far east and Pacific islands; it is said to have been imported into Britain on bones and animal hides from India (Goater, 1986) and has been intercepted on a variety of ships' cargoes (Aitken, 1984). Introduced.

*Thylacoptila pauosema* (Meyrick), collected by Duffey and by Kirke, occurs in the Old World tropics and the Caribbean and has been reared on *Cassia*, which is now present on Ascension. Introduced.

**Pterophoridae.** *Megalorhipida defectalis* (Walker) was collected by Kirke near Traveller's Hill; it is a pantropical species that feeds on *Commicarpus*. Doubtful.

*Trichoptilus wahlbergi* (Zeller), collected by Duffey and by Kirke, is an Old World tropical species in a genus that is represented on many remote islands. It is recorded as feeding on *Ipomoea* (Robinson & Kirke, 1990) and so may have colonized the island naturally and utilized the indigenous *Ipomoea pes-caprae* L. However, it also feeds on *Oxalis*, which is probably not indigenous but was established on the island by the late 19th century (Hemsley, 1885), so *T. wahlbergi* might have been introduced with this plant. Doubtful.

**Lycanidae.** *Lampides boeticus* (L.) has been repeatedly recorded from the island, was included in the collection obtained by Bowden and was seen in numbers by Kirke. The species is widespread in warm regions of the Old World, and is a long-distance migrant that occurs in New Zealand, Hawai'i and St Helena as well as Ascension, which it presumably reached naturally. However, the larvae apparently always feed on seeds of legumes, and the species may not have maintained a population on the island in its pristine state; it now breeds on gorse *Ulex europaeus* L., which was introduced in 1850 as browse for cattle and horses (Dr E. Duffey, *in litt.*). We consider the status of *L. boeticus* in the past as doubtful.

**Nymphalidae.** *Cynthia* (or *Vanessa*) *cardui* (L.) has been recorded by McLachlan (1878), Stüder (1889), and by J. Packer (*in litt.*) in 1963, 1969 and 1971. The species is almost cosmopolitan; it is a well-known migrant and in 1939 a swarm was recorded in mid-Atlantic 1,600 km west of St Helena (Johnson & Bowden, 1973). The species presumably reaches Ascension naturally from time to time, but although it feeds on a range of plants, it may not maintain a population even now; a similar situation obtains on Bermuda (Ferguson *et al.*, 1991). On Ascension its status in the past must remain doubtful.

*Hypolimnas misippus* (L.), recorded by Duffey, Wollaston (1879) (as *H. bolina*) and also by Packer (*in litt.*), who in 1963 found them around an isolated pocket of *Ageratum conyzoides* and *Ipomoea pes-caprae* near Spoon Crater. The latter plant is indigenous on Ascension, as is *Portulaca*, on which the larvae of *H. misippus* are known to feed (Williams, 1969). *H. misippus* is an African and Asian migrant species, and has been recorded more than once in mid Atlantic between the Equator and the Cape Verde islands (Walker, 1931). It is thus likely to be a natural colonist of Ascension, though it evidently becomes numerous only after the occasional rains and may well have become extinct on the island from time to time. Indigenous.

**Danaidae.** *Danaus chrysippus* (L.): a single individual was recorded in 1971 by Packer (1983). There is, however, a slight doubt about the identification (John Packer, *in litt.*). *D. chrysippus* is an Afrotropical and Oriental species which feeds mainly on Asclepiadaceae; it is evidently only a vagrant to Ascension, and as with vagrant birds and dragonflies, we exclude it from the analysis.

*Danaus plexippus* (L.) was recorded from Ascension by Clark (1932); unlike Robinson & Kirke (1990) we consider the natural arrival of this species on Ascension as meteorologically improbable

and feel that the record should be ignored unless a specimen can be traced.

**Geometridae.** A species of *Scapula* was recorded by Duffey. Doubtful.

**Sphingidae.** *Acherontia atropos* (L.). A specimen collected on Green Mountain in 1973 is now in the Georgetown Museum (Robinson & Kirke, 1990). This Afrotropical species is a well-known migrant which has also reached St Helena (Melliss, 1875); it is only a vagrant on Ascension.

**Noctuidae.** The noctuids are an important group on Ascension, and six subfamilies are represented. It is noteworthy that all of these include polyphagous species known as migrant pests. All six groups have reached Norfolk Island (Holloway, 1977), all were recorded by Fox (1978) as transoceanic immigrants to New Zealand from Australia, and all but the plusiines were represented among the immigrants to Willis Island in the Coral Sea recorded by Farrow (1984). We suspect that most of the species colonized Ascension naturally, but it is possible that some of them are frequent natural immigrants and temporary breeders rather than permanent breeding residents (cf. Holloway, 1977; Farrow, 1984). It must also be remembered that many of the species also infest crops, so the possibilities for human introduction with plants are considerable.

(1) **Noctuinae.** *Agrotis ipsilon* (Hufnagel), collected by Kirke on Green Mountain, is a cosmopolitan polyphagous species feeding mainly on herbaceous plants (including many crops); it has been recorded as feeding on guava (*Psidium guajava* L.) (Holloway, 1977), an invasive shrub on Ascension. *A. ipsilon* is well known as a migrant and has been recorded as travelling long distances with locusts in the Middle East (Johnson, 1969). We consider it as probably indigenous on Ascension, though it may not have maintained a permanent population in the past (cf. Ferguson *in* Ferguson *et al.*, 1991).

*Agrotis segetum* (Denis & Schiffermüller), which was collected by Duffey and by Kirke, and also recorded by McLachlan (1878) as very destructive on the island, feeds extensively on root vegetables. It is a widespread Eurasian species, and although it is well known as a migrant it seems unlikely to have reached Ascension naturally. Introduced.

(2) **Hadeninae.** *Mythimna loreyi* (Duponchel) recorded by McLachlan (1878), Waterhouse (1881) and Duffey, is a grass-feeder from the Afrotropical and Oriental regions, mainly in the subtropics and including a number of Atlantic islands. It is known as a migrant. Indigenous.

(3) **Amphipyritinae.** *Callopietria* sp. was recorded by McLachlan (1878) but Robinson & Kirke consider this to be an error.

*Spodoptera exigua* (Hübner), collected by Waterhouse, Duffey and Kirke, is an 'armyworm', the most cosmopolitan species in the genus and well known in Africa as a polyphagous pest and long distance migrant, with flights of over 2,400 km recorded (Johnson, 1969; Brown & Dewhurst, 1975; Ferguson *et al.*, 1991). Indigenous.

*Spodoptera littoralis* (Boisduval) has been recorded by McLachlan (1878), Waterhouse (1881), Duffey and Robinson & Kirke. McLachlan commented that when it appears in numbers on the island it 'clears everything before it'. This highly polyphagous pest species is widespread in Africa and occurs in the Mediterranean region and on many islands of the Indian and Atlantic Ocean (Brown & Dewhurst, 1975). Indigenous.

(4) **Heliothinae.** *Helicoverpa armigera* (Hübner) was recorded by Duffey, included in the collection sent to Bowden, and collected by Kirke and by us. It is a well known Old World tropical and subtropical migrant polyphagous pest. The species is likely to have reached Ascension naturally, but it is recorded as being sometimes transported with vegetables (Bretherton, Goater & Lorimer, 1983). Doubtful.

(5) **Plusiinae.** *Chrysodeixis dalei* (Wollaston), found by McLachlan (1878) and by Kirke, is otherwise known only from St Helena (Robinson & Kirke, 1990). It is not clear whether this is a species really endemic to the two islands, or whether it has been transported from St Helena to Ascension by humans, or whether the two

populations are independently derived from an African population of *C. acuta* (Walker). Doubtful.

*Ctenoplistia limbirena* (Guenée), collected by Duffey and by Kirke, is an Oriental and Afrotropical species also occurring on St Helena. It is polyphagous and sometimes a pest of potatoes. Doubtful.

*Thysanoplistia orichalcea* (Fabr.) collected by Duffey, McLachlan, Waterhouse and Kirke, is a polyphagous pest distributed in the Old World tropics and subtropics, including the Macaronesian islands. It is known as a migrant, and has reached Britain in association with *Helicoverpa armigera* (Bretherton *et al.*, 1983). Indigenous.

*Trichoplistia ni* (Hübner), recorded by Waterhouse (1881) and by Kirke, is cosmopolitan and polyphagous; it is sometimes a pest of crucifers. It is known as a migrant, and is sometimes associated with *Spodoptera exigua* (Bretherton *et al.*, 1983). Indigenous.

(6) **Catocalinae.** *Anomis flava* (Fabr.), recorded under several names in the past and also collected by Kirke, is a pantropical species that is mentioned by Farrow (1984) as an immigrant to Willis Island; the larvae feed on Malvaceae. Doubtful.

*Hypena masurialis* (Hübner), recorded by Waterhouse, Duffey and Robinson & Kirke, is from the Old World tropics and has been recorded as feeding on *Commelina*, which is now present on Ascension. Doubtful.

*Melipotis famelica* (Guenée). Specimens included in the collection received by Bowden in 1974 were identified as this species by Adrian Riley (*in litt.*). This has prompted re-examination of the material collected by Kirke and recorded by Robinson & Kirke (1990) as *M. obliquivia* (Hampson). Robinson informs us (*in litt.*) that the two species appear indistinguishable and suggests that as *famelica* Guenée is the older name it should be the one adopted. *M. famelica* occurs in North America and the Caribbean and seems to be the only New World lepidopteran established on Ascension. Introduced.

#### SIPHONAPTERA

**Pulicidae.** Duffey recorded *Xenopsylla aff. gratiosa* Jordan & Rothschild. This species has been found on procellariiform seabirds on the Canaries and Salvage Islands. Indigenous.

#### DIPTERA

Diptera are less well known as migrants than the large swarming Orthoptera and Lepidoptera, but their capacity for long distance dispersal is shown both by their frequent occurrence in samples obtained with nets suspended from aircraft, kites and ships (Hardy & Milne, 1938; Glick, 1939; Gressitt & Yoshimoto, 1966; Peck, 1994a) and by their success in colonizing isolated island groups such as Hawai'i (Howarth & Mull, 1992). The Diptera recorded from Ascension include a number of widespread genera that may well have colonized the island by air, while a few may have arrived by rafting.

**Culicidae.** *Culex (Culex) quinquefasciatus* was collected by us in 1995. Dahl mentioned larvae belonging to this genus in the tank at Traveller's, and mosquitoes are now troublesome in Georgetown and at Two Boats. Doubtful.

**Sciaridae.** An unidentifiable female obtained in Ravine Cave in 1995 is the first sciarid recorded from the island. Sciaridae are among the commonest Diptera at high levels in the air (Glick, 1939) and comprised over 70% of the insects caught by Peck (1994a, b) in both aerial and pleuston (water surface) nets carried on boats between islands in the Galápagos. Indigenous.

**Phoridae.** *Megaselia curtineura* (Brues) is the dominant phorid on Ascension. A. Roberts found two individuals in 1987 and we collected specimens in many sites in 1990 (Table 1); the species was also obtained in the pipe trap in Daly's Crags in 1995. *M. curtineura* is now widely distributed in warm areas but may have originated in tropical Africa. The larvae are polyphagous saprophage in habits. On Ascension the species is abundant and shows a polymorphism in rectal papilla number that has not been seen elsewhere (Disney, 1991); this suggests character release on Ascension, where relatively few competing species are likely to have been present. Members of the genus are often found at high altitudes in the air. Indigenous.

*Megaselia scalaris* Loew. This species was added to the Ascension



fauna in 1995, a single male being collected on Boatswainbird Island. *M. scalaris* is a polyphagous saprophage tramp species that has been carried around the world by man; its restricted distribution on Ascension suggests that it was introduced on a guano boat.

**Syrphidae.** *Eristalis aeneus* Scop. This coastal species was recorded by Dahl (1892), who commented that the specimens belonged to a variety widely distributed on oceanic islands. Indigenous.

*Eristalis tenax* (L.) is a cosmopolitan species found by Duffey; it occurs in North and South Africa, the Canary Islands and St Helena, and is known as a migrant. However, it requires damp places for reproduction. Doubtful.

*Eumerus obliquus* (Fabr.), recorded by Duffey, is an African species with an endemic subspecies on St Helena. Natural colonization is thus plausible, but the possibility of introduction with plants—either from St Helena or South Africa—cannot be ruled out, and comparison of specimens would be of interest. Doubtful.

*Ischiodon aegyptius* (Wiedemann) was collected in 1995 near Spoon Crater. Dahl (1892) mentioned finding a new species of '*Xanthogramma* (*Syrphus* Bigot)' which is probably the same species. *I. aegyptius* is a predator on aphids and is an African species which has also been found on St Helena. Doubtful.

**Ephydriidae.** *Atissa pygmaea* (Haliday) was found by us at the South Gannet Flow Pools. This is a maritime Afrotropical, Neotropical and Holarctic species that also occurs on St Helena. Its diet is unknown, but some members of the family are able to eat cyanobacteria while others eat algae (Foote, 1995): both these resources are available in its coastal habitat. As with *Hecamede brasiliensis* (see below) we consider this species to be indigenous.

*Hecamede brasiliensis* Cresson, a species occurring in both Afrotropical and Neotropical regions, was found by us at the South Gannet Flow Pools, and in 1995 also on *Euphorbia origanoides* inland from Hummock Point. Dahl's (1892) mention of a new species of *Hecamede* that he found on dead flying fish and on *E. origanoides* doubtless refer to *H. brasiliensis*; Cogan (1976) also mentioned it as occurring on both Ascension and St Helena. Species of *Hecamede* appear to be specialists on carrion (Bohart & Gressitt, 1951; Foote, 1995) a resource that has probably been available on the beaches of Ascension more or less continuously. The wide distribution of members of the genus on oceanic islands (Mathis, 1993) indicates great powers of dispersal. Members of the family are among the most abundant Diptera in high-level aerial samples (Holzapfel & Harrell, 1968; Johnson, 1969), but Cogan (1976) commented on the possibilities for long range sea dispersal for littoral ephydriids; we think that *H. brasiliensis* probably reached Ascension from Africa by rafting. Indigenous.

*Placopsidella ternocephala* Kertész. A single female was obtained in 1995 on *Euphorbia origanoides* inland from Hummock Point. Secure specific identification is not possible without a male, but *P. ternocephala* occurs on a number of Atlantic islands and is the most likely species (W.N. Mathis, *in litt.*). Indigenous.

**Drosophilidae.** *Drosophila (Sophophora) simulans* Sturt. was recorded by Duffey, and in 1995 we trapped two males in Packer's Hole Cave. Females—probably of the same species—were obtained on Boatswainbird Island and at Lava Lake. These flies are often intercepted in ships' cargoes (Aitken, 1984). Introduced.

*Drosophila buzzatii*, Patterson & Wheeler was found by us. It is an originally New World species associated with *Opuntia*, and was doubtless introduced with its host plant.

*Zaprionus* sp. We found a female referable to the *vittiger* group; *Z. vittiger* is widespread in Africa and occurs on St Helena. Introduced.

**Chloropidae.** *Cadrema pallida* (Loew) was found by us in Packer's Hole cave in 1995. This is a circumtropical species that also occurs on St Helena. Its larvae exploit a wide variety of decaying animal matter, including decaying shellfish and barnacles on driftwood washed ashore (Sabrosky, 1976). This is evidently a halophilic species and it may have reached Ascension by rafting, although Peck (1994a) caught two individuals of the genus in aerial nets carried by boats in the Galápagos. Indigenous.

*Siphunculina striolata* (Wiedemann) (= *signata* (Wollaston)), found in 1995 on *Euphorbia origanoides* on South Gannet Hill, is a circumtropical species also occurring on many islands around the world, including St Helena and the Cape Verde Islands. Members of this genus have been reared from mammal dung and from bird nests. Indigenous.

**Agromyzidae.** *Liriomyza brassicae* (Riley) was collected on the island by Simon Fowler (pers. comm.). This leafminer is a pest of brassicas and is clearly introduced.

**Muscidae.** The first records of this family are by Osbeck (1771) who visited the island in 1752 and recorded '*Musca vulgarissima*' and '*Musca nivea*', species that we cannot identify with confidence. *Musca domestica* L. (recorded by Dahl as *M. basilaris* Macq.) is a cosmopolitan species; our specimen is referable to subspecies *domestica* rather than to one of the afrotropical subspecies (A.C. Pont, 1991 and *in litt.*) so the species may be assumed to be introduced.

*Synthesiomia nudiseta* (Wulp) was found by us. This is a common pantropical filth fly that prefers carrion for larval food (Bohart & Gressitt, 1951). Our specimens were from barren lava areas, suggesting that the species is not totally dependent on refuse produced by humans. Dr Pont is of the opinion that it probably reached the island with human aid, but we feel that natural colonization cannot be excluded. Doubtful.

**Calliphoridae.** *Chrysomya albiceps* (Wiedemann), which was recorded by Dahl (as *Lucilia albiceps*) apparently on dead flying fish and elsewhere, is found in warm parts of the Old World. It was recorded on St Helena in the last century, but recent captures there are all of *C. chloropyga* (Wiedemann), an Afrotropical species, suggesting past confusion both there and on Ascension. Although calliphorids have undoubtedly been taken to some islands by humans, natural colonization must also occur, since there are endemic species on remote islands such as Hawai'i and Norfolk Island. Calliphorids sometimes undertake long-distance migrations (Johnson, 1969), have been caught in aerial nets carried by boats at sea (Peck, 1994a) and were among the earliest colonists of Surtsey (Lindroth *et al.*, 1973). For the moment we treat *Chrysomya* sp. as of doubtful origin.

*Lucilia sericata* (Meigen) was recorded by Duffey, and the identity of the specimens concerned has been confirmed by Nigel P. Wyatt. The records by Dahl (1892) of *L. latifrons* and by Waterhouse (1881) of *L. caesar* (L.) may also refer to *L. sericata*, which is a widespread sheep maggot fly, typical of temperate regions but also abundant on St Helena. Introduced.

**Sarcophagidae.** *Sarcophaga haemorrhoidalis* (Fallén) sensu Meigen (= *S. cruentata* Meigen) was recorded by Waterhouse (1881), but Dahl (1892) considered the identification to be incorrect; Dahl himself found two species of sarcophagids, but did not give names. Duffey recorded *S. exuberans* Pandellé, and Thomas Pape has identified specimens collected by us as *S. exuberans*. He comments, however (*in litt.*), that the non-Madagascan Afrotropical populations of *S. exuberans* authors', occurring in subsaharan Africa, Ascension and St Helena, constitute a species distinct both from *S. exuberans* in other areas and from *S. exuberansoides* Zumpt from Madagascar. The species was recently named *Liosarcophaga babiyari* Lehrer, 1995, but the valid name is *Sarcophaga redux* Walker, 1849 (Pape, *in litt.*, 10 April 1996). Species of the genus have been caught from aircraft at high altitudes (Glick, 1939) and natural aerial colonization of Ascension by *Sarcophaga exuberans* authors' seems possible. However, since the species could also have been introduced with livestock, we treat it as of doubtful origin.

*Sarcophaga* sp. Our collections from remote sites also included specimens of a different, small species of *Sarcophaga* which cannot be identified because they are female, but which do not belong to any of the cosmopolitan species known from St Helena or the Cape Verde Islands (Pape, *in litt.*). Doubtful.

**Hippoboscidae.** *Olfersia aenescens* Thomson, recorded by Duffey, is a subcosmopolitan species recorded from many kinds of seabirds and is undoubtedly indigenous to Ascension; it was probably this

species recorded as *Hippobosea nigra* by Osbeck (1771). Specimens referable to the genus *Olfersia* collected by us in 1995 have not yet been identified. Dahl (1892) recorded *Ornithomyia* sp. from *Fregata aquila*; we feel that there is a possibility of confusion with *Olfersia aenescens* and therefore ignore this record.

**Milichiidae.** *Desmometopa varipalpis* Malloch. Duffey listed *Desmometopa tarsalis* Loew, but Sabrosky (1983) records *D. varipalpis* from Ascension (probably on the basis of Duffey's material) and mentions that *varipalpis* has often been mistaken for *tarsalis*, which is actually confined to the New World and Oceania. *D. varipalpis* is now cosmopolitan and has apparently been carried around the world by shipping. The larvae are associated with sewage and rotting plant material. Introduced.

*Leptomotopa latipes* (Meigen), found in 1995 on Boatswainbird Island, is widespread in the Holarctic and also in Africa including the Cape Verde Islands. It has been reared from human faeces and from bird nests. It is likely to have reached Ascension with seabirds. Indigenous.

*Milichiella lacteipennis* (Loew), found by us, is widespread in the tropics and breeds on decaying vegetation as well as dung (Bohart & Gressitt, 1951). Although Sabrosky (1976), discussing the St Helena fauna, commented that the scavenging flies of this family have been spread around the world by man, it is noteworthy that they are native to Hawai'i (Howarth & Mull, 1992) and are sometimes abundant in aerial samples (Holzapfel & Harrell, 1968). Doubtful.

**Canaceidae.** *Canace* sp. Dahl (1892) recorded this on lava cliffs rising straight from the water. The family has radiated in both Hawai'i and the Galápagos (Howarth & Mull, 1992; Peck, 1991), indicating that these seashore flies disperse effectively, probably by rafting. Even without precise identification we consider the species as probably indigenous.

## NOTE ADDED IN PROOF

We have recently heard that a second species of gecko (Squamata, Gekkonidae) may be present on Ascension, but we are not aware of an identification.

In an attempt to control the mesquite *Prosopis*, two species of bruchid beetles have now been introduced to the island by Simon V. Fowler; they are *Algarobius prosopis* (Le Conte) and *Neltumius arizonensis* (Schaeffer).

During a visit to Ascension in July 1996 in connection with the biological control project, Dr Fowler collected a number of insects, mainly off *Prosopis*. Some of these have now been identified and represent new records for the island. Dr Fowler has kindly allowed us to mention them here. Neither these species nor the bruchids have been included in the numerical totals in the text, Table 2 or the Appendix. The species concerned are:

Homoptera, Psyllidae: *Heteropsylla reducta* Caldwell & Martorell. A Caribbean species which feeds on *Prosopis juliflora*. Like the next species and the last two, it was presumably introduced along with the mesquite.

Homoptera, Coccidae: *Coccus longulus* (Douglas). Collected from *Prosopis*. A tropicopolitan and polyphagous species known as a pest of *Leucaena* sp. in the Pacific region.

Heteroptera, Miridae: *Phytocoris* sp. and *Rhinacloa* sp. These were both beaten off *Prosopis*.

Heteroptera, Pentatomidae: species close to *Thyanta*.

Coleoptera, Scolytidae: *Hypothenemus* sp. near *squamosus* (Hopkins). Collected from twigs of *Prosopis*. *H. squamosus* is a New World species feeding on Leguminosae.

Hymenoptera, Encyrtidae: *Isodromus timberlakei* Annecke. Beaten off *Prosopis*.