



Origin of the inland Acari of Continental Antarctica, with particular reference to Dronning Maud Land

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The extant Acari occurring on the inland mountain ranges and nunataks of Continental Antarctica comprise only pre-Pleistocene endemic Prostigmata and Cryptostigmata of which the Prostigmata are the probable earlier colonists. The inland acarofauna of Continental Antarctica has a different origin from that of Maritime Antarctica, though both are the relict descendants of a Mesozoic acarofauna, which has been radically depleted by one or more Mesozoic and/or Cenozoic glacial events.

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ADDITIONAL KEY WORDS: — Acari – Antarctica – biogeography – endemism – immigration – origin.

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INTRODUCTION

Antarctica covers *c.*14 million km² (Laws, 1984), a huge and sparsely inhabited area where plants and invertebrates are restricted to the ice-free terrain on nunataks, mountain ranges, rocky coasts and offshore islands (Gressitt, 1964). Early estimates put this ice-free area at *c.*2% of the Antarctic land surface area (Gressitt, 1964), though more recent studies suggest a figure closer to *c.*5.7% (Fox & Cooper, 1994).

The polar ice cap which dominates the topography and climate of Antarctica is a relatively recent feature, but Antarctica was glaciated on at least one previous occasion and subsequently deglaciated as a result of both world climate changes and latitudinal migration caused by continental drift (e.g. Parrish, 1990; Gould, 1993). For example, as part of Pangaea, Antarctica was cold and glaciated during much of the Carboniferous, but became deglaciated, wet and seasonally humid during the Jurassic disintegration of the supercontinent, and subsequently clad in a polar broad-leaved forest and sub-tropical savanna up to the Eocene. Antarctica became isolated from the rest of Gondwana during the Miocene after which the pre-Miocene lush vegetation was replaced by tundra and eventually the ice cap, which considerably expanded and thickened 1.8 to 0.12 million years ago during the Pleistocene. The current climate is relatively severe, compared with the comparatively mild and more humid early post-Pleistocene of *c.*100 000 years ago.

The fossil record suggests that Antarctica supported rich plant and animal communities during the Palaeocene and Eocene, which were largely obliterated by subsequent cooling and ice cap expansion (van Zinderen-Bakker, 1970; Chaloner & Creber, 1989; Creber, 1990). The extant antarctic biota is restricted to ice-free mountains and nunataks and includes a few algae, mosses, lichens and invertebrates. The impoverished fauna is dominated by nematodes, insects and mites, the ascendant taxa of hostile, hot and/or cold environments including deserts, exposed mountain ridges and the polar regions (Gressitt, 1965; Danks, 1981; Freckman & Virginia, 1991). Although the extant invertebrates may have much in common with those of other cold hostile environments their origins are debatable. For example, are they of pre- or post-Pleistocene (glaciation) origin? Furthermore do they have affinities with the faunas of other (particularly Gondwanan) continents?

A compounding problem is that 'the Antarctic' *per se* is a huge area which includes three biogeographic provinces each with unique plant and animal communities (e.g. Hedgpeth, 1969; Greene *et al.*, 1970; Lewis-Smith, 1984; Longton, 1988; Hattersley-Smith, 1991; Wardle, 1991). Continental (= Eastern or Greater) Antarctica covers the greater part of mainland Antarctica but excludes the Antarctic Peninsula, which along with the S. Shetland, S. Orkney and S. Sandwich archipelagos constitute Maritime (= Western or Lesser) Antarctica. The other Southern Oceanic islands south of the 45°S parallel, excluding Tierra del Fuego and New Zealand, make up the remaining sub-Antarctic province.

This study considers the origins of the terrestrial fauna of Continental Antarctica, but focuses on the mites or Acari which being represented by over 100 species, is the most diverse known invertebrate group within the region (e.g. Gressitt, 1967; Pugh 1993). Not all mites need be considered in this context. For example the ticks (Metastigmata = Ixodida) and feather mites (Psoroptida, Astigmata = Acaridida) are parasitic and/or nidicolous and so likely to be dispersed by their hosts, while some coastal mites *may be* dispersed by ocean currents (e.g. Wallwork, 1984; Pugh,

1993, 1994). Removal of these groups leaves only the free-living mites associated with inland mountains and nunataks which have no intimate associations with other animals (including man). Little is known regarding the origin of these 'inland' Acari other than most species are perhaps endemic to the region, in contrast to most of the other terrestrial Antarctic faunal groups which are presumed post-Pleistocene immigrants (e.g. Wallwork, 1967, 1984; Convey, 1996).

There are a number of problems associated with the study of this inland Continental Antarctic free-living fauna. Firstly the majority of records come from two sectors, namely 'Maud' (30°E 30°W) and 'Scott' (150°E 150°W) on the opposite side of the continent (*sensu* Pugh, 1993) (see Fig. 1). Twelve species of Acari have been reported from Maud sector and 14 from Scott, while in contrast each of the remaining four sectors has a maximum of three recorded species (Pugh 1993). This is likely to reflect the greater amount of data available from Maud and Scott sectors and for this reason the present study concentrates upon Maud Sector, a largely ice-covered region with ice-free habitats on numerous nunataks and mountain range peaks along a 900 km transect parallel to the coast and 100 to 200 km inland.

The mites occurring on the ice-free terrain of Maud Sector are compared with similar inland faunas throughout the Continental and Maritime Antarctic as well as the sub-Antarctic islands to determine the origin of the inland Antarctic fauna as a whole. Concentration upon a small fauna of only twelve species generates further problems, in that these species may show little evidence of relationships with those present in other regions (e.g. Gressitt, 1967). To counteract these difficulties several lines of enquiry will be addressed. Firstly which groups are/are not represented amongst the fauna and what are the possible origins of these groups. Secondly what

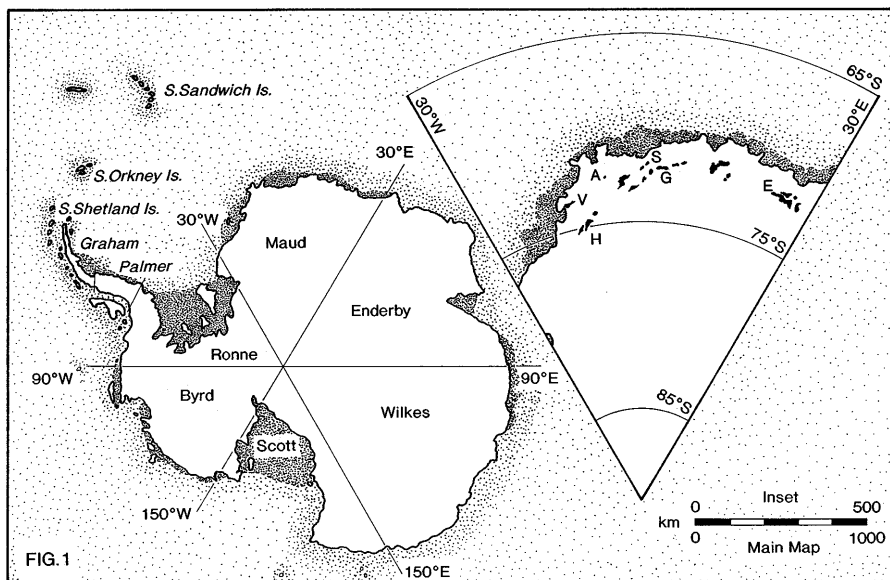


Figure 1. The study area. Main map: Roman type - Continental Antarctic sectors, italics - Maritime Antarctic areas. Ice shelves are heavily shaded. Inset map: Heavy shading - ice shelves, black - mountain ranges. Data are available for the following mountain ranges (west to east): H = Heimfrontfjella, V = Vestfjella, A = Ahlmannryggen, S = H.U. Sverdrupfjella, G = Gjelsvikfjella and E = eastern Dronning Maud (Sør Rondane Mountains).

is the (antiquity of) the habitats selected by these mites and could present day dispersal mechanisms account for the post-Pleistocene distribution of species amongst them. Thirdly what is the occurrence of both endemism and commonality within the Antarctic acarofauna? Finally, by considering whether this extant and impoverished antarctic acarofauna evolved by adaptation and speciation of relatively few species or has been derived from selective obliteration of a much larger and diverse fauna.

MATERIAL AND METHODS

Data regarding acarine distribution within Maud Sector have been obtained from the literature (Bowra, Holdgate & Tilbrook, 1966; Strandtmann, 1967; Strandtmann & Sømme, 1977; Sømme, 1978, 1980, 1986; Ryan *et al.*, 1989; Marshall, Newton & Crafford, 1994; Hiruta & Ohshima, 1995). The broader distribution patterns of all inland species and their higher taxa were derived from Pugh (1993), after the removal of all data relating to dubious, ill-determined and non-indigenous species (see Pugh, 1994).

Records of Antarctic mites were assigned to eleven regions (e.g. Greene *et al.*, 1970; Lewis-Smith, 1984; Longton, 1988; Hattersley-Smith, 1991; Pugh 1995) (Fig. 1). The six mainland areas radiating from the South Pole (90°S) to the coast conveniently contain different mountain ranges and constitute Continental Antarctica. These include Maud from 30°W to 30°E, Enderby (30°E–90°E), Wilkes (90°E–150°E), Scott (150°E–150°W), Byrd (150°W–90°W) and Ronne (90°W–30°W), which terminates at a northern limit between Cape Adams (75°00'S, 62°34'W) and the English Coast (73°24'S, 72°00'W). The Antarctic peninsula and its offshore islands north of the Cape Adams-English Coast line, includes southern Palmer and northern Graham regions, delimited by a line between Cape Jeremy (62°24'S, 68°50'W) and Cape Agassiz (68°28'S, 62°37'W). This region of the Antarctic mainland together with the S. Shetland, S. Orkney and S. Sandwich Island Groups comprises 'Maritime Antarctica'. Data from the sub-Antarctic islands, i.e. all other Southern Oceanic islands south of 45°S, excluding Tierra del Fuego, the Falkland Islands and the offshore islands of New Zealand north of 52°S, were used to establish possible outgroups (Pugh, 1993). These islands are less than million years old and/or were glaciated during the Pleistocene (e.g. Bellair, 1965; Varne, Gee & Quilty, 1969; Verwoerd, 1971; Sugden & Clapperhan, 1977), and so provide good comparators by having a relatively young fauna.

Faunistic similarities between the different sectors and islands were established by means of cluster analysis using a simple weighted-mean pair-group analysis (= WMPGA) computation (Sokal & Sneath, 1963), and a species or group present or not-recorded algorithm of x^2/yz , where x represents the number of taxa common to any two areas, while y and z are the total number of taxa in each. A more discriminatory present or absent algorithm was not applicable because the Antarctic fauna has not been studied systematically and the absence of particular records may simply reflect the lack of data (Pugh, 1993).

Similarities at specific, generic and familial levels were established for inland Prostigmata (= Actinedida) and Cryptostigmata (= Oribatida) by the removal of coastal records from the original data (Pugh, 1993). The Mesostigmata (= Gamasida) have been recorded from Maritime Antarctica but not from Continental

Antarctica and the one record of free-living Acaridia (Astigmata = Acaridida) was omitted. Complementary principal coordinate analysis was not appropriate because no suitable components could be determined. There were neither common physiological comparators nor common morphological traits covering the groups involved. Similarly, longitudinal/latitudinal parameters are wholly inappropriate, while species diversity, density and habitat descriptors are too vague or biased to be of use.

RESULTS

Ten of the twelve species of Acari recorded from Maud Sector are Prostigmata and two are Cryptostigmata (Table 1). On the basis of species range, the known distribution sites may be divided by cluster analysis into two groups which are relatively homogeneous (within group χ^2/yz coefficients of $.18 < .75$), but distinct from each other (between group coefficient of $.065$). These groups are (a) Vestfjella and Heimfrontfjella (V & H in Fig. 1) which share *Nanorchestes bifurcatus* and *Eupodes tottanfjella*, and (b) Ahlmannryggen, H.U. Sverdrupfjella, Gjelsvikfjella and the Sør Rondane mountains (A, S, G & E in Fig. 1), all of which share *Eupodes angardi* and *Maudheimia wilsoni*. Two species, *Nanorchestes brekkeristae* and *Tydeus erebus* exhibit disjunct distributions between the two groups.

TABLE 1. Distributions of mites on six mountain regions in Dronning Maud Land (see Fig. 1)

Family and species	Mountain Ranges ¹							Habitats ²
	V	H	A	S	G	E	O	
PROSTIGMATA								
Nanorchestidae								
<i>Nanorchestes antarcticus</i> Strandtmann			+				U	C
<i>N. bellus</i> Strandtmann & Sømme				+			M	C
<i>N. bifurcatus</i> Strandtmann	+	+				+	*	C B
<i>N. brekkeristae</i> Strandtmann & Sømme	+			+			*	C B
Eupodidae								
<i>Eupodes angardi</i> Strandtmann & Sømme			+	+	+	+	*	B R
<i>E. tottanfjella</i> Strandtmann	+	+					*	C B R
<i>E. winsnesi</i> Strandtmann & Sømme				+			*	C B R
<i>Protoreunetes maudae</i> Strandtmann	+						S	C B
Tydeidae ³								
<i>Tydeus erebus</i> Strandtmann		+	+		+	+	*	C B R
<i>T. setsukose</i> Strandtmann	+						S	C B R
CRYPTOSTIGMATA								
Maudheimiidae								
<i>Maudheimia petronia</i> Wallwork				+			*	C
<i>M. wilsoni</i> Dalenius			+	+	+	+	S	C

Note: ¹Mountain ranges listed as follows from west to east:

V = Vestfjella, H = Heimfrontfjella, A = Ahlmannryggen, S = H. U. Sverdrupfjella, G = Gjelsvikfjella, E = Eastern Dronning Maud (Sør Rondane Mountains), O = Outside Maud Sector, including Macquarie I., S = Scott Sector and U = Ubiquitous (Antarctic and sub-Antarctic), all others (*) are endemic to Maud Sector.

²Habitats: C = chalikosystems, B = bryosystems, R = bird rookeries.

³*T. wilkesi* in Pugh (1993) (sic) is attributable to Ronne Sector.

Data from: Bowra *et al.* (1966), Strandtmann (1967), Strandtmann & Sømme (1977), Sømme (1978, 1980, 1986), Ryan *et al.* (1989), Marshall *et al.* (1994); Hiruta & Ohyama (1995).

The *in toto* inland acarofaunas of Continental and Maritime Antarctica comprise 40 species (Tables 2 & 3) though some, e.g. *Edwardzetes* and *Magellozetes* spp. may be of coastal origin (P. Convey, personal communication). The faunas are dominated by the Prostigmata, with 12 genera from 6 families, and the Cryptostigmata, with 8 genera from 7 families. Although only marginally more species have been recorded from the Maritime Antarctic than the Continental Antarctic (40 vs. 28 species), the major difference between the two regions is the degree of endemism associated with each. For example over 85% of Continental species are endemic, compared with only about half those of the Maritime fauna while generic endemism is low in both regions (Table 2). This trend is repeated if the Prostigmata and Cryptostigmata are treated separately (Table 3), though in the Cryptostigmata endemism is high among the Continental fauna and low among the Maritime equivalent.

Cluster analysis (Fig. 2) indicates that the Prostigmata show no evidence of a 'Continental Antarctic species cluster' because there are no species common to either Wilkes or Byrd and the other sectors. This leaves Graham Land, S. Shetland S. Orkney and S. Sandwich Islands sharing common *Nanorchestes*, *Eupodes*, and *Ereynetes* species and forming a 'Maritime cluster' which is loosely associated with a Maud/Ronne grouping as well as a more distant Palmer/Enderby/Scott one. There is however considerable outgrouping with the sub-Antarctic islands between these two distant clusters.

The Maritime cluster persists at the generic level where there is also a distinct

TABLE 2. Free-living inland Antarctic Acari. Figures show numbers of endemic+non-endemic species of each genus per zone

Order	Family	Genus	Antarctic zone			
			Con.	Mar.	Total	
MESOSTIGMATA	None — all coastal					
PROSTIGMATA	Nanorchestidae	<i>Nanorchestes</i>	3+2	3+1	5+2	
		<i>Eupodes</i>	4+0	4+1	8+1	
	Eupodidae	<i>Protereunetes</i>	2+0	—	2+0	
		<i>Stereotydeus</i>	6+1	1+1	7+1	
	Penthalodidae	<i>Coccorhagidia</i>	2+0	—	2+0	
	Rhagidiidae	<i>Rhagidia</i>	—	0+2	0+2	
		<i>Ereynetes</i>	—	0+1	0+1	
	Ereynetidae	<i>Apotrophytydeus</i> #	—	3+0	3+0	
		<i>Paratriophytydeus</i> #	—	1+0	1+0	
		<i>Paratydealus</i> #	—	1+0	1+0	
		<i>Pretriophytydeus</i>	—	0+1	0+1	
		<i>Tydeus</i>	4+0	—	4+0	
	CRYPTOSTIGMATA	Brachychthoniidae	<i>Liochthonius</i>	—	0+2	0+2
		Oppiidae	<i>Oppia</i>	—	2+1	2+1
		Podacaridae	<i>Antarcticola</i>	1+0	—	1+0
Haplozetidae		<i>Maculobates</i>	—	1+0	1+0	
Ceratozetidae		<i>Edwardzetes</i>	—	0+1	0+1	
		<i>Magellozetes</i>	—	0+1	0+1	
Maudheimiidae #		<i>Maudheimia</i> #	2+0	—	2+0	
Mycobatidae		<i>Antarctozetes</i>	—	0+1	0+1	
ASTIGMATA	Saproglyphidae	<i>Neocalvolia</i>	—	1+0	1+0	
Total endemic+non endemic species:			24+3	17+13	40+14	
Percentage of endemic species			85.7%	42.5%	74.1%	

Key: Con = Continental and Mar = Maritime Antarctica # = endemic taxa.

TABLE 3. Occurrence of endemic acarine taxa from inland Antarctica, Gondwanaland, Arctic and Alpine refugia. The numbers show endemic+non endemic taxa and the degree of endemic taxa per zone (rounded to nearest percentage). Antarctic data from Table 2 and others from literature sources as indicated below. Endemicity estimates for the Cryptostigmata are used to suggest whether the different provinces or regions are pre-Pleistocene refugia

Province or Region	Order				Refugia
	PROSTIGMATA		CRYPTOSTIGMATA		
	species	genus	species	genus	
Continental Antarctica	22+3 88%	0+6 0%	3+0 100%	1+1 50%	YES
Maritime Antarctica	13+8 62%	3+6 33%	3+6 25%	0+6 0%	NO?
Neotropical (High Andes) ^d	—	—	85%	21%	YES
Australian (New Zealand) ^{a & e}	—	—	82%	17%	YES
Ethiopian (Southern Africa) ^e	—	—	50%	11%	NO?
Alpine (Austrian Alps) ^c	—	—	16%	2–5%	NO
Arctic (North America) ^b	28	5–10%	7%	<2%	NO

Data from: ^aSpain & Luxton (1971); ^bDanks (1981); ^cSchatz (1983); ^dBalogh & Balogh (1990); ^eBalogh & Balogh (1992).

Palmer/Continental (minus Ronne) grouping. All are based on a maximum of six, but more usually one to three common genera, again *Nanorchestes*, *Eupodes* and *Ereynetes* are the most common denominators. There is however considerable outgrouping within the two Maritime and Continental clusters and little evidence of a common locus. The clusters at familial level are enhanced generic ones, i.e. Maritime island/Graham Land, Maud/Scott and Palmer/Byrd/Enderby with reduced outgrouping.

Within the Cryptostigmata there are no taxa common to Enderby, Wilkes, Byrd, Ronne and Palmer regions, but there are generally greater similarities between the other sectors and islands when compared with the Prostigmata. Continental Maud and Scott sectors form a cluster at all levels, but cannot be related to the other Maritime areas because the common denominator is two species of the genus *Maudheimia*, which along with the parent family Maudheimiidae, are unique to Continental Antarctica. Graham Land, S. Shetland, S. Orkney and S. Sandwich Is. form a consistent Maritime Antarctic cluster.

DISCUSSION

Antiquity and origin of higher taxa

The inland Continental and Maritime Antarctic acarofaunas are remarkably impoverished, comprising only 54 known species (Tables 2 & 3), and severely disharmonic in that several major groups are absent. The groups not represented include the Eleutherogonina (Prostigmata), Mesostigmata, numerous families within the Cryptostigmata, and with the exception of one species, the Astigmata. The ascendant Prostigmata and Cryptostigmata are ancient taxa, pre-dating the Cretaceous disintegration of Gondwana and may even date back to the Devonian (Krivolutsky, 1979; Bernini, 1986; Krivolutsky & Druk, 1986; Norton *et al.*, 1988).

Indeed, Mesozoic continental drift may account for some of the current global distribution patterns within these groups (e.g. Hammer & Wallwork, 1979). In contrast the Anactinotrichida, including the Mesostigmata, are of relatively recent, possibly Tertiary origin (Bernini, 1991) and are thus possibly 'too young' to have reached Continental Antarctica after it separated from the rest of Gondwana.

Age(s) of selected habitat(s)

The minimum requirements for free-living Antarctic mites and other meiofauna

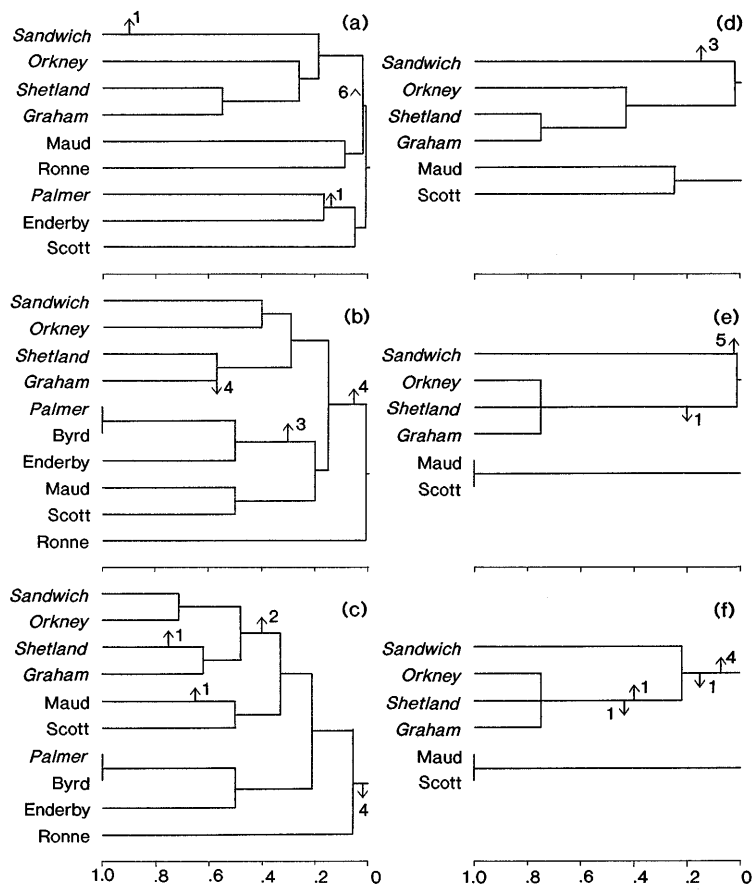


Fig.2 Similarities among inland Antarctic acarofaunas by cluster analysis. Diagram show cluster associations for x^2/yz similarity coefficients between the different Continental (roman type) and Maritime Antarctic (italic) areas of two major free-living groups of mites at three different taxa levels.

Figure 2. Similarities among inland Antarctic acarofaunas by cluster analysis. Diagram show cluster associations for x^2/yz similarity coefficients between the different Continental (roman type) and Maritime Antarctic (italic) areas of two major free-living groups of mites at three different taxa levels. (a) Prostigmata species, zero associations for Wilkes and Byrd. (b) Prostigmata genera, zero association for Wilkes. (c) Prostigmata families, zero association for Wilkes. (d) Cryptostigmata species, zero associations for Enderby, Wilkes, Byrd, Ronne and Palmer. (e) Cryptostigmata genera, zero associations for Enderby, Wilkes, Byrd, Ronne and Palmer. (f) Cryptostigmata families, zero associations for Enderby, Wilkes, Byrd, Ronne and Palmer. Arrows show position and number of outgroupings with sub-Antarctic islands. Note: Orkney = South Orkney Is., Sandwich = South Sandwich Is., Shetland = South Shetland Is.

are: (1) Small quantities of organic (food) material, (2) protection from prolonged high winds and sufficient heat trapping to allow promote survival in often very low sub-zero temperatures, and (3) moisture, the scarcity of which is often the limiting factor for Antarctic life (e.g. Gressitt, 1964; Janetschek, 1967; Sømme 1978, 1985; Ryan *et al.*, 1989; Kennedy, 1993). There is a limited range of Antarctic habitats which can provide such conditions, including recently deposited faecal material, corpses and other debris left by birds in isolated rookeries; older but post-Pleistocene 'bryosystems' which include clumps of macrophyte vegetation, and pre-Pleistocene or even pre-Cretaceous 'chalikosystems' of bare gravel and only scattered microphytes (Janetschek, 1963; Gressitt, 1965, 1967; van Zinderen-Bakker, 1970). The Eupodidae and Tydeidae of Maud Sector are generally distributed throughout all available habitats (Table 1). In contrast, the Nanorchestidae do not occur in bird rookeries while two species, *N. antarcticus*, *N. bellus* and the two *Maudheimia* spp. show a clear preference for the older chalikosystems (Dalenius & Wilson, 1958; Strandtmann, 1967, 1982; Wallwork, 1967; Strandtmann & Sømme, 1977; Sømme, 1980; Marshall, Newton & Crafford, 1994; Hiruta & Ohyama, 1995).

Because colonization of inland Continental Antarctica is limited to geographically scarce ice-free habitats, as well as by the severe climate and isolation from other continents (and thus sources of other biota), the process is probably restricted to relatively ice-free interglacial periods. The most recent glaciation maximum was during the Pleistocene (1.8–0.12 million years ago), so the extant fauna must comprise either pre-Pleistocene (endemic) or post-Pleistocene (immigrant) species. Habitat selection is biased towards the 'older' pre-Pleistocene chalikosystems, particularly at generic level but it is not clear whether the present distribution patterns are truly pre-Pleistocene or a result of post-Pleistocene diversification. This may be clarified by considering whether present day dispersal mechanisms could account for the observed distribution patterns.

Contemporary dispersal mechanisms

Dispersal of Antarctic terrestrial plants and invertebrates is mediated by mechanisms beyond the control of individuals (Ellis-Evans & Walton, 1990). The main natural dispersive agents are wind, water and birds, because there are no human-mediated introduced or dispersed species amongst the inland fauna (Pugh, 1994).

Wind

Important for the long-range dispersal of polar microbes, plant propagules and non-polar mites (Ellis-Evans & Walton, 1990; Schatz, 1991). Antarctic mites tend to live in protected niches under stones and amongst vegetation (Gressitt, 1965; Pugh, 1994), where wind-mediated transport is not likely to be effective. Furthermore, unlike other resistant invertebrates including nematodes, rotifers or tardigrades, Antarctic mites do not possess an anhydrobiotic resting/dispersal stage (c.f. Ashwood-Smith, 1970 Block, 1982; Pickup, 1988, 1990; Sømme, 1985; Kinchin, 1994), which would allow them to survive the extremely severe cold and desiccating conditions present in the aerial plankton (Wallwork, 1984).

Water

Ocean currents may effect the dispersal of some coastal temperate mites (Schatz, 1991), but they cannot distribute inland Antarctic species which are separated from the sea by extensive ice shelves.

Birds

A variety of species, particularly the Antarctic petrel *Thalassoica antarctica* (Gmelin) (Procellariidae) have been suggested as effective distribution vectors for a variety of mites and other Antarctic invertebrates (e.g. Taylor, 1954; Dalenius & Wilson, 1958; Falla, 1960; Bowra Holdgate & Tilbrook, 1966; Wallwork, 1973). It is more likely however that free-living invertebrates and especially mites occur in bird colonies simply because these are organically enriched by faeces, microbes, feathers, egg remains and corpses (Gressitt, 1965; Gressitt & Shoup, 1967). Direct bird-mediated transportation has never been demonstrated.

All three dispersal mechanisms are problematical over short range and are unlikely to have been effective for post-Pleistocene immigration from the other Gondwanan continents, even using the older Southern Oceanic islands as 'stepping stones' as observed in some sub-Antarctic insect faunas (e.g. Chown, 1992). The fauna (Table 2) is restricted to Pachygnathina, Eupodina (Prostigmata) and Cryptostigmata, that is groups with comparatively poor dispersal attributes. Groups with good dispersal attributes for example the phoretic Mesostigmata and parasitic Eleutherengonina (Prostigmata) (e.g. Mitchell, 1967; Binns, 1982; Athias-Binche, 1994), are absent. Their exclusion may be the result of an absence of suitable insect hosts and/or prey.

The evidence presented so far merely confirms the previously suggested pre-Pleistocene origin of the Antarctic Acari (e.g. Wallwork, 1967, 1973, 1984). But it has not been established whether these species are themselves pre-Pleistocene or more recent descendants of pre-Pleistocene ancestors. This question may be approached by considering the degree of endemism in different taxa.

Endemism

The significance of endemism may be considered via two routes. First, by comparing its occurrence at specific and generic levels in the same taxa within different geographical regions. In this case amongst Acari, principally Cryptostigmata, within Antarctic and other comparable Gondwanan refugia, as well as cold high altitude/latitude environments. Second by comparing its occurrence between unrelated taxa from the same (Antarctic) region which have known, or at least suspected origins. Both will be considered.

Geographical endemism

Two species, *Eupodes winsnesi* and *Maudheimia petronia* are unique to a particular mountain range, H.U. Sverdrupfjella in western Dronning Maud Land, while a total of seven species (= 58%) are endemic to Maud Sector. Previous studies on endemism amongst Antarctic oribatid mites suggested that moderate (60%) specific and low (30%) generic endemism were indicative of a post-Pleistocene origin (Gressitt, 1961; Wallwork, 1973). Similar figures may be obtained from the *in toto* inland fauna, i.e. c.74% at specific and c.19% at generic levels (Table 2). But such conclusions are

misleading and when the data are broken down both taxonomically into Prostigmata and Cryptostigmata as well as geographically into Maritime and Continental Antarctica, they show remarkably diverse trends (Table 3) indicative of rather heterogeneous data.

The Continental Antarctic Prostigmata and Cryptostigmata together with the Continental Antarctic Prostigmata are dominated by endemic species while the Maritime Antarctic Prostigmata comprise a larger number of species also recorded from the sub-Antarctic islands. There are different and significantly more endemic species of both Prostigmata and Cryptostigmata in the Continental Antarctic than in the Maritime Antarctic (Tables 2 & 3). The endemic Antarctic biota in general includes both pan-Antarctic Mesozoic palaeoendemics and neoendemics which have recently entered the Maritime Antarctic from South America and are not found east of the Trans-Antarctic mountains (Schweiger, 1958). This implies that the Continental Antarctic acarofauna may be predominantly Palaeoendemic, whilst that of the Maritime Antarctic is Neoendemic.

Despite the apparently high levels of specific endemism along the Continental fauna, all four recorded genera of Prostigmata have a cosmopolitan distribution, only *Maudheimia* and its parent family Maudheimiidae (Cryptostigmata) are endemic to the region (Balogh & Balogh, 1992). *Maudheimia* is a montane genus, with a very disjunct distribution, with *M. wilsoni* endemic to the Maud Sector while *M. petronia* has a very broad distribution extending to Victoria Land in the Scott Sector (Dalenius & Wilson, 1958; Sømme, 1986; Ryan *et al.*, 1989; Marshall *et al.*, 1994; Hiruta & Ohyama, 1995). It is likely that the two *Maudheimia* species are synonymous (L. Coetzee, personal communication), and their spatially separated populations represent the fragments of a formerly extensive generic distribution continuous over a range of 5000 km surrounding the Polar Plateau. The persistence of *Maudheimia* as such widely dispersed populations is evidence of the genus being endemic and a possible Gondwanan relic.

Endemism relative to Gondwana, Alpine and Arctic refugia

The reported levels of specific endemism for Continental Antarctica, especially that for the Cryptostigmata, appear to be very high. But such data need to be compared to those of other related mites from pre-Pleistocene refugia in other parts of the world. Although the acarofaunas of the Southern Hemisphere are not particularly well documented there are useable data for the Cryptostigmata which will be addressed here (see Table 3).

Gondwanan refugia include the Neotropical high Andes (over 1000 m), the Ethiopian Cape Province over 1000 m, a region at least partly isolated by the Kalahari and Namib deserts, and the Australasian New Zealand (e.g. Briggs, 1987). Specific endemism is relatively high amongst the Andean and New Zealand Cryptostigmata (82–85%), but the complementary generic endemism is rather low (17–21%), though this may simply reflect the scarcity of records and a predominance of type localities amongst the data (e.g. Spain & Luxton, 1971). Specific endemism is estimated at only 50% for the South African Cryptostigmata, based on a low (11%) generic endemism. Comparable or higher levels of endemism are evident amongst vascular plant communities associated with the same Gondwanan refugia, for example 73% in Southern Africa and 81% in New Zealand (Major, 1988). These data suggest that the Andes, New Zealand, Cape Province and the nunataks of

Continental Antarctica are pre-Pleistocene refugia and contain predominantly (pre-Pleistocene) endemic Cryptostigmata.

High altitude/latitude refugia show a remarkably different trend as exemplified by the Austrian Alps and the North American Arctic where, amongst the Cryptostigmata, specific endemism is low (7–16%) and generic endemism very low (2–7%). Again, similar levels of specific endemism are evident for the vascular plant communities of these refugia, for example 0.5% in the Arctic and 13–18% in the eastern and western Alps (Major, 1988). Such figures suggest that neither region are refugia and do not contain significant pre-Pleistocene components, but are dominated by post-Pleistocene immigrant species of both Cryptostigmata and vascular plants.

Endemism in other Antarctic faunas

The antiquity of some higher taxa within the Antarctic fauna may be determined from their relative degrees of generic and specific endemism (e.g. White, 1984; Watling & Thurston, 1989; Greenslade, 1995). For example, high levels of specific endemism (>90%) and moderate to low levels of generic endemism (measured as 70% in fishes, 60% in Continental springtails, 39% in amphipods and 14% in pycnogonids) are indicative of pre-Pleistocene relicts. In contrast, a moderate specific (42–57%) and very low (<5%) generic endemism as illustrated by the polychaetes (Annelida) and Maritime springtails, indicates a taxon which has developed *in situ* since the Pleistocene, or is of post-Pleistocene origin.

Taking figures of 80% and 40% to mark the divisions between high, medium and low levels of endemism, the marine and terrestrial faunas of Antarctica may be divided into two groups. Group A is characterized by a high specific endemism and moderate to low generic endemism typical of relict taxa with a pre-Pleistocene origin, while Group B is identified by moderate specific and moderate to low generic endemism typical of post-Pleistocene immigrants (Table 4). The two groups are

TABLE 4. Endemism amongst the Antarctic fauna. Data are ranked by specific endemism and split into two groups (A & B), with group A showing high (80%+) specific and moderate (40–80%) or low (<40%) generic endemism, while group B shows moderate specific and moderate or low generic endemism

Group	Taxa	Endemism (%)		Reference
		Specific	Generic	
A	Cryptostigmata (Continental)	100	50	present study
	Pisces	95	70	Andriashev (1965)
	Collembola (Continental)	91	60	Greenslade (1995)
	Amphipoda	90	39	Knox & Lowry (1977)
	Pycnogonida	>90	14	Fry (1964)
	Prostigmata (Continental)	88	0	present study
B	Echinodermata — Echinoidea	77	25	Pawson (1969b)
	Echinodermata	73	27	Eckman (1953)
	Isopoda & Tanaidacea	66	10	Kussakin (1967)
	Prostigmata (Maritime)	62	33	present study
	Echinodermata — Holothuroidea	58	5	Pawson (1969a)
	Bryozoa	58	—	Bullivant (1969)
	Annelida — Polychaeta	57	5	Knox & Lowry (1977)
	Collembola (Maritime)	42	0	Greenslade (1995)
	Cryptostigmata (Maritime)	25	0	present study

clearly discrete at generic ($P = .05 < .1$) and even more so at specific ($P < .01$) levels (Mann-Whitney U-test, Sokal & Rohlf, 1995).

Although the marine fauna may be assigned to either group the terrestrial fauna shows a remarkably clear trend in that the Continental Antarctic Cryptostigmata, Prostigmata and Collembola all belong to pre-Pleistocene endemic Group A, whilst their Maritime Antarctic counterparts are all Group B post-Pleistocene immigrants. This apparent distinction between the terrestrial arthropod (especially acarine) faunas of Continental and Maritime Antarctica is corroborated by the separate geological origins of the two regions (e.g. Dalziel & Elliot, 1982; Storey *et al.*, 1988), and may be examined further by considering the faunistic similarities within and between the two provinces.

Similarities within the Antarctic acarofauna

The cluster analysis (Fig. 2) indicates that the Prostigmata comprise a distinct Maritime locus with some outgrouping to the sub-Antarctic islands and a diffuse often broken Continental grouping instead of a distinct locus. The contrary is true of the Cryptostigmata which form essentially separate Continental and Maritime Antarctic loci, of which the latter exhibits intermittent outgrouping with the relatively young sub-Antarctic island faunas at all three taxa levels. This corroborates the previously described low levels of endemism among the Maritime oribatids and confirms that they share a close affinity with those of the sub-Antarctic islands (Wallwork, 1967). In contrast, the Continental oribatids comprise only two *Maudheimia* spp. endemic to Maud and Scott Sectors which exhibit perfect generic and familial similarities with no evidence of outgrouping (Fig. 2d-f, Tables 1 & 2).

Similarities between Antarctic and other acarofaunas

The genera *Eupodes*, *Nanorchestes*, *Protoreunetes* and *Tydeus* are all cosmopolitan (e.g. Strandmann, 1971; Krantz, 1978; Pugh, 1993), whilst *Maudheimia* is the only genus of endemic (cryptostigmatic) Acari on Continental Antarctica. *Maudheimia* has no known relatives in Southern Africa, the region which abutted western Dronning Maud Land when Africa and Antarctica were joined to form Gondwana, to immediately support a Gondwanan origin. There are however related genera on other Gondwanan fragments including one *Crassoribatula* sp. (Oribatulidae) from New Zealand, one *Areozetes* sp. (Areozetidae) in Peru and another questionable congeneric record from Sri Lanka (L. Coetzee, personal communication). This indicates a probable common Gondwanan and ancient (pre-Pleistocene) origin for the *Areozetes*, *Crassoribatula* and *Maudheimia* group.

Origin: speciation vs. faunal obliteration

A suite of survival strategies have been reported in Antarctic mites as adaptations to the severe climate of the region. These are principally cold-tolerance strategies as adaptations to low temperatures and prolonged life histories to compensate for restricted periods of growth and reproduction (e.g. Block, 1990; Convey, 1994). But

such characteristics are necessarily pre-adaptations and provide few clues as to the origin of a species. Close relatives of extant species did not necessarily become extinct during encroaching glaciation because of deficient survival strategies, but because they were in the wrong place at the wrong time.

For example the terrestrial fauna of Scott Sector is more diverse on high (1000–2000 m) mountains and nunataks than on the coastal fringe where climate, soil and food conditions are apparently better (Janetschek, 1963). These data were originally construed as the replacement of a (pre-glaciation) ancestral fauna by more tolerant or resistant descendants on the higher mountains (Janetschek, 1963). But oribatid mites and Antarctic invertebrates are characterized by slow reproduction and low fecundity (e.g. Norton, 1994; Convey, 1996), factors which are indicative of slow speciation (e.g. Barton, 1988), so that the extant fauna could not have arisen during the last 10 000 years of the post-Pleistocene.

There is an alternative origin for the montane fauna of Scott Sector which can be applied to that of Maud Sector and Continental Antarctica in general. There was a severe and broad spectrum obliteration of low altitude pre-glacial habitats and biota caused by ice-sheet advance and thickening during periods of glaciation. Some montane Acari survived this encroaching glaciation amongst chalikosystem habitats isolated on high altitude mountains and nunataks. Both mites and lichens endured the extreme cold associated with high altitude, during 'warm' interglacial and 'colder' glaciation periods, including the severe Pleistocene one, and were essentially pre-adapted to the comparatively milder present-day Antarctic climate.

This hypothesis is supported by the disjunct distributions of Antarctic inland (montane) Acari. For example *Nanorchestes brekkeristae* and *Tydeus erebus* on separate mountain ranges within Maud Sector; *Protoreunetes maudae*, *Tydeus setsukoae* and *Maudheimia petronia* in both Maud and Scott Sectors, while *N. antarcticus* is widely scattered across Antarctica. Such distribution patterns cannot be accounted for in a post-Pleistocene time span and clearly indicate that Antarctic mountains and nunataks are refugia supporting the scattered remnants of one-time more widely dispersed populations which have survived the Pleistocene glacial maximum on montane chalikosystem habitats. All other species and members of the extant species occurring at lower altitudes were obliterated by earlier Pleistocene or even Carboniferous expansion and thickening of the Antarctic ice cap.

CONCLUSIONS

The few mite species which occur on the inland mountain ranges and nunataks of Continental Antarctica are dis-harmonic members of the Pachygnathina, Eupodina and Cryptostigmata, i.e. ancient Cenozoic taxa which pre-date the disintegration of Gondwana. One family, the Maudheimiidae (Cryptostigmata), is exclusive to Continental Antarctica and of probable Gondwanan origin, though all other families contain predominantly temperate, tropical or cosmopolitan species. Antarctic mites have limited powers of self dispersal and the absence of those with better dispersal attributes, i.e. the Eleutherengonina and Mesostigmata, which have parasitic or phoretic juveniles, may be related to a lack of suitable hosts and/or prey. In addition the Mesostigmata possibly evolved after the Cenozoic disintegration of Gondwana and so never reached Continental Antarctica.

A post-Pleistocene origin of the inland Antarctic acarofauna at generic or specific

levels is unlikely as suggested by problems associated with modern day dispersal, disparate adjacent Continental and Maritime faunas and inferred slow speciation. It is more probable that these often locally endemic or disjunct species represent the relict remnants of ancient pre-Pleistocene, or even pre-Tertiary endemic acarofaunas. All of these palaeoendemic mites survived one or more major glaciation events as isolated populations among 'ancient' chalikosystem refugia on mountains and nunataks, while all low altitude faunas were obliterated. It is only since the end of the most recent Pleistocene glaciation event that the different mite species have colonized other 'younger' ice-free niches of bryosystems and debris associated with bird colonies.

The Prostigmata show disjunct species distribution patterns, both at specific level within Maud Sector and at specific, generic and familial levels between Continental and Maritime Antarctica. In contrast, the Cryptostigmata show a more consistent Continental/Maritime grouping at all three taxonomic levels. This implies that the Prostigmata are relicts of an earlier pan-Antarctic fauna than the Cryptostigmata and perhaps pre-date the Antarctic Cryptostigmata. But although the Continental Cryptostigmata are undoubtedly endemic to the region, the Maritime species may share a common origin with the relatively young faunas of the sub-Antarctic islands.

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