A Review of the World Distribution of Oribatid Mites (*Acari: Cryptostigmata*) in Relation to Continental Drift

By MARIE HAMMER *and* JOHN A. WALLWORK

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Synopsis

A survey is presented of the patterns of world distribution of *oribatid mites,* mainly at the generic level. Evidence is presented to show that the oribatids are an ancient group, and recent genera have an evolutionary history extending back to the *Jurassic* and probably earlier. Sixteen percent of recent genera are cosmopolitan in distribution, and this element in the world fauna can be identified with that which was present in *Pangaea.* With the gradual break-up of Pangaea, genera arose with a more restricted distribution – firstly in *Gondwanaland* and *Laurasia* – and subsequently in the main continental masses as we know them today. All of these elements can be identified in the recent oribatid fauna of the world. Circum-polar and pan-tropical distribution patterns provide evidence of previous Gondwanan and Laurasian connexions, and evidences of faunal intermixing at the boundaries of these two former super-continents are found in the faunas of *India,* north-west *Pakistan* and *Japan.* The origin of the oribatid fauna of *oceanic islands* is discussed and it is suggested that the source area for the fauna of the South Pacific is probably South-east Asia and that dispersal has occurred over seas, via island "stepping stones".

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Contents

Introduction

The moss mites, or oribatids, are small arachnids which live a free existence, mainly in soils but not infrequently in wet biotopes. They are widely distributed around the world, although little attention has been paid so far to any patterns that may occur on a global scale and, more particularly, to how such patterns have arisen. If we believe, for instance, that the oribatids are a very ancient group of animals, with an evolutionary history extending back many millions of years into geological time, we must consider the possibility that the global distribution of this fauna has been influenced by changes in world climate and topography which have occurred during this time. Such changes have been brought about principally by the movements of continents which have been occurring at least since the Jurassic, 150 million years ago. At this time, the earth's major land masses were much closer together than they are today, forming the supercontinent of Pangaea. The faunal continuities that existed then would have been disrupted by the subsequent break-up of Pangaea and, eventually, the separation of Laurasia and Gondwanaland into eastern and western components. If oribatid stocks persisted and continued to evolve while these events were occurring, even up to the present day, we might expect to find evidence for the effects of continental drift in the global patterns of distribution that we can observe today. For example, stocks which were widely distributed across Pangaea, if they have persisted to the present day, would be expected to show a cosmopolitan distribution, or a relict of such. Stocks which evolved in Gondwanaland could be expected to be widely distributed across the southern hemisphere today, in South America, Africa, India and Australasia — but not commonly outside these regions. Similarly, a Laurasian fauna would have a distribution which essentially encompassed North America, Greenland and Eurasia. Evidence for such patterns would be provided by the existence of harmonic faunas (see page 10) in two or more regions which are now geographically isolated.

Alternatively, we must also consider the possibility that the present distribution patterns of oribatid mites are recent phenomena — the products of dispersal agencies which have been operating, perhaps, since the Pleistocene. Such dispersal must have taken place across the wide expanses of ocean which now separate the continents of the world, and the agencies involved could be air currents, water currents, transport by birds, or introduction by Man. Such agencies are essentially random ones, and result in unbalanced, dysharmonic faunas (see p. 7).

The evidence for continental drift is, in our opinion, overwhelming (see readings from Scientific American, entitled 'Continents Adrift', introduced by J. Tuzo Wilson 1971). We will also present evidence that the oribatids are a very ancient group of terrestrial animals. The main purpose of this review is to examine the extent to which present-day distribution patterns of these arachnids may be interpreted within the context of continental drift.

It is recognized at the outset that the oribatid fauna of certain parts of the world, notably China, India and Australia, is very incompletely known, and our analyses have been limited, sometimes severely, by this fact. However, we believe that enough information is available from many parts of the world to allow a broad framework to be developed, even though subsequent discoveries of new taxa and new distribution records will undoubtedly modify the ideas presented in this paper. Some of these ideas have already been developed by Hammer in her works on the oribatid fauna of South America, North America, Greenland, New Zealand, north-west Pakistan, south-east Asia (unpublished) and the Pacific, and by Wallwork in relation to the subAntarctic fauna (full details of the relevant publications are given in the Bibliography). In this review, these ideas are developed further in a global context, and as a first approach we have modified the distribution data given by Balogh (1972) and Ghilarov & Krivolutsky (1975) in the light of the most recent records available. This task has been made easier by the kind cooperation of Dr. E. Piffl (Vienna) who has placed at our disposal his very extensive, unpublished distribution records. We wish to express our sincere thanks to Dr. Piffl for providing such an invaluable, if hitherto unpublicized service to Acarology. We would also like to thank Mrs. H. Price-Thomas (Westfield College) for the art work.

The antiquity of oribatids

If the distribution patterns of oribatid mites have been influenced by continental drift, then this must be an ancient group of animals. What evidence do we have for the antiquity of this group?

It could be inferred that the oribatids are an ancient group because of their wide distribution in the world, but this is essentially a circular argument — oribatids are an ancient group because they are widely distributed, and they are widely distributed because they are an ancient group. The hard evidence that we are looking for must come from the fossil record.

Until quite recently, fossil oribatids were known only from amber deposits of the Oligocene (Sellnick, 1918) — too recent for our purposes. Not long ago, however, Krivolutsky (1973) recovered fossil oribatids from Jurassic and Cretaceous deposits in Russia. These include representatives of such families as the Camisiidae, Trhypochthoniidae, Cymbaeremaeidae and Plateremaeidae which have a cosmopolitan distribution today. The validity of these finds has recently been confirmed by the discovery of a member of the cosmopolitan aquatic genus *Hydrozetes* in a deposit of Lower Jurassic age in southern Sweden (Sivhed & Wallwork, in prep.). These records provide positive evidence that families of oribatids that we can recognize today were present during the Jurassic and undoubtedly earlier. There is no reason to doubt that they would be widely spread across a continuous land mass which was Pangaea. With the break-up of Pangaea, they would be carried on drifting continents to all parts of the globe, and should be present as a cosmopolitan element in the oribatid fauna of the world today.

Global patterns of distribution

It is not sufficient, for the development of our argument, merely to identify a cosmopolitan element in the world oribatid fauna. Continental drift has changed the positions of the earth's land masses relative to each other and, in many cases, has increased their isolation. We might expect to find, therefore, in addition to a cosmopolitan element in the world oribatid fauna, stocks which are clearly Gondwanan or Laurasian in origin together with elements, perhaps of more recent origin, which have evolved in, and are restricted to, one particular land mass.

Using the distribution records available to us, we have attempted to identify these various elements at the generic level. We have deliberately chosen to deal with genera, rather than species or families, in most of our analyses because we believe that the distribution patterns of groups of related species (= genera) are more meaningful than those of individual species or super-generic groups. In Table 1, 696 genera are classified according to their known distribution; this represents over 90 % of the oribatid genera described to the present time. The remainder have not been included in our analyses for various reasons, i.e. their taxonomic status or distribution records are questionable.

In Table 1, two groups of oribatids are recognized: the Inferiores and the Superiores. The former are the 'primitive' oribatids, numbering some 110 genera, which include an appreciable number of aquatic or hygrophilous groups, such as *Malaconothrus, Trimalaconothrus, Trhypochthonius, Platynothrus, Heminothrus* and *Hypochthonius.* The latter are the so-called 'higher' oribatids, supposedly of more recent evolutionary origin, and primarily terrestrial in habit. Complete lists of genera used in the compilation of Table 1 are given in the Appendix.

The data presented in Table 1 raise a number of interesting points which will be discussed in subsequent sections of this paper. For the moment, we are content to make the following statements. Firstly, that an appreciable cosmopolitan element (16 %) is present in the world oribatid fauna, and we are identifying this with the fauna which was present in Pangaea. Secondly, on a percentage basis, the cosmopolitan group is much more strongly represented among the Inferiores than among the Superiores. This is to be expected if we subscribe to the view that the cosmopolitan group represents the relicts of an ancient Pangaean fauna. Thirdly, the number of genera which are restricted to a particular land mass or region belong, in the main, to the Superiores — this is again consistent with the idea that recent large-scale overseas dispersal is not occurring.

The cosmopolitan fauna

As already noted, the cosmopolitan fauna includes a substantial number of primitive oribatid genera — the Inferiores. A good example of the cosmopolitan distribution of one of these primitive oribatids is provided by *Mucronothrus nasalis* (Fig. 1).

Mucronothrus nasalis was first described by Willmann (1929) from moss in a spring on the small island of Herdla, near Bergen, Norway. Since then it has been encountered in many localities around the world and will no doubt be found in more localities by future investigations (Fig. 1). This species has a very distinctive biotope; it is always found in cold springs or icy melt-water at high altitudes. Its wide distribution and its restriction to freshwater biotopes suggest that its only way of dispersal has been by continental drift; a conclusion advanced by Hammer (1965) and subsequently supported by the morphological studies of Travé (1971, 1973). Travé examined populations from various parts of the world, such as East Greenland, Lappland, Denmark, Pyrenees, the Andes of South

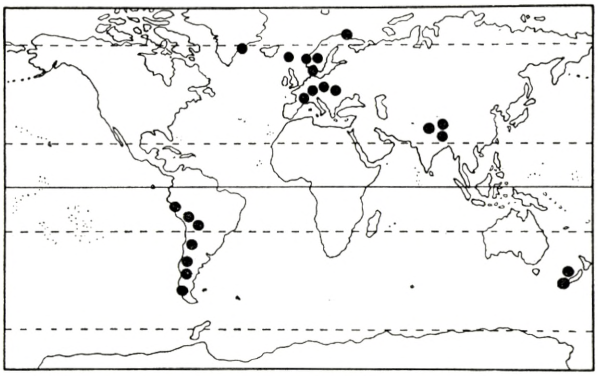

Fig. 1. The world distribution of *Mucronothrus nasalis* (Willm.).

Table 1. The distribution of oribatid genera on a world-wide basis, expressed as numbers restricted to a particular geographical area.

	Oribatei Inferiores	Oribatei Superiores	Total
Cosmopolitan	35 (32 %)	74 (13 %)	109 (16 %)
Gondwanan	21 (19 %)	81 (14 %)	102 (15 %)
Laurasian	14 (13 %)	44 (7 %)	58 (8 %)
Central/South America	5 (5 %)	97 (16 %)	102 (15 %)
Palaearctic	13 (12 %)	87 (15 %)	100 (14 %)
Africa	7 (6 %)	50 (8 %)	57 (8 %)
South-east Asia	7 (6 %)	34 (6 %)	41 (6 %)
New Zealand	4 (4 %)	43 (7 %)	47 (7 %)
Australia/ New Guinea	2 (2 %)	23 (4 %)	25 (4 %)
Japan	0	12 (2 %)	12 (2 %)
North America	2 (2 %)	36 (6 %)	38 (5 %)
Antarctic	0	5 (1 %)	5 (1 %)
Totals	110	586	696

America, and New Zealand, and found very little variation between them. This is a species which has evidently existed, unchanged, through long periods of geological time, possibly since the Permian glaciation, 200 million years ago. Its stability may be due, in part, to its extreme adaption to the low temperatures in its preferred habitat with no competition from other species, but it may also be due to the species being parthenogenetic.

The distribution of *Mucronothrus nasalis* is typical of many species and genera of Oribatei Inferiores. As already indicated, an aquatic mode of life is not uncommon among these groups and, in view of this fact, we are of the opinion that their cosmopolitan distribution cannot be attributed to dispersal by random agencies. Taking into account that we are considering here the most ancient of the oribatids, from an evolutionary standpoint, it seems more likely that their present world-wide distribution is a reflection of their earlier presence in Pangaea.

At the same time, it must be pointed out that Pangaea was not solely the provenance of the Inferiores. Earlier in this paper it was noted that groups of Oribatei Superiores, such as the Cymbaeremaeidae, Plateremaeidae and the genus *Hydrozetes* existed in the Jurassic and probably earlier. These groups have a cosmopolitan distribution today, and they are old enough to have been present in Pangaea, and for their present distribution to be explained in terms of continental drift. This is particularly true of the freshwater genus *Hydrozetes* which, because of the mode of life, is not susceptible to random dispersal. Unfortunately it is, at this time, impossible to say anything about global distribution patterns of 'primitive' and 'advanced' Superiores. It seems plausible to suggest, therefore, that there is a cosmopolitan element in the world oribatid fauna which can be identified with stocks that existed in Pangaea. The evidence for this suggestion comes from: (a) the fossil record which establishes the antiquity of the oribatids, (b) ecological preferences which limit the ability of these mites to disperse over large expanses of inhospitable land or water, and (c) the fact that the cosmopolitan group of oribatids contains an appreciable proportion of hygrophilous Inferiores — precisely those oribatids which are the most ancient and the least susceptible to random dispersal.

The Gondwanan element

The Gondwanan fauna is here considered to comprise those genera which are widely distributed today in the major land masses of the southern hemisphere: South America, Africa, India, certain parts of south-east Asia, Australia, New Zealand and Antarctica. It is believed that these land masses were once joined together as the super-continent of Gondwanaland,* and that the oribatid genera they have in common arose during this period of land continuity. As can be seen from Table 1, this is a substantial element in the world oribatid fauna, and much of it ranges through the western (South America) and eastern (Africa, south-east Asia etc.) parts of former Gondwanaland. The lists given in the Appendix show that 17 out of 21 Inferiores genera, and 51 out of 81 Superiores, have such a distribution. The remainder occur only in the eastern part but are widely distributed here and may well represent an element which arose after the Afro-American separation (see later).

In order to examine these patterns in more detail, we must now look more closely at the composition of the oribatid fauna in different parts of the southern hemisphere, and we start with New Zealand.

New Zealand oribatids

Our knowledge of the oribatid fauna of New Zealand is based mainly on the extensive studies carried out by Hammer (1966, 1967a, 1968a). The relationships between this fauna and that of comparable biotopes in South America can be studied with reference to earlier collections made by this same author in the Andes Mountains (Hammer, 1958, 1961, 1962a & b).

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*) Here and in the following Gondwanaland means Gondwanaland *sensu lato*.

If the New Zealand faunal province is taken to include Campbell Island and the Auckland Islands, a list of some 140 oribatid genera can be recorded from here, and about a third of these have not been reported from outside this province (see Appendix). These records, if they are confirmed, indicate a high degree of generic endemism in the New Zealand oribatid fauna. Endemism at the specific level is also very high. Hammer (op. cit.) identified a total of about 330 species of which 250 (75 %) were described for the first time. Most of these new species are probably endemic to the New Zealand area.

Endemism of these orders of magnitude indicates a comparatively isolated fauna, although it must be stressed that the oribatid fauna of Australia is virtually unknown and there may be, as yet, undetected relationships here. These, if they exist, will merely have the effect of expanding the New Zealand faunal province into an Australasian province, but we hesitate to suggest that this will prove to be the case. Later in this paper, it will be shown that there is very little evidence to indicate that there are strong affinities between the New Zealand oribatid fauna and that of regions to the north. More pertinent to our argument is the relationship of the New Zealand fauna with that of South America. Hammer (op. cit.) identified a group of 17 species in the New Zealand fauna which occur in the Andes of South America — but nowhere else, as far as we know. This is a significant find and, in seeking an explanation, two alternative possibilities must be considered.

The first of these alternatives is that the 17 species common to the Andes and to New Zealand have been transported across the southern hemisphere in recent times by some random agency, such as ocean currents, wind or attached to migrating birds. Such a possibility seems very unlikely for a number of reasons. In the first instance, the distance between New Zealand and South America is very great, and it is doubtful if small terrestrial arthropods, such as oribatids, could survive the desiccation which would occur during wind dispersal. In support of this, it must be pointed out that aerial plankton samples taken over southern oceans have proved to be largely negative, and no living oribatids have been reported from them. These mites would also be unable to survive the long immersion in sea water if they drifted on ocean currents; again, there are large stretches of ocean between New Zealand and South America which are devoid of island 'stepping stones'. Furthermore, the possibility of transportation by birds appears to be remote since, as far as we know, bird migration between New Zealand and South America is, at the very least, uncommon. Finally, if some random agency is responsible, the oribatids which are common to New Zealand and South America should form a dysharmonic group — a chance assemblage of unrelated species. There is evidence that this is not so, and this evidence strongly supports the second of the two alternatives which must be considered.

The second alternative is that the present distribution of these 17 species is a relict of an ancient pattern which was established when New Zealand and South America had direct land connexions as parts of Gondwanaland. Brundin (1966) has argued strongly along these lines to explain the distribution patterns of Chironomidae in the southern hemisphere, and his arguments are borne out by our findings. The evidence in question is provided by the distribution patterns of species belonging to two genera of Oribatei Inferiores, namely *Trimalaconothrus* and *Crotonia.*

The genus *Trimalaconothrus* occurs in fresh water and moist biotopes in many parts of the world. Its members can be divided into two distinct species-groups on the basis of the number, and insertion pattern, of the setae on the genital plates of the adult. For ease of reference we refer to these as the '*novus*' and '*opisthoseta*' species-groups. In the '*novus*' group there are 5 or more setae on each genital plate and these are inserted equidistant from each other along the median margin; all these setae are retrorse, i.e. directed posteriad. In the '*opisthoseta*' group there are only 4 or 5 setae on each genital plate, 3 or 4 of which are inserted along the median

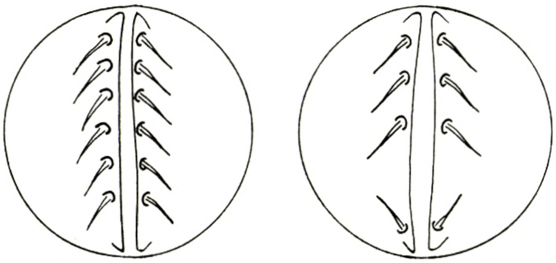

Fig. 2. Schematic representation of the genital chaetotaxy in the 'novus' and 'opisthoseta' groups of the genus *Trimalaconothrus.* (a) 'novus' group, (b) 'opisthoseta' group.

margin of the anterior part of the plate and are retrorse; the remaining seta is remote from the anterior group and is inserted near the posteromedian angle of the plate; it is antrorse. These two conditions are illustrated in Fig. 2.

Species belonging to the '*novus*' group are common in Europe (e.g. *T. novus, T. saxosus, T. vietsi*). The group is also present in South America (*T. novus, T. crispus*) and New Zealand (*T. novus, T. crispus, T. longirostrum, T. sacculus*) (Hammer, 1968a). The '*opisthoseta*' group, on the other hand, has a more restricted distribution. It does not appear to occur in Europe or Asia, but it is present in New Zealand (*T. opisthoseta, T. platyrhinus, T. oxyrhinus, T. angustirostrum*) and in South America (*T. platyrhinus, T. oxyrhinus*) (Hammer, 1962a, 1966, 1968a).

The presence of both the '*novus*' and '*opisthoseta*' groups in New Zealand and South America suggests that the *Trimalaconothrus* fauna of these two now remote regions is a harmonic one, i.e. that the similarities have not arisen through chance dispersal. This suggestion is supported by the fact that (a) both species-groups are represented by more than one species (often 2 or 4) in each of the two geographical regions, and (b) not only are both species-groups present in both regions, but each group is represented, in part, by the same species in the two regions. This degree of faunal continuity could be expected if land connexions had previously existed between New Zealand and South America, but not otherwise.

It is interesting to speculate why the distribution patterns of the two species-groups should differ on a world-wide scale; the '*novus*' group being cosmopolitan, whereas the '*opisthoseta*' is Gondwanan. It could be inferred that the '*novus*' group arose first as part of the Pangaean fauna, and that the '*opisthoseta*' group arose later in Gondwanaland after this super-continent had been separated from Laurasia. To prove this, it is necessary to show that the '*novus*' group is more 'primitive' than the '*opisthoseta*' group. There is some evidence that this is the case. As already noted, species belonging to the '*novus*' have at least 5 genital setae on each plate (the number is often 6, but it may be as high as 12). In contrast, the number of genital setae in the '*opisthoseta*' group is only 4 or 5. Now, during the phylogenetic evolution of the oribatids, there has been a tendency for a reduction in the number of genital setae to occur. This has occurred on a broad scale, as evidenced by the fact that the vast majority of the Superiores have 6 or fewer setae on each genital plate in the adult, whereas numbers in excess of 6 are commonly encountered in the Inferiores. It has also occurred independently within various groups of oribatids e.g. Euphthiracaroidea, Nothroidea, Carabodoidea, Oribatuloidea, although it is not always easy to determine which is the primitive and which is the derivative condition in some of these groups. Nevertheless, there is little doubt that the Inferiores are a more ancient group than the Superiores and that the trend in genital chaetotaxy has been regressive rather than progressive. This being the case, we have grounds for suggesting that the '*opisthoseta*' group of *Trimalaconothrus* species has a more recent evolutionary origin than the '*novus*' group.

The existence of two or more different morphological types within a group of related species (a genus) is a very useful phenomenon as far as the zoogeographer is concerned, for it allows for the identification of harmonic (and dysharmonic) patterns of distribution. This phenomenon exists in the second of the two examples we are considering in this section, namely the genus *Crotonia.*

Crotonia is a very distinctive genus (Ramsay &

Luxton, 1967) with a distribution which is confined, according to present records, to parts of former Gondwanaland and certain oceanic islands in the southern hemisphere. There are about 15 species belonging to this genus which have been described adequately, and several others for which only limited information is available. These species fall into one or other of two very distinct morphological types, designated the '*cophinarius*' and '*unguifera*' groups. These two groups may be distinguished by the distribution of setal apophyses on the posterior region of the notogaster in the adult, as illustrated in Fig. 3.

The genus *Crotonia* occurs in New Zealand (Michael, 1908; Hammer, 1966; Wallwork, 1966; Spain & Luxton, 1971), South America (Beck, 1962b; Balogh & Csiszar, 1963), East Africa (Berlese, 1916), St. Helena (Wallwork, 1977), and the Pacific (Berlese, 1910; Jacot, 1934b). In Fig. 4 this distribution pattern is analysed in terms of the '*cophinarius*' and '*unguifera*' groupings. Several interesting points emerge from this figure and these may be summarized briefly as follows. Firstly, it seems likely that the genus *Crotonia* evolved in the Australia/New Zealand region. Three distinct pieces of evidence lead to this conclusion: (1) the richest representation of species occurs here, (2) one of these species is a fossil form from the Caenozoic of Victoria — this argues against a recent immigration into Australasia from some other source area, and (3) the only closely related genera, *Austronothrus* and *Holonothrus,* only occur in the New Zealand region.

The most significant point arising from the pattern depicted in Fig. 4, however, is that both the '*cophinarius*' and '*unguifera*' groups occur in New Zealand, South America and, almost certainly, in East Africa (see also Table 2). In other words, the *Crotonia* fauna of these three parts of former Gondwanaland is harmonic. For the reasons already advanced in the case of *Trimalaconothrus,* this harmony provides evidence for faunal and geographical continuity between New Zealand, South America and Africa at some earlier time.*

Fig. 3. The distribution of posterior notogastral apophyses in two morphological groupings of the genus *Crotonia.* (a) 'unguifera' group, (b) 'cophinarius' group.

In contrast, the *Crotonia* fauna on oceanic islands is dysharmonic. When it occurs, the genus is represented either by species of the '*cophinarius*' group or by species of the '*unguifera*' group — but not by both (Table 2). This difference between the composition of the *Crotonia* fauna on continental, as compared with oceanic, land masses suggests that different dispersal mechanisms have been involved. The dysharmonic nature of the oceanic island fauna indicates dispersal by some random agency (see later).

As mentioned earlier, it is appropriate to consider Campbell Island and the Auckland Islands as part of the New Zealand faunal province. The justification for this can now be explained.

These islands lie to the south of New Zealand on the edge of the subAntarctic zone. Indeed, some authors (but not us) regard Campbell Island as lying within this zone. In any event, the islands provide possible 'stepping stones' for faunal movement between New Zealand and the subAntarctic and, as such, are of obvious interest to the zoogeographer. Unfortunately, taxonomic study on the oribatids of these islands has only just begun. Wallwork (1964a, b & c; 1966) has recorded 19 species from Campbell Island, and Wallwork & Ramsay (in prep.) have identified 40 species from the Auck-

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*) If dispersal by some random agency has taken place from continent to continent the distribution pattern would be discontinuous, not harmonic.

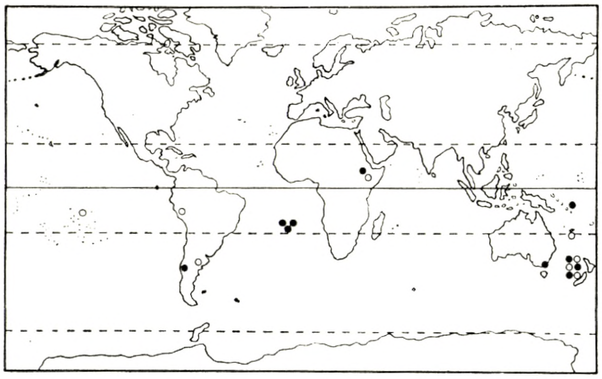

Fig. 4. The distribution of the genus *Crotonia*. ● = 'cophinarius' group; ○ = 'unguifera' group.

Table 2. The world distribution of species belonging to the genus *Crotonia.*

	'unguifera' group	'cophinarius' group
Australia & New Zealand	*C. unguifera* (Mich.) *C. obtecta* (P.-C.) *C. caudalis* (Hamm.)	*C. cophinarius* (Mich.) C. brevicornuta (Wallw.) *C. ramus* (Womersl.) *C. brachyrostrum* (Hamm.)
South America	*C. flagellata* (Bal. & Cz.) *C. pulcher* (Beck)	*C. chiloensis* (Wallw.)
East Africa	*C. rothschildi* (Berl.)	*C. alluaudi* (Berl.)
St. Helena		*C. lanceolata* (Wallw.) *C. brassicae* (Wallw.) *C. perforata* (Wallw.)
Marquesas	*C. nukuhivae* (Jac.)	
New Hebrides		*C. melanesiae* (Wallw.)
New Caledonia	*C. camelus* (Berl.)	

land Islands. While these records do not provide a completely representative picture of the total oribatid fauna of these islands, they do indicate strong links with the New Zealand fauna. This is illustrated by the data presented in Table 3 which lists the genera so far recorded from Campbell Island and/or the Auckland Islands, and their occurrence in New Zealand and elsewhere. The list comprises 28 genera of which 24 are certainly common to the Auckland Islands and New Zealand. Furthermore, 12 of the 13 genera recorded from Campbell Island also occur in New Zealand.

Table 3. The distribution of oribatid genera in the New Zealand region.

	Camp-bell	Auck-land	New Zealand	Other
Andacarus	+	+	+	Gondwanaland
Neophthiracarus	+	+	?	Gondwanaland
Notophthiracarus		+	+	Gondwanaland
Zeanothrus		+	+	Gondwanaland
Holonothrus	+		+	SubAntarctic
Crotonia	+		+	Gondwanaland
Pedrocortesia	+	+	+	Gondwanaland
Eutegaeus	+	+	+	Gondwanaland
Neseutegaeus		+	+	
Halozetes	+	+	+	Gondwanaland
Austrocarabodes		+	+	
Globoppia	+	+	+	Gondwanaland
Oppia	+	+	+	Cosmopolitan
Lanceoppia		+	+	Gondwanaland
Belloppia		+	+	Australia
Paroppia		+	+	
Clavazetes		+	+	
Scheloribates	+	+	+	Cosmopolitan
Antarctozetes		+	+	Gondwanaland
Campbellobates	+	+	+	
Neomycobates		+		SubAntarctic
Macrogena	+	+	+	
Parafurcobates		+	+	
Eupelops		+	+	Cosmopolitan
Pedunculozetes		+	+	Gondwanaland
Tumerozetes		+	+	
Edwardzetes		+	+	Cosmopolitan
Totobates	+	+	+	Gondwanaland

It is evident from Table 3 that many of the genera which have a distribution extending southwards from New Zealand are Gondwanan in origin, i.e. they also occur in South America. This suggests the interesting possibility that faunal continuities may, at one time have existed, between New Zealand and South America via Antarctica.

It is now time to turn our attention to other parts of the former Gondwanaland, notably the tropical zone which encompasses South America, Africa and parts of south-east Asia.

South American and African oribatids

The number of genera with a distribution restricted to the American part of former Gondwanaland is 102, of which 5 belong to the Inferiores and 97 to the Superiores (Table 1 and Appendix). In marked contrast, there are only 57 genera which, as far as is known, are restricted to the African part of former Gondwanaland (7 Inferiores and 50 Superiores). It may seem surprising that these two large, essentially tropical, continents should differ so much in this respect, and there are two possible explanations, at least. Firstly, although there are no quantitative data to support this, it appears that a greater range of biotopes has been sampled in South America compared with Africa. Our knowledge of the South American oribatids is based on the collections of Hammer throughout the Andes Mountains, of Beck in lowland tropical forest, and of Balogh who described oribatids from marsh and forest areas in Argentina and Peru (see Bibliography). On the other hand, most of the genera recorded from Africa by Balogh and by Wallwork (see Bibliography) have been described from the equatorial forest region. Secondly, the lower degree of generic endemism shown by the African fauna, compared with that of South America, may be a reflection of the less isolated position of Africa. The spread of genera through the eastern part of former Gondwanaland would be facilitated by the relatively late separation of some of the land blocks which formed part of this region, and by the fact that such spread is essentially latitudinal and would not be severely checked by climatic barriers. We estimate that the following genera have a distribution which is eastern Gondwanan, i.e. they extend eastwards from Africa into parts of south-east Asia (including India and Ceylon) and/or Australia and New Zealand: —

Haplacarus
Cyrthermannia
Eremaeozetes
Basilobelba
Gibbicepheus
Trichocarabodes
Tegeozetes
Pseudotocepheus
Rhynchoppia
Machadobelba
Cosmobates
Allozetes
Paralamellobates
Trichogalumna

To our knowledge, these genera do not occur outside the regions of former eastern Gondwanaland specified above.

If we now look at the position of South America, we have a rather different situation. After the Cretaceous Afro-American separation, the only terrestrial dispersion route would be northwards — to North America *via* Central America. The difficulties involved in this pattern of dispersal are twofold. First, the spread is longitudinal and, hence, climatic barriers might be limiting. Secondly, the connexion between north and south America is narrow and undoubtedly has been severed and rejoined several times in the past. As far as we can determine, there are no oribatid genera which have a distribution *only* encompassing north, central and south America, and only 5 genera (*Charassobates, Gymnobatoides, Nasobates, Cosmozetes* and *Schalleria*) which occur both in central and south America. Admittedly, our knowledge of the Central American fauna is poor, but the information we have at our disposal does not suggest that the South American oribatid fauna has been able to disperse as readily as the fauna of eastern Gondwanaland.

These faunal differences between western and eastern parts of former Gondwanaland should not allows us to lose sight of the undoubted similarities which also exist between the oribatids of these two regions. We estimate that more than 50 % of the Gondwanan fauna is distributed across the western and eastern parts, i.e. of the 102 genera identified as Gondwanan (Table 1), 68 occur both in South America and eastern parts of former Gondwanaland. It is at present not possible to show a closer relationship between South America and Africa due to incomplete knowledge of well known genera

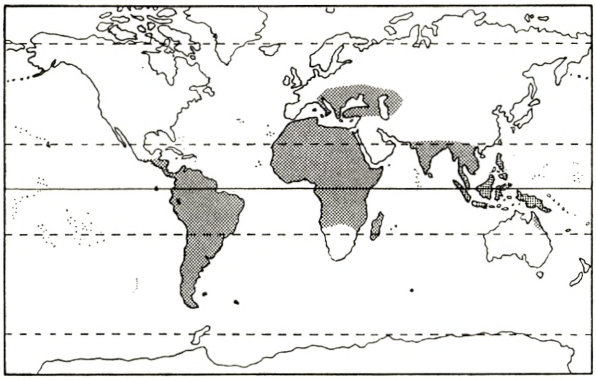

Fig. 5. The approximate world distribution of the Lohmanniidae (excluding the cosmopolitan genus *Lohmannia*).

in Africa, from where Balogh, the most active acarologist there, mainly has published new genera.

An inspection of the generic lists given for South America and Africa in the Appendix reveals some interesting points which, subsequently, may or may not be valid. However, we consider them worthy of attention at this time. First, it seems possible that South America may be the centre of evolution of genera belonging to the Microzetidae. This family presently comprises 34 genera of which 19 are restricted to South America. In contrast, only 4 genera belonging to this family are restricted to Africa. Secondly, if we compare the representation of Galumnidae in South America and Africa, we find that 8 out of the 28 genera comprising this family are African, whereas only 2 are limited to South America.

It may be argued, with justification, that these findings are rather artificial, and reflect the interest (and competence) of the taxonomist who is dealing with these particular collections. It is admitted that both the Microzetidae and Galumnidae present problem to the taxonomist, and many finds may have gone unrecorded for this reason. On the other hand, it must be pointed out that our knowledge both of the Microzetidae in South America and the Galumnidae in Africa comes largely from the detailed studies of Balogh (see Bibliography) and this, to some extent, would eliminate any personal bias.

Identification of genera belonging to the family Lohmanniidae (*sensu lato*) presents fewer problems, and here we can be confident that the records are reasonably accurate. The family contains 22 genera, 12 of which occur in Africa and of these, 4 are restricted to this continent. By comparison, only 4 lohmanniid genera have been recorded from Central and South America, with only 2 restricted to these regions. This family has evidently achieved a greater degree of evolutionary radiation in Africa than in South America, although as Fig. 5 shows, the family has a wide distribution in those parts of the world which belonged, formerly, to Gondwanaland. The Figure shows that the family also occurs in southern Europe, south and central Asia, and is represented in this part of the Palaearctic by *Thamnacarus, Cryptacarus, Papillacarus, Asiacarus* and the cosmopolitan *Lohmannia.* The first three of these genera occur commonly in Africa and other parts of former east Gondwanaland. Taking into account the wide distribution of the Lohmanniidae in former Gondwanaland (compared with the very localized distribution in what was formerly part of Laurasia), it is suggested that the three genera in question may have extended their range from Africa into the Palaearctic. This extension could have occurred when the African and/or Iranian plate moved northwards and established a connexion with the eastern part of former Laurasia.

A similar explanation may be advanced to account for the presence of other Gondwanan genera in Laurasia. Examples of these are *Licnoliodes* (in southern Spain), *Stachyoppia* (in USSR) and *Austrocarabodes* (in the eastern Mediterranean and central Asia).

Oribatids of south-east Asia

The patterns and origins of oribatid distribution in south-east Asia are difficult to interpret for a number of reasons. If we define this region to include India and Ceylon, Malayasia, Thailand, Viet-Nam and the islands of the East Indies, it is probable that we are dealing with an area which is partly Gondwanan and partly Laurasian in origin. This region contains thousands of islands in which the climate is tropical or subtropical. Here, rates of speciation could be high due to many different ecological niches and, indeed, Hammer (unpublished) has noted that many distinct but related species occur in Malayasia and Java, despite the fact that land continuity between these two areas was broken only 10,000 years ago. This rate of speciation suggests that, although the region as a whole contains an appreciable element of Gondwanan oribatids, the fauna of the various islands or island groups within the region is a young one. This is borne out by Hammer's unpublished records from Java; the 96 genera identified can be assigned as follows: —

Cosmopolitan:	41 (43 %)
Gondwanan:	39 (41 %)
South-east Asian:	8 (8 %)
Endemic:	7 (7 %)
Laurasian:	1 (1 %)

These data underline the significant contribution made by the Gondwanaland element to the oribatid fauna of Java, and the discovery of only 7 new genera (the 'endemics') is a reflection of the 'youth' of this fauna.

Referring back to Table 1, it may be noted that the number of genera restricted to south-east Asia, as a whole, is 41 — a figure which is only a little lower than that for New Zealand or for Africa or for the whole of Laurasia. Earlier, attention was drawn to the large number of genera which appear to be endemic to New Zealand; this was interpreted as a result of the comparatively isolated position of these islands. Some support is given to this idea by the south-east Asian oribatids. An examination of the lists given in the Appendix reveals that of a total of 41 genera restricted to this area in general, 23 have been recorded from only one locality, compared with only 18 which occur in two or more separate localities. This is to be expected if (a) the fauna of the individual islands or island groups is a young one, and has not yet had time to disperse, or (b) that there are barriers to dispersal within the region as a whole. Possibly both of these mechanisms are operating to produce the distribution patterns we have described.

We must now consider how the appreciable Gondwanan element arrived in south-east Asia. It is suggested that this element was brought into the region as land masses from former Gondwanaland moved north-eastwards, bringing with them their characteristic oribatid fauna. Of these land masses, New Zealand appears to be an unlikely source for its fauna has little similarity to that of south-east Asia. About 33 of the genera recorded from New Zealand by Hammer can be classified as Gondwanan and less than a dozen of these have been reported from south-east Asia: —

Andacarus
Austrocarabodes
Ramusella
Amerioppia
Rostrozetes
Lamellobates
Pedrocortesella

As far as the oribatid fauna of Australia is concerned, there is so little information that it would be unwise to speculate on its affinities. We are faced with a similar problem with the Indian fauna, although we believe that this subcontinent may be of crucial importance as a source of the Gondwanan element in the south-east Asian fauna. Drs. Bhaduri (Calcutta) and Chakrabarti (Darjeeling) have kindly supplied us with a check-list of Indian oribatid genera identified to the present time. While this list will undoubtedly be extended as our knowledge of the Indian fauna increases, it is perhaps worthy of mention at this point in time. The list comprises 64 identifiable genera which can be assigned as follows: —

Cosmopolitan:	39 (61 %)
Gondwanan:	17 (27 %)
Laurasian:	5 (8 %)
South-east Asia:	3 (5 %)

Of the 17 genera identified as Gondwanan, 11 (i.e. over 50 %) also occur in other parts of south-east Asia: —

Malacoangelia
Annectacarus
Javacarus
Papillacarus
Allonothrus
Archegozetes
Cyrthermannia
Striatoppia
Lamellobates
Paralamellobates
Rostrozetes

In proportionate terms, this is a much higher contribution to the south-east Asian fauna than that provided by the New Zealand fauna. There are indications, therefore, that India may have provided an important pathway for the extension of Gondwanan genera into south-east Asia.

The presence of a Laurasian element in the Indian oribatid fauna should not pass without comment. This element consists of the following genera which are widely distributed across the former Laurasia or the present Palaearctic part of it: —

Gehypochthonius
Hermannia
Conoppia
Ommatocepheus
Amerus

The occurrence of this element in a region which is essentially Gondwanan in origin suggests that when India drifted north-eastwards, after the separation of Gondwanaland, and established contact with the eastern part of Laurasia, some oribatid genera from the latter may have extended their range southwards. Here, then, there is a mixing of Laurasian and Gondwanan faunas. The frontier along which these two faunas come together is an extensive one, ranging from the Mediterrranean to south-east Asia. Already, we have drawn attention to faunal pathways which may have been established *via* the African or Iranian plates. Now, our enquiry shifts further eastward, particularly to north-west Pakistan where we might expect to find further evidence of Laurasian/Gondwanan intermingling.

The oribatid fauna of north-west Pakistan has been intensively studied by Hammer (1977). From a geographical point of view, this region is more closely associated with the Palaearctic than is India and, indeed, may originally have been part of Laurasia. This is reflected in the composition of its oribatid fauna. Hammer has identified a total of 86 genera, which can be assigned as follows: —

Cosmopolitan:	50 (58 %)
Laurasian (or Palaearctic):	17 (20 %)
Gondwanan:	10 (12 %)
Endemic:	9 (10 %)

If these figures are compared with those for India given earlier, it appears that the Gondwanan element is becoming diluted, and the Laurasian element strengthened as we move northwards. This is completely in accord with the drift hypothesis. It is to be expected that zones of faunal intermixing would occur where parts of the former Gondwanaland and Laurasia establish geographical continuity, provided that climatic barriers do not intervene. As a result of her studies, Hammer was able to conclude that 'North-West Pakistan seems to be the meeting point of the Laurasian and Gondwanaland faunas. The genera *Oxyoppia, Amerioppia, Ramusella, Brachioppiella, Zetomotrichus, Nannerlia, Gerloubia, Paralamellobates, Lamellobates* and *Trichogalumna* belong to the former Gondwanaland. They came probably to the Asian continent with the Iranian and/or the Indian plates when these, in the Tertiary period, drifted northwards from their former position on the north-east and the south-east coast of Africa and came in contact with the Asian plate.'*

Another meeting point for Laurasian and Gondwanan faunas appears to be Japan. As far as the oribatid fauna is concerned, this is one of the most intensively studied areas in the Far East (see the papers by Aoki and his co-workers listed in the Bibliography). A total of 141 genera has been recorded from these islands which border the eastern part of Laurasia. An analysis of this list reveals the following components: —

Cosmopolitan:	72 (51 %)
Laurasian (or Palaearctic):	32 (23 %)
Gondwanan:	18 (13 %)
Endemic:	12 (8 %)
South-east Asian:	7 (5 %)

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*) Travé (1976b) found circumtropical genera well represented in the Himalayas.

The similarities between this breakdown and that given earlier for the oribatid fauna of north-west Pakistan are immediately apparent. The contributions of the cosmopolitan, Laurasian and Gondwanan elements are remarkably similar in the two cases. In both also, the proportion of endemic genera is low, indicating a lack of isolation. Here again, therefore, in Japan we may have a meeting point for the Laurasian and Gondwanan faunas. It is possible that the Gondwanan element has found its way into Japan *via* the mainland and south-east Asia. However, the fact that Japan appears to share very few genera with south-east Asia may argue against this. On the other hand, it must be pointed out that our knowledge of the south-east Asian oribatid fauna is derived mainly from the islands of Indonesia and New Guinea and much more information is required about the fauna of mainland Malaysia and China before we can clarify distribution patterns in this region as a whole. From the work of Aoki (1974a, 1975a) a list of 17 oribatid genera can be compiled from the Korean peninsula, of which only 3 have not be reported from Japan. Again, 4 out of 11 genera recorded from west Malayasia (Aoki, 1976b) are known from Japan. However, it would be unwise to draw any conclusions about faunal affinities on the basis of these very limited studies. They suggest the possibility of faunal continuities, but no more than this.

Returning now to the broader scope of our enquiry, it is suggested that the available evidence, reviewed in the foregoing pages, clearly indicates that the distribution patterns of oribatids in the southern hemisphere have been influenced by continental drift. Naturally, we now consider the question: can the same interpretation be applied to oribatids in the northern hemisphere?

The Laurasian element

The Laurasian element in the world oribatid fauna is considerably smaller than the Gondwanan one that we have just been considering. From Table 1 it can be calculated that there are about 200 genera with a distribution which is confined, essentially, to the northern hemisphere (i.e. those classified as Laurasian, Palaearctic and North American), compared with over 390 which are restricted to parts of former Gondwanaland now located in the southern hemisphere. The reason for this discrepancy may well lie in the fact that the land masses of former Laurasia occupy temperate latitudes and have done so since the Cretaceous, while those of former Gondwanaland are, and were, mainly tropical. It is to be expected, therefore, that evolutionary rates would be higher in the southern hemisphere with its numerous favourable environment conditions than in the north.

According to the theory of continental drift, the separation of land masses occurred later in the polar regions than in the tropics. Thus, if continental drift has influenced distribution patterns of oribatid mites, we can expect faunal continuities to be more evident in polar regions than in the tropics. This should be particularly the case in the north polar region, where the Arctic ocean is surrounded by land masses.

The family Ameronothridae which occurs commonly in the northern hemisphere is now considered to include the single genus *Ameronothrus* with 9 species (Schubart, 1975). These species fall into four distinct morphological groups, designated the *marinus, maculatus, lineatus* and *lapponicus* groupings (Table 4). The distribution patterns of these species in the northern hemisphere have recently been reviewed by Schulte (1975), and the following conclusions emerge from this review. Firstly, 5 of the 9 species are either circumpolar, or occur on both sides of the Atlantic. Secondly, the species that occur in only one geographical region have a more southerly distribution and, thirdly, each of the four species groupings is represented on both sides of the Atlantic, or in the west and the east of the Arctic. Figure 6 shows the circum-polar distribution of *Ameronothrus nigrofemoratus,* a member of the '*lineatus*' group; similar patterns are also shown by *Ameronothrus maculatus, marinus* and *lapponicus.* These patterns are indicative of a

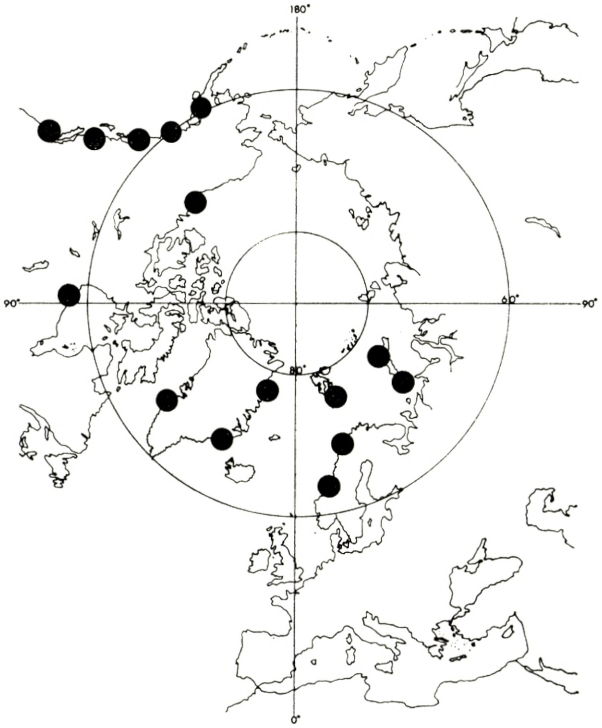

Fig. 6. The distribution of *Ameronothrus nigrofemoratus* in the north polar region.

Table 4. Species groups of the Ameronothridae (from Schubart, 1975).

Ameronothrus marinus group
    A. bilineatus (Mich.)
    A. marinus (Banks)
    A. schusteri Schub.

Ameronothrus maculatus group
    A. maculatus (Mich.)
    A. schneideri (Oudms.)

Ameronothrus lineatus group
    A. lineatus (Thorell)
    A. nigrofemoratus (Koch)
    A. schubarti Weigm. & Sch.

Ameronothrus lapponicus group
    A. lapponicus Dal.

harmonic distribution of the Ameronothridae as a whole, and this leads to the conclusion that the stock or stocks from which these four groupings have arisen had an ancient distribution, continuous across the former Laurasia. This is consistent with that part of the drift hypothesis which maintains that North America, Greenland and Eurasia were in direct land connexion until the Eocene.

The Ameronothridae set the pattern for many other groups of oribatids which occur in the northern hemisphere, and Hammer (1952a, 1955b, 1967b) has shown that a 55 % similarity, at the species level, exists between the oribatid faunas of northern Canada and Europe, and a 63 % similarity between those of Alaska and Europe. These species are mainly cold temperate or Arctic in distribution, and undoubtedly were able to survive periods of glaciation during the Pleistocene and probably earlier. Evidence for this ability to survive glaciation comes from two sources: (1) the oribatid fauna of Greenland, and (2) Arctic-alpine oribatids.

Greenland oribatids

Our knowledge of the oribatid fauna of Greenland comes from the work of Hammer (1944, 1946, 1952b, 1953, 1954, 1960) and of Strenzke (1952, 1955). The main points emerging from these studies may be summarized as follows. Firstly, although the number of species recorded to date, less than 90, is rather low, it is considerably higher than comparable latitudes in the southern hemisphere. Secondly, virtually all of the Greenland species also occur in other localities of the north polar region (Alaska, northern Canada, northern Eurasia); only one species, *Iugoribates gracilis* Selln., appears to be endemic to Greenland. *I. gracilis* has been recorded from several localities all of which are characterized by low precipitation, and this species may be a relic from a period of drier climate (Hammer, 1955a). Thirdly, the possibilities of the recent recolonization of Greenland from neighbouring land masses seem remote. There is no geological evidence for any recent land bridge connexions: accidental introductions of oribatids by Norsemen from Iceland cannot provide a complete answer since subfossil oribatids from Greenland peat pre-date these immigrants. Greenland's isolation by icy seas also renders the prospect of recent ocean dispersal unlikely. In conclusion, Greenland's oribatid fauna appears to be a relic of an ancient fauna which was distributed widely across the northern part of former Laurasia.

Arctic-alpine oribatids

During the Pleistocene, much of the north temperate region was covered by ice, and cold-adapted species of oribatids, which are now largely restricted to Arctic localities, may have had a more extensive distribution southwards. If this has been the case, we might expect to find relics of this fauna discontinuously distributed in alpine localities of the temperate zone today. Some evidence is available to support this expectation and this can be illustrated by the known distribution of a species of Inferiores, *Platynothrus punctatus,* as shown in Fig. 7. From this it can be seen that the species occurs, for the most part, north of latitude 60° but isolated finds have been recorded further south, notably in Great Britain and the European Alps (Seyd, 1962, 1964, 1966). These finds are invariably in alpine situations and can be interpreted as relics of a former continuous distribution which existed during a glacial period. The same is true of at least one other oribatid, *Calyptozetes sarekensis,* (Seyd, 1964) and we can find parallels, here, in the southern hemisphere. For example, the genus *Cryptobothria,* originally described from the subAntarctic locality of Macquarie Island, has subsequently been recorded at high altitudes much further north, in New Guinea (Balogh, 1970). This appears to be but one representative of a fauna which had a continuous distribution in earlier, glacial, periods.

The existence of these glacial relics is evidence that certain species of oribatids are adapted to live in cold environments and could well have survived through an Ice Age.

Palaearctic oribatids

Referring back to Table 1, it may be noted that the number of genera restricted to the Palaearctic region represents a considerable contribution to the world oribatid fauna. The Palaearctic is, of course, an enormous land mass with a climate that ranges from the Mediterranean to the Arctic, and with biotopes that grade from forest to desert. It is not surprising, therefore, with this great variety of niches available, that the oribatids should have undergone extensive phylogenetic evolution. Much of this evolution would appear to have taken place in the western part of the Palaearctic (i.e. west of the Urals), to judge from present distribution records. Sixty-two of the 100 genera occur only in the west, compared with 20 which occur only in the east, and 18 which have a wide distribution across the whole of the Palaearctic. This may be a reflection of the fact that environmental conditions are more favourable in the west than in the east, but it may also indicate the greater amount of attention paid to the western fauna by taxonomists.

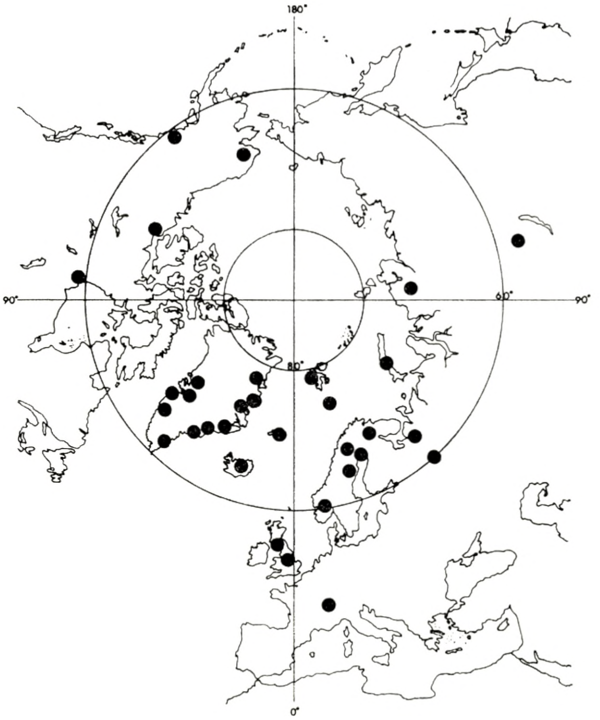

Fig. 7. The distribution of *Platynothrus punctatus.*

The Palaearctic appears to be the centre of evolution of the belboid oribatids which are grouped within the families Damaeidae, Belbidae and Belbodamaeidae. All of the 17 genera comprising these three families, with the exception of the cosmopolitan *Belba* and *Metabelba,* occur only in the northern hemisphere and 12 are restricted to the Palaearctic. It is also interesting to note that the belboid groups have not been recorded from Japan. Earlier in this paper, attention was drawn to the appreciable Laurasian element in the oribatid fauna of Japan, and it is surprising that this element does not include any belboids. No ready explanation is available for this.

North American oribatids

As we have already seen, considerable faunal similarities exist between northern Canada, Alaska, Greenland and northern Eurasia. The same appears to be true of much of the eastern United States and western Europe: two regions which are very similar with regard to climate and vegetation. The separation of North America from Eurasia occurred later than the Cretaceous separation of the southern continents and, as a consequence, faunal continuities across Laurasia would have been maintained to a more recent time than those between South America and Africa. It is perhaps not surprising, therefore, that the number of oribatid genera endemic to North America is relatively low, although it must be pointed out that there are many biotopes in this region which remain to be investigated.

A list of the genera restricted to North America is given in the Appendix. There is little in the list worthy of comment except, perhaps, to note that the liacaroid oribatids, comprising the families Tenuialidae, Liacaridae, Xenillidae, Astegistidae, Multoribulidae, Metrioppiidae and Gustaviidae, may have undergone a major evolutionary development here. Of the 36 genera presently included in these families, 20 occur in North America and 5 (*Leuroxenillus, Stenoxenillus, Stonyxenillus, Metapyroppia* and *Paenoppia*) are restricted to this region. At a lower taxonomic level, it has also been suggested (Norton & Metz, 1977) that box-mites belonging to the cosmopolitan genus *Euphthiracarus* have achieved their greatest evolutionary success in North America, to judge by the number of species there.

Oribatid fauna of oceanic islands

Oceanic islands are of much more recent origin than the land masses we have been considering so far, and the composition of their oribatid fauna is of considerable interest from this point of view. It is generally believed among zoogeographers that oceanic islands receive their faunas from the nearest continental masses by means of random overseas dispersal, and that the similarity between a continental and an oceanic fauna is inversely related to the distance from the mainland. The agencies of dispersal are essentially of four kinds, water or air currents, transport by migrating birds, or accidental introduction by Man. These agencies are non-selective in the sense that they do not produce an island fauna which is a faithful reflection, as far as its specific or generic composition is concerned, of the continental fauna. In other words, the island fauna is dysharmonic, and consists of an assemblage of unrelated forms which occur together because of their enhanced abilities or opportunities for overseas dispersal. An example of dysharmony on a restricted scale has already been provided by the distribution of the genus *Crotonia* on St. Helena and in the Pacific. We can now turn our attention to the 'dilution' phenomenon which occurs on oceanic islands with particular reference to (a) the subAntarctic islands, and (b) the islands of the Pacific.

SubAntarctic oribatids

The subAntarctic region consists of an arc of islands extending from Macquarie in the east to South Georgia in the west. Apart from Macquarie and South Georgia, these islands are oceanic and the origins of their oribatid fauna are of great interest. The islands, or groups of islands, in question are Heard, Kerguelen, Crozet and Marion/P. Edward, and their disposition has been indicated in Fig. 8. One striking feature of the oribatid faunas of each of these islands is the very low degree of endemism at the specific level (Wallwork, 1972a, Travé, 1976a). Comparisons of the specific (and sub-specific) compositions of these faunas indicate appreciable similarities, particularly between neighbouring island groups. Thus, the percentage of species common both to Kerguelen and Crozet is 41.4, while the percentage for Kerguelen and Macquarie is 31.1, and that for Crozet and Marion is 31.0 (Travé, 1976a). Even the two islands most remote from each other, Macquarie and Marion, have nearly one-third of their oribatid species in common (Travé, 1976a). These similarities suggest that these island oribatid faunas constitute a part, at least, of a single zoogeographical province, and that their source area may well have been Macquarie or a locality along the Macquarie Ridge. It is very probable that the oribatid fauna of Macquarie has not been fully described, and even greater similarities with the oribatid faunas of the oceanic islands will be evident when this has been done. The low degree endemism on these islands means that dispersal from Macquarie, if indeed this has occurred, is likely to have been a recent, post-Pleistocene phenomenon, and that it has occurred either by wind or water (Wallwork, 1973). The 'dilution' phenomenon which can be expected to occur as a result of this type of dispersal is not clearly evident in these subAntarctic islands, however. This emerges if pairs of islands, or groups, are ranked according to increasing mutual distance and, at the same time, the percentage faunal similarities are also recorded:

Macquarie: Heard :: 23.8 %
Macquarie: Kerguelen :: 31.1 %
Macquarie: Crozet :: 20.7 %
Macquarie: Marion :: 29.6 %

Clearly, there is no consistent 'dilution' effect as the distance between the islands increases. There are various reasons for this (Travé, 1976a) of which two seem to be important. Firstly, the inclusion of Heard Island in this sequence undoubtedly distorts the effect. Although Heard is the closest, of the islands considered, to Macquarie, it is small, almost completely covered with ice, and collections of oribatids from this island are few. Only 6 species of oribatids have been recorded from here and 5 of these also occur on Macquarie (Wallwork, 1970b). Secondly, a point to which we have already referred, namely that the total oribatid fauna of Macquarie has probably not yet been described. Support is given to this possibility by the fact that species of small body size, such as members of the genera *Liochthonius* and *Oppia,* which have been recorded from Kerguelen and Crozet, are not on the lists from Macquaire, and may have been overlooked in collecting. If these groups are, indeed, present on Macquarie, the faunal similarities between this island and Kerguelen and Crozet would be enhanced.

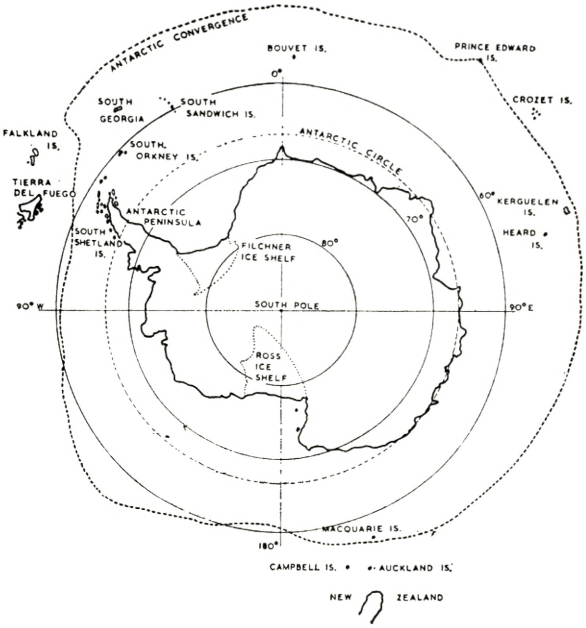

Fig. 8. Map of the south polar region to show the principal biogeographical zones.

Pacific oribatids

Our knowledge of the oribatid fauna of the Pacific islands is mainly derived from the work of Jacot (1934 a & b) on collections from the Marquesas and Hawaii, and Hammer's studies on the fauna of Fiji, Tonga, West Samoa and Tahiti (Hammer, 1971, 1972, 1973).

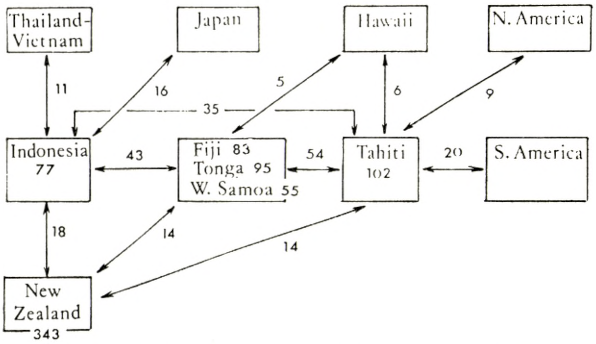

Fig. 9. The number of oribatid species common to various parts of the Pacific region. (Numbers within boxes indicate the total oribatid fauna known up to the present time).

Immediately, a distinction can be made between the fauna of the northern and the southern parts of this region. As a whole, the islands in the southern part of the Pacific ocean have many oribatid species in common — over 50 % similarity in most cases. In contrast, the oribatid fauna of the more northerly Hawaiian group, as far as it is known, appears to be very isolated and has little in common with the fauna of the islands of the south Pacific.

The extent of the similarities, at the species level, between the oribatid faunas of various parts of the Pacific is shown, schematically, in Fig. 9. The following tentative conclusions can be drawn from this analysis: —

1. There appears to be a clear relationship between the fauna of Indonesia and that of the islands of the south Pacific.

2. The 18 species which are common to Indonesia and New Zealand include 8 cosmopolitan species and 2 species which are probably recent introductions. If we exclude these from consideration, the faunal similarities between these two regions are low. Further, New Zealand seems to be a less important source area for south Pacific oribatids than does Indonesia.

3. The 'dilution' effect, mentioned earlier, appears to be demonstrated here. Thus, moving eastwards from Indonesia, the number of species common with the Fiji/Tonga/W. Samoa group is 43, while that for Tahiti is 35. Further, Tahiti shares only 20 species with the more remote South American mainland, and 9 species with the even more distant North America. Finally, Jacot's (1934a) survey of Hawaiian oribatids suggests that there is virtually no similarity between this fauna and that of the American mainland.

It appears likely that the oribatids of the south Pacific originated from Indonesia or the Malayasian region although, at the moment, we have very little evidence to suggest how this dispersal occurred. The islands of the south Pacific are, of course, of more recent origin than the continents, but some of them go back at least to the Jurassic — dating of ocean floors by the Glomar Challenger indicates as much (Oxburgh, 1974). Certainly, dispersal occurred through some random agency — wind, water, birds or Man; the distribution of the genus *Crotonia* in the New Hebrides and the Marquesas, mentioned earlier, supports this idea. It is tempting to suggest that human agencies may have been involved in the spread of oribatids from south-east Asia into the Pacific, bearing in mind the waves of human migration which have evidently occurred over the centuries in this part of the world. However, the oribatid fauna of the Pacific islands pre-dates the occurrence of Man, and some genera are endemic. It is more likely that dispersal has occurred by sea, *via* logs or other flotsam, and the groups of islands in the south Pacific could have provided 'stepping stones' for such dispersal. Much more information about the oribatids of the south Pacific and south-east Asia is required before we can say any more about dispersal mechanisms and pathways.

Concluding remarks

In the preceding pages we have presented evidence and arguments which suggest that the global patterns of distribution of oribatid mites should be interpreted within the context of continental drift. Relicts of an ancient fauna are present today which have probably existed for a period of 150—200 million years. These relicts live alongside groups which have evolved during later times but whose distribution is entirely compatible with the movements and separation of continental masses since the Permian period.

Critics of this interpretation may point to the considerable amount of human traffic that has occurred over the centuries between various parts of the world. Such traffic involving, as it does, not only people but their accustomed food plants and associated soil, inevitably provides pathways of dispersal for oribatids. Thus, investigations at Plant Quarantine stations in the U.S.A. have shown that oribatids are being introduced alive in considerable numbers by Man from all parts of the world (Hammer, 1969). Again, a survey of the oribatid fauna of St. Helena, an oceanic island in the south Atlantic with strong European associations, has revealed that the number of endemic and non-endemic species are approximately equally represented. The non-endemic element is very largely European in origin, with but a small African component (Wallwork, 1977). This strongly suggests that human traffic from Europe has had a strong influence on the composition of the oribatid fauna of this island. Finally, there is a small element in the New Zealand oribatid fauna which has probably been introduced from Europe (e.g. *Platynothrus peltifer, Ceratozetes gracilis, Scapheremaeus patella, Acrogalumna longiplumus, Nothrus silvestris, Scutovertex minutus* and *S. sculptus*).

With the exception, perhaps, of St. Helena, these introductions do not appear to have had any measurable influence on the global patterns of distribution that have been described in the preceding pages. The available evidence points to these patterns having been established over millions of years. Human agencies are measured over hundreds of years of history, and hence are relatively recent phenomena. Certainly, the distribution patterns of oribatids on the major land masses of the world were established long before Man came on the scene. Fundamental to our arguments is the antiquity of the oribatids, a group whose age is measured in terms of geological, rather than historical, time. The fossil record confirms this.

The oribatids of St. Helena may present a special case. Only 48 species, representing 27 genera and 22 families, have been recorded from this island, although it has been argued that this is a representative record (Wallwork, 1977). Clearly, when dealing with such a species-poor fauna, the 'introduced' element will figure large when compared, say, with that of the much richer fauna of New Zealand. It is hardly reasonable to generalise from such localized distortions.

Bibliography

Aoki, J-i.: 1970a. A peculiar new species of the genus *Phyllhermannia* collected at Mt. Fuji (Acari: Hermanniidae). Bull. Nat. Sci. Mus. Tokyo, 13, 71–75.

- 1970b. The oribatid mites of the islands of Tsushima. Bull. Nat. Sci. Mus. Tokyo, 13, 395–442.
- 1973a. Oribatid mites from Mt. Poroshiri in Hokkaido, North Japan. Ann. Zool. Japon., 46, 241–252.
- 1973b. Oribatid mites from Iriomote-jima, the southernmost island of Japan (I). Mem. Nat. Sci. Mus. Tokyo, 6, 85–101.
- 1974a. Oribatid mites from Korea. I. Acta. Zool. Hung., 20, 233–241.
- 1974b. New species and record of oribatid mites from Hokkaido, North Japan. Bull. Nat. Sci. Mus. Tokyo, 17, 149–156.
- 1974c. Oribatid mites from Iriomote-jima, the southernmost island of Japan (II). Mem. Nat. Sci. Mus. Tokyo, 7, 129–134.
- 1974d. The first record of the intertidal oribatid genus, *Fortuynia,* from Asia. Ann. Zool. Japon., 47, 170–174.
- 1975a. Oribatid mites from Korea (Acari). II. Acta Zool. Hung., 21, 233–239.
- 1975b. Taxonomic notes on some little known oribatid mites of Japan. Bull. Nat. Sci. Mus. Ser. A (Zool.), 1, 57–65.
- 1975c. Two species of the primitive oribatid genus *Gehypochthonius* from Japan. Ann. Zool. Japon., 48, 55–59.
- 1976a. The oribatid mites of Pseudosasa-grass zone at the highest point of the island of Yaku-shima, south Japan. Mem. Nat. Sci. Mus. Tokyo, 9, 145–150.
- 1976b. Oribatid mites from the IBP study area, Pasoh Forest Reserve, West Malayasia. Nature and Life in Southeast Asia, 7, 39–59.

Aoki, J-i. & Fujikawa, T.: 1969. Description of a new species of the genus *Hafenferrefia* Jacot (Acari, Tenuialidae). Taxonomic notes on oribatid mites of Hokkaido. I. Ann. Zool. Japon., 42, 216–219.

- 1971a. Occurrence of a Japanese representative of the North American genus *Megeremaeus* (Acari, Megeremaeidae). Taxonomic notes on oribatid mites of Hokkaido. IV. Ann. Zool. Japon., 44, 109–112.
- 1971b. A new species of the genus *Allodamaeus* Banks (Acari, Gymnodamaeidae). Taxonomic notes on oribatid mites of Hokkaido. V. Ann. Zool. Japon., 44, 113–116.
- 1972. A new genus of oribatid mites exhibiting both the characteristic features of the families Charassobatidae and Cymbaeremaeidae (Acari: Cryptostigmata). Acarologia, 14, 258–267.

Aoki, J-i. & Fukuyama, K.: 1976. A peculiar new species of the genus *Suctobelbella* (Acari, Oribatida) from Japan. Ann. Zool. Japon., 49, 209–212.

Aoki, J-i. & Ohkubo, N.: 1974. A proposal of new classification of the family Oripodidae (*s. lat.*), with description of new species. Bull. Nat. Sci. Mus. Tokyo, 17, 117–147.

Aoki, J-i. & Suzuki, K.: 1970. A new species of the genus *Pedrocortesella* from Japan (Acari, Cryptostigmata). Bull. Nat. Sci. Mus. Tokyo, 13, 117–120.

Aoki, J-i. & Yoshida, K.: 1970. A new oribatid mite, *Cosmohermannia frondosus* gen. n. et sp. n. from Yaku-shima island. Bull. biogeogr. Soc. Japan, 26, 1–4.

Balogh, J.: 1958. Oribatides nouvelles de l'Afrique tropicale. Rev. Zool. Bot. Afr., 58, 1–34.

- 1959a. Some oribatid mites from eastern Africa (Acari: Oribatidae). Acta Zool. Hung., 5, 13–32.
- 1959b. Oribates (Acari) nouveaux d'Angola et du Congo Belge (1ère sér.). Publ. cult. Co. Diam. Ang., 48, 91–108.
- 1960a. Oribates (Acari) nouveaux d'Angola et du Congo Belge (2ème sér.). Publ. cult. Co. Diam. Ang., 51, 15–40.
- 1960b. Descriptions complémentaires d'Oribates (Acari) d'Angola et du Congo Belge (1ère sér.). Publ. cult. Co. Diam. Ang., 51, 89–105.
- 1960c. Oribates (Acari) nouveaux de Madagascar (1ère sér.). Mem. Inst. Sci. Madagascar, 14, 7–37.
- 1961a. Descriptions complémentaires d'Oribates (Acari) d'Angola et du Congo (2ème sér.). Publ. cult. Co. Diam. Ang., 52, 67–73.
- 1961b. The scientific results of the First Hungarian Expedition to East Africa. 4. Acarina, Oribatei. Ann. Hist. Nat. Mus. Nat. Hung., 53, 517–524.

- 1961c. Some new Oribatidae from Central Africa (Acari). Ann. Univ. Sci. Budapest (Biol.), 4, 3–7.
- 1962a. New Microzetids from eastern Peru (Acari: Oribatei). Ann. Hist. Nat. Mus. Nat. Hung., 54, 405–417.
- 1962b. New oribatids from Madagascar (Acari). Ann. Hist. Nat. Mus. Nat. Hung., 54, 418–427.
- 1962c. Some new Lohmanniids from Peru (Acari: Oribatei). Opusc. Zool. Budapest, 4, 59–61.
- 1962d. Acari Oribates. Résultats scientifiques de l'I.R.S.A.C. en Afrique orientale. Ann. Mus. Roy. Afr. Centr. (Zool.), 110, 90–131.
- 1962e. Recherches sur la fauna endogée de Madagascar. VII. Oribates (Acariens) nouveaux. Nat. malgache, 13, 121–151.
- 1963. Oribates (Acari) nouveaux d'Angola et du Congo (3ème sér.). Publ. cult. Co. Diam. Ang., 68, 33–48.
- 1970. New oribatids from New Guinea. II. Acta Zool. Hung., 16, 291–344.
- 1972. The Oribatid Genera of the World. Akad. Kiado, Budapest, 188 pp.
- & Csiszar, J.: 1963. The zoological results of Gy. Topal's collectings in south Argentina. 5. Oribatei (Acarina). Ann. Hist. Nat. Mus. Nat. Hung., 55, 463–485.

Beck, L.: 1962a. Beiträge zur Kenntnis der neotropischen Oribatiden-fauna. 1. *Eohypochthonius* und *Cosmochthonius* (Arach., Acari). Senck. biol., 43, 227–236.

- 1962b. Beiträge zur Kenntnis der neotropischen Oribatiden-fauna. 2. Nothridae, Camisiidae, Heterobelbidae (Arach., Acari). Senck. biol., 43, 385–407.
- 1962c. Beiträge zur Kenntnis der neotropischen Oribatiden-fauna. 3. *Dampfiella* (Arach., Acari). Senck. biol., 43, 475–487.
- 1963. Zur Ökologie und Taxionomie der neotropischen Bodentiere. I. Zur Oribatiden-fauna Perus. Zool. Jb. Syst., 90, 289–392.
- 1964. Beiträge zur Kenntnis der neotropischen Oribatiden-fauna. 4. *Haplozetes* und *Peloribates* (Arach., Acari). Senck. biol., 45, 161–183.

Berlese, A.: 1910. Brevi diagnosi di generi e specie nuovi di Acari. Manipulus, 6, 346–388.

- 1916. Centuria prima di Acari nuovi. Redia, 12, 19–67.

Brundin, L.: 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges. Kgl. Sv. Vet. Ak. Handl., 4, 11, 1–472.

Ghilarov, M. S. & Krivolutsky, D. A.: 1975. Sarcoptiformes. Akad. Nauk. SSSR. 491 pp.

Hammer, M.: 1944. Studies on the oribatids and collemboles of Greenland. Medd. Grønland, 141, 1–210.

- 1946. Oribatids. *In* The Zoology of East Greenland. Medd. Grønland, 122, 1–39.
- 1952a. Investigations on the microfauna of northern Canada. Part I. Oribatidae. Acta Arct., 4, 1–108.
- 1952b. The Oribatid and Collembola fauna in some soil samples from Søndre Strømfjord. Ent. Medd., 26, 404–414.
- 1953. Collemboles and oribatids from the Thule District (north-west Greenland) and Ellesmere Island (Canada). Medd. Grønland, 136, 1–16.
- 1954. Collemboles and oribatids from Peary Land (north Greenland). Medd. Grønland, 137, 1–28.
- 1955a. Some aspects of the distribution of microfauna in the Arctic. Arctic, 8, 115–126.
- 1955b. Alaskan Oribatids. Acta Arct., 7, 5–36.
- 1958. Investigations on the oribatid fauna of the Andes Mountains. I. The Argentine and Bolivia. Biol. Skr. Dan. Vid. Selsk., 10, 129 pp.
- 1960. A few more oribatids from Greenland and Lappland. Ent. Medd., 29, 360–363.
- 1961. Investigations on the oribatid fauna of the Andes Mountains. II. Peru. Biol. Skr. Dan. Vid. Selsk., 13, 157 pp.
- 1962a. Investigations on the oribatid fauna of the Andes Mountains. III. Chile. Biol. Skr. Dan. Vid. Selsk., 13, 96 pp.
- 1962b. Investigations on the oribatid fauna of the Andes Mountains. IV. Patagonia. Biol. Skr. Dan. Vid. Selsk., 13, 37 pp.
- 1965. Are low temperatures a species-preserving factor? Illustrated by the oribatid mite *Mucronothrus nasalis* (Willm.). Acta Univ. Lund., 2, 1–10.
- 1966. Investigations on the oribatid fauna of New Zealand. Part I. Biol. Skr. Dan. Vid. Selsk., 15, 108 pp.
- 1967a. Investigations on the oribatid fauna of New Zealand. Part II. Biol. Skr. Dan. Vid. Selsk., 15, 64 pp.
- 1967b. Some oribatids from Kodiak Island, near Alaska. Acta Arct., 14, 25 pp.
- 1968a. Investigations on the oribatid fauna of New Zealand. Part III. Biol. Skr. Dan. Vid. Selsk., 16, 96 pp.
- 1968b. Transantarctic relationships within oribatids. Proc. XIII Int. Congr. Ent., Moscow, 348–350.
- 1969. Oribatids found at Plant Quarantine Stations in the U.S.A. Vid. Medd. dansk. naturh. Foren., 132, 63–78.
- 1970. A few oribatid mites from Easter Island. Pacif. Insects, 12, 279–289.
- 1971. On some oribatids from Viti Levu, the Fiji Islands. Biol. Skr. Dan. Vid. Selsk., 16, 60 pp.
- 1972. Investigation on the oribatid fauna of Tahiti, and on some oribatids found on the atoll Rangiroa. Biol. Skr. Dan. Vid. Selsk., 19, 65 pp.
- 1973. Oribatids from Tongatapu and Eua, the Tonga Islands, and from Upolu, Western Samoa. Biol. Skr. Dan. Vid. Selsk., 20, 70 pp.

– 1977. Investigations on the oribatid fauna of North-West Pakistan. Biol. Skr. Dan. Vid. Selsk. 21, 71 pp.

– (unpublished). Investigations on the oribatid fauna of Java.

Holdgate, M. W.: 1964. Terrestrial ecology in the Maritime Antarctic. *In* Antarctic Biology. Hermann, Paris, 181–194.

Jacot, A. P.: 1934a. Some Hawaiian Oribatoidea (Acarina). Bull. B. P. Bishop Mus., 121, 3–99.

– 1934b. Some Tyroglyphina (Sarcoptiformes) of the Marquesas Islands. Bull. B. P. Bishop Mus., 114, 211–238.

Krivolutsky, D. A.: 1973. The evolutionary ecology trends and tempo of evolution in Palaearctic Oribatei. Proc. 3rd. Int. Congr. Acarology, Prague, 1971, 91–94.

Michael, A. D.: 1908. Unrecorded Acari from New Zealand. J. Linn. Soc. (Zool.), 30, 134–149.

Norton, R. A. & Metz, L. J.: 1977. *Euphthiracarus humeralis* n. sp. (Acarina: Oribatei) from central North Carolina. J. Georgia Ent. Soc., 12, 52–56.

Oxburgh, E. R.: 1974. The plain man's guide to plate tectonics. Proc. Geol. Ass., 85, 299–357.

Ramsay, G. W. & Luxton, M.: 1967. A redescription of the type specimen of *Crotonia* (= *Acronothrus*) *obtecta* (O. Pickard-Cambridge, 1875) and a discussion of its taxonomic relationships. J. Nat. Hist., 1, 473–480.

Schubart, H.: 1975. Morphologische Grundlagen für die Klärung der Verwandtschaftsbeziehungen innerhalb der Milbenfamilie Ameronothridae (Acari, Oribatei). Zoologica, 123, 24–91.

Schulte, C.: 1975. Holarktische Artareale der Ameronothridae (Acari, Oribatei). Inst. Meeresforsch. Bremerh., 15, 339–357.

Sellnick, M.: 1918. Die Oribatiden der Bernsteinsammlung der Universität Königsberg. Schr. Phys.-ökon. Ges. Königsberg, 59, 21–42.

Seyd, E. L.: 1962. The moss mites of Kinder Scout, Derbyshire (Acari: Oribatei). J. Linn. Soc. Lond. (Zool.), 44, 585–591.

– 1964. A further record of *Calyptozetes sarekensis* (Trägårdh, 1910) from Britain (Acari: Oribatei). Entomologist, 18–19.

– 1966. The moss mites of a Lakeland peak (Acari: Oribatei). Entomologist, 140–143.

Sivhed, U. & Wallwork, J. A.: (in prep.). An early Jurassic oribatid mite from southern Sweden.

Spain, A. V. & Luxton, M.: 1971. Catalog and bibliography of the Acari of the New Zealand subregion. Pacif. Insects Monogr., 25, 179–226.

Strenzke, K.: 1952. Zur Systematik westgrönländischer Oribatiden. Zool. Anz., 149, 89–96.

– 1955. Microfaune du sol de l'eqe Groenland. I. Arachnides. Expéditions Polaires Françaises. Missions Paul Emile Victor. Actual. Sci. Indust., 1232, 11–84.

Travé, J.: 1971. The specific stability and the chaetotactic variations in *Mucronothrus nasalis* (Willm.) (Oribatei). Proc. 3rd. Int. Congr. Acarology, Prague, 1971, 303–309.

– 1973. Les variations chaetotaxiques dans quelques populations de *Mucronothrus nasalis* (Willm.) (Oribatei). Acarologia, 15, 521–533.

– 1976a. Les Oribates (Acariens) des archipels de Kerguelen et Crozet: essai biogéographique. *In:* Biologie et Biogéographie des milieux terrestres des iles Crozet et Kerguelen. CNFRA, 41, 61–72.

– 1976b. Himalaya. Écologie – Ethnologie. Centre National de la Recherche Scientifique, 268.

Tuzo Wilson, J.: 1971. Editor of: Continents Adrift. Readings from Scientific American.

Wallwork, J. A.: 1960–1963. Some Oribatei from Ghana. Parts I–XIII. Acarologia, vols. 2–5.

– 1963. The Oribatei (Acari) of Macquarie Island. Pacif. Insects, 5, 721–769.

– 1964a. Insects of Campbell Island. Cryptostigmata (Oribatei): Oppiidae. Pacif. Insects Monogr., 7, 138–147.

– 1964b. Insects of Campbell Island. Appendix. *Campbellobates acanthus* n. gen. n. sp. Pacif. Insects Monogr., 7, 601–606.

– 1964c. On the genus *Totobates* Hammer 1961 (Acarina: Oribatidae). Pacif. Insects, 6, 741–746.

– 1965. The Cryptostigmata (Acari) of Antarctica, with special reference to the Antarctic Peninsula and South Shetland Islands. Pacif. Insects, 7, 453–468.

– 1966. More oribatid mites (Acari: Cryptostigmata) from Campbell I. Pacif. Insects, 8, 849–877.

– 1970a. Acarina-Cryptostigmata of South Georgia. *In:* SubAntarctic Entomology, particularly of South Georgia and Heard Island. Pacif. Insects Monogr., 23, 161–178.

– 1970b. Acarina-Cryptostigmata of Heard and Kerguelen. *In:* SubAntarctic Entomology, particularly of South Georgia and Heard Island. Pacif. Insects Monogr., 23, 179–182.

– 1972a. Some cryptostigmatid mites (Acari: Cryptostigmata) from Crozet Islands. Pacif. Insects, 14, 27–37.

– 1972b. Distribution patterns of cryptostigmatid mites (Arachnida: Acari) in South Georgia. Pacif. Insects, 14, 615–625.

– 1973. Zoogeography of some terrestrial micro-Arthropoda in Antarctica. Biol. Rev. 48, 233–259.

– 1977. Order Cryptostigmata (Acari). *In:* Fauna of St. Helena, IV. Tervuren.

Willmann, C.: 1929. Oribatiden von der Inseln Herdla. Bergen Mus. Årb., 5, 1–6.

Appendix

Lists of genera used in the compilation of Table 1

COSMOPOLITAN

O. INFERIORES

Ctenacarus
Aphelacarus
Archoplophora
Mesoplophora
Hoplophorella
Hoplophthiracarus
Phthiracarus
Steganacarus
Entomotritia
Oribotritia
Euphthiracarus
Microtritia
Rhysotritia
Parhypochthonius
Eohypochthonius
Hypochthonius
Hypochthoniella
Cosmochthonius
Trichthonius
Haplochthonius
Sphaerochthonius
Brachychthonius
Eobrachychthonius
Liochthonius
Sellnickochthonius
Lohmannia
Epilohmannia
Nothrus
Camisia
Heminothrus
Platynothrus
Mucronothrus
Trhypochthonius
Malaconothrus
Trimalaconothrus

Total 35

O. SUPERIORES

Masthermannia
Nanhermannia
Hermanniella
Liodes
Gymnodamaeus
Plateremaeus
Belba
Metabelba
Cepheus
Microzetes
Nellacarus
Eremulus
Fosseremus
Eremobelba
Zetorchestes
Liacarus
Xenillus
Cultroribula
Gustavia
Carabodes
Tectocepheus
Dolicheremaeus
Machuella
Multioppia
Oppia
Oppiella
Quadroppia
Suctobelba
Suctobelbella
Suctobelbila
Banksinoma
Heloribates
Hydrozetes
Limnozetes
Cymbaeremaeus
Scapheremaeus
Micreremus
Licneremaeus
Passalozetes
Scutovertex
Oripoda
Dometorina
Eporibatula
Hemileius
Liebstadia
Oribatula
Phauloppia
Scheloribates
Zygoribatula
Haplozetes
Peloribates
Protoribates
Xylobates
Chamobates
Heterozetes
Ceratozetes
Edwardzetes
Humerobates
Trichoribates
Mycobates
Punctoribates
Eupelops
Peloptulus
Oribatella
Tegoribates
Achipteria
Anachipteria
Neoribates
Protokalumma
Acrogalumna
Allogalumna
Galumna
Pergalumna
Stictozetes

Total 74

GONDWANALAND

(E = eastern, W = western)

O. INFERIORES

Andacarus (E + W)
Cryptoplophora (E + W)
Neophthiracarus (E + W)
Notophthiracarus (E + W)
Protophthiracarus (E + W)
Indotritia (E + W)
Malacoangelia (E + W)
Annectacarus (E + W)
Cryptacarus (E) + USSR
Haplacarus (E)
Javacarus (E + W)
Meristacarus (E + W)
Mixacarus (E + W)
Papillacarus (E) + Bulgaria
Thamnacarus (E) + USSR
Torpacarus (E + W)
Crotonia (E + W)
Afronothrus (E + W)
Allonothrus (E + W)
Archegozetes (E + W)
Fossonothrus (E + W)

Total 21

O. SUPERIORES

Cyrthermannia (E)
Phyllhermannia (E + W)
Orbiculobates (E + W)
Plasmobates (E + W)
  + Japan
Teleioliodes (E + W)
Pedrocortesella (E + W)
Pedrocortesia (E + W)
Phereliodes (E + W)

Licnodamaeus (W) + Mediterranean
Microtegaeus (E + W)
Eremaeozetes (E)
Eutegaeus (E + W)
Neoeutegaeus (E + W)
Nodocepheus (E + W)
Plenotocepheus (E)
Topalia (E + W)
Megazetes (E + W)
Orthozetes (E + W)
Rugozetes (E + W)
Szentivanyella (E + W)
Reteremulus (E)
Heterobelba (E + W)
Basilobelba (E)
Furcoppia (E)
Austrocarabodes (E + W) + Mediterranean, Asia
Gibbicepheus (E)
Machadocepheus (E)
Trichocarabodes (E)
Tegeozetes (E)
Pseudotocepheus (E)
Beckiella (E + W)
Dampfiella (E + W)
Amerioppia (E + W)
Brachioppia (E + W)
Brachioppiella (E + W)
Globoppia (E + W)
Lanceoppia (E + W)
Lyroppia (E + W)
Oxyoppia (E + W)
Ramusella (E + W)
Striatoppia (E) + USSR
Rhynchoppia (E)
Rhynchoribates (E + W)
Suctoribates (E)
Austrogneta (E + W)
Tecteremaeus (E + W)
Machadobelba (E)
Fortuynia (E + W)
Halozetes (E + W)
Caloppia (E)
Neotrichozetes (E + W)
Calobates (E + W)
Gerloubia (W) + Pakistan
Incabates (E + W)
Maculobates (E + W)
Nannerlia (E) + Pakistan
Setobates (E)
Tuberemaeus (E)
Cosmobates (E)
Lauritzenia (E + W)
Magyaria (E)
Rostrozetes (E + W)
Totobates (E + W)
Vilhenabates (E)
Pedunculozetes (E + W)
Allozetes (E)
Antarctozetes (E + W)
Magellozetes (E + W)
Uracrobates (E + W)
Podoribates (E + W)
Rykella (E)
Lamellobates (E + W)
Plakoribates (E)
Paralamellobates (E)
Physobates (E + W)
Galumnella (E + W)
Galumnopsis (E + W)
Flagellozetes (E)
Leptogalumna (E + W)
Orthogalumna (E + W)
Trichogalumna (E)

Total 81

LAURASIA

O. INFERIORES

Acaronychus
Palaeacarus
Tropacarus
Maerkelotritia
Protoribotritia + Japan
Gehypochthonius + Japan, Maldive I.
Heterochthonius
Synchthonius
Atopochthonius
Pterochthonius
Eulohmannia
Perlohmannia
Neonothrus
Trhypochthoniellus

Total 14

O. SUPERIORES

Hermannia
Platyliodes
Poroliodes
Allodamaeus
Damaeus
Epidamaeus
Porobelba
Conoppia
Eupterotegaeus
Ommatocepheus
Oribatodes
Protocepheus
Eremaeus
Hafenferrefia
Hafenrefferia
Tenuiala
Tenuialoides
Adoristes
Dorycranosus
Astegistes
Furcoribula
Ceratoppia
Metrioppia
Pyroppia
Autogneta
Caleremaeus
Oribella
Ameronothrus
Lucoppia
Calyptozetes
Ceratozetella
Ceratozetoides
Diapterobates
Fuscozetes
Melanozetes
Oromurcia
Propelops
Sphaerozetes
Ophidiotrichus
Lepidozetes
Scutozetes
Parachipteria
Parakalumma
Pilogalumna

Total 44

CENTRAL/SOUTH AMERICA

(C = central, S = south)

O. INFERIORES

Aedoplophora (C)
Perutritia (S)
Brasiliotritia (S)
Euryacarus (C)
Xenolohmannia (S)

Total 5

O. SUPERIORES

Ampullobates (C)
Hermannobates (S)
Sacculobates (S)
Solenozetes (S)
Hamotegeus (S)
Pareutegaeus (Juan Fernandez)
Charassobates (C + S)
Acaroceras (S)
Anakingia (S)
Austrozetes (S)
Brazilozetes (S)
Calozetes (S)
Cosmozetes (C + S)
Dinozetes (S)
Fusozetes (S)
Licnozetes (S)
Mystacozetes (S)
Mysterozetes (S)
Plumozetes (S)
Phylacozetes (S)
Protozetes (S)
Rhabdozetes (S)
Schalleria (C + S)
Schizozetes (S)
Stylozetes (S)
Undulozetes (S)
Pseuderemulus (S)
Andesamerus (S)
Staurobates (S)
Stauroma (S)
Haplobelba (S)
Lamellozetes (S)
Amazoppia (S)
Ceratorchestes (S)
Comeremaeus (S)

Cerocepheus (Juan Fernandez)
Cubabodes (Cuba)
Neocarabodes (S)
Phyllocarabodes (S)
Spathulocepheus (S)
Cavernocepheus (S)
Aeroppia (S)
Borhidia (Cuba)
Chavinia (S)
Cuneoppia (S)
Enantioppia (S)
Gittella (S)
Karenella (S)
Octoppia (S)
Sacculoppia (S)
Trapezoppia (S)
Yungaseremaeus (S)
Sternoppia (S)
Synoppia (S)
Neosuctobelba (S)
Arceremaeus (S)
Andeseremaeus (S)
Cristeremaeus (S)
Schusteria (S)
Glanderemaeus (S)
Mikizetes (S)
Stelechobates (C)
Gymnobatoides (C+S)
Parapirnodus (S)
Pteroripoda (Cuba)
Andeszetes (S)
Areozetes (S)
Cantharozetes (S)
Drymobates (C)
Fissurobates (S)
Mancoribates (S)
Monoschelobates (S)
Multoribates (S)
Urubambates (S)
Conozetes (S)
Paraxylobates (S)
Tuxenia (S)
Nasobates (C+S)
Ceratobates (S)
Cuspidozetes (S)
Furcobates (S)
Geminozetes (S)
Granizetes (S)
Hamobates (S)
Lobozetes (S)
Porozetes (S)
Viracochiella (S)
Dynatozetes (S)
Mochlozetes (S)
Arcozetes (S)
Cultrobates (C)
Fenestrobates (S)
Williamszetes (S)
Epactozetes (S)
Truncozetes (S)
Erogalumna (S)
Kratzensteinia (C)

Total 97

PALAEARCTIC

O. INFERIORES

Zachvatkinella (E+W)
Amuracarus (E)
Palaeacaroides (E)
Beklemishevia (E)
Gilarovella (E)
Adelphacarus (W)
Protoplophora (E+W)
Paratritia (W)
Mesotritia (E+W)
Mixochthonius (W)
Ammemochthonius (W)
Asiacarus (E)
Collohmannia (W)

Total 13

O. SUPERIORES

Aleurodamaeus (W)
Plesiodamaeus (W)
Licnobelba (W)
Hypodamaeus (E+W)
Paradamaeus (W)
Spatiodamaeus (E+W)
Allobelba (W)
Metabelbella (W)
Neobelba (W)
Parabelbella (E+W)
Subbelba (E+W)
Belbodamaeus (E+W)
Damaeobelba (E+W)
Hungarobelba (E+W)
Hypocepheus (W)
Tritegeus (W)
Polypterozetes (W)
Arenozetes (E)
Miracarus (W)
Christovizetes (E)
Amerobelba (W)
Mongaillardia (W)
Rastellobata (W)
Ctenobelba (W)
Damaeolus (W)
Amerus (W)
Proteremaeus (E)
Tricheremaeus (W)
Belorchestes (W)
Litholestes (W)
Microzetorchestes (W)
Saxicolestes (W)
Strenzkea (W)
Hafenrefferiella (W)
Birsteinius (E+W)
Procorynetes (W)
Odontocepheus (W)
Niphocepheus (W)
Lamellocepheus (W)
Epimerella (W)
Mystroppia (E+W)
Trizetes (W)
Tuberoppia (E)
Allosuctobelba (E+W)
Rhyncobelba (W)
Sucteremaeus (E)
Ussuribata (E)
Proteremella (W)
Cosmogneta (W)
Parautogneta (E)
Kaszabobates (E)
Spinozetes (W)
Selenoribates (W)
Thalassozetes (W)
Hypovertex (E)
Neoscutovertex (W)
Provertex (W)
Ghilarovus (E+W)
Pallidacarus (E)
Cryptoribatula (E)
Pirnodus (W)
Haloribatula (W)
Metaleius (W)
Paraleius (W)
Pseudoppia (W)
Romanobates (W)
Siculobata (W)
Simkinia (E)
Symphauloppia (W)
Topobates (W)
Baloghiella (E)
Euzetes (W)
Balzania (W)
Ghilarovizetes (E)
Globozetes (E+W)
Minunthozetes (E+W)
Permycobates (W)
Joelia (W)
Unduloribates (E+W)
Umbellozetes (E)
Cerachipteria (W)
Pseudachipteria (W)
Centroribates (W)
Cryptogalumna (W)
Dicatozetes (W)
Psammogalumna (E+W)
Vaghia (W)

Total 87

AFRICA

O. INFERIORES

Archeonothrus
Prototritia
Phyllochthonius
Dendracarus (Madagascar)
Heptacarus
Millotacarus (Madagascar)
Paulianacarus (Madagascar)

Total 7

O. SUPERIORES

Issaniella
Licnoliodes (Mediterranean)
Acanthozetes
Hymenozetes (Madagascar)
Oxyzetes
Rhopalozetes (Madagascar)
Hymenobelba (Madagascar)
Pteramerus (Madagascar)
Multoribula
Trichoppia (Madagascar)
Carabocepheus

Congocepheus
Gymnobodes
Tuberocepheus
(Madagascar)
Leptotocepheus
Longocepheus
Papillocepheus
Trichocepheus
Granuloppia
Hexoppia
Papillonotus
Ramuloppia
Stachyoppia + USSR
Tectoppia
Teratoppia
Trematoppia (Madagascar)
Ramogneta
Rhaphigneta
Scutoverticosus
Zetomotrichus + Pakistan
Zetorchella
Lamellarea
Benoibates
Haploripoda
Capilloppia
Grandjeania
Heteroleius
Muliercula
Pilobatella
Pilobates
Africoribates
Farchacarus
Achipterina
Ctenogalumna
(Madagascar)
Heterogalumna
Pilizetes
Sphaerogalumna
Taeniogalumna
Trachygalumna
Xenogalumna (Madagascar)

Total 50

SOUTH-EAST ASIA

O. INFERIORES

*Arthroplophora
Austrotritia
*Terratritia
Sabacarus
*Lepidacarus
*Nesiacarus
*Vepracarus

Total 7

O. SUPERIORES

Sadocepheus
Compactozetes + N.G., N.
*Dudichella
Xiphobelba + N.G.
Aokiella + N.G.
*Archegocepheus
Leobodes
Acrotocepheus + N.G.
Eurostocepheus
*Fissicepheus
Megalostocepheus + N.G.
Otocepheus + N.G.
*Cryptoppia
*Heteroppia
Lasiobelba
*Porrhoppia
*Fenestrobelba
Oxyamerus + N.G.
*Limnozetella
*Brachyoripoda
Protoripoda + N.G.
Brassiella + N.G.
*Nasozetes
*Rhabdoribates
Sellnickia + N.G., N.Z.
Acutozetes + N.G.
*Cribrozetes
*Indoribates
*Phalacrozetes
*Setoxylobates
*Trachyoribates
*Frischia
Unguizetes
*Flagellozetes

Total 34

* Recorded from only one locality

NEW ZEALAND

O. INFERIORES

Novonothrus
Holonothrus
Austronothrus
Zeanothrus

Total 4

O. SUPERIORES

Tikizetes
Bornebuschia
Neseutegaeus
Pterozetes
Tumerozetes
Cuspitegula
Maorizetes
Pseudoceratoppia
Clavazetes
Neotocepheus
Belloppia + Tasmania
Hamoppia
Laminoppia
Membranoppia
Miroppia
Operculoppia
Paroppia
Polyoppia
Solenoppia
Tripiloppia
Zeasuctobelba
Tuparezetes
Adhaesozetes + Tonga I
Capillibates
Bulleremaeus
Campbellobates
Crassoribatula
Grandjeanobates
Ingella
Paraphauloppia
Subphauloppia
Angullozetes
Magnobates
Baloghobates
Macrogena
Onychobates
Parafurcobates
Parahypozetes
Zealandobates
Tutorozetes + Tasmania
Cryptobothria + New Guinea
Mycozetes
Neomycobates

Total 43

NEW GUINEA AUSTRALIA

O. INFERIORES

Meristolohmannia (A)
Nothrolohmannia (N.G.)

Total 2

O. SUPERIORES

New Guinea:

Flammaeremaeus
Papuazetes
Gressittolus
Hardybodes
Apotomocepheus
Papuacepheus
Pseudantarcticola
Arthrovertex
Symbioribates
Cosmopirnodus
Birobates
Fenichelia
Hammerabates
Reductobates + Australia
Tentaculozetes
Porogalumnella
Ceratokalumma

Total 17

Australia:

Porrhotegaeus
Notoppia
Constrictobates
Plumobates
Reticuloppia
Austrachipteria

Total 6

JAPAN

O. INFERIORES

Total 0

O. SUPERIORES

Cosmohermannia
Crypoceramerus
Costeremus
Dendrozetes
Meriocepheus
Nippobodes
Nemacepheus
Trichotocepheus
Tokunocepheus
Coropuculia
Allomycobates
Prionoribatella

Total 12

NORTH AMERICA

O. INFERIORES

Synichotritia
Epilohmannoides

Total 2

O. SUPERIORES

Heterodamaeus
Jacotella
Licnocepheus
Veloppia
Sphodrocepheus
Ametroproctus
Kalyptrazetes
Gymnodampia
Epieremulus
Caenosamerus
Megeremaeus
Opsioristes
Raphidosus
Leuroxenillus
Stenoxenillus
Stonyxenillus
Metapyroppia
Paenoppia
Exechocepheus
Rhinosuctobelba
Eremobodes
Kodiakella
Exoribatula
Exoripoda
Gymnobates
Neogymnobates
Spinoppia
Alloribates
Boreozetes
Dentizetes
Parapelops
Adoribatella
Ferolocella
Holokalumma
Holozetes
Neorizetes

Total 36

ANTARCTICA

O. INFERIORES

Total 0

O. SUPERIORES

Macquarioppia
Alaskozetes
Podacarus
Antarcticola
Maudheimia

Total 5

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Biologiske Skrifter

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5. Manton, I., and Leadbeater, B. S. C.: Fine-structural Observations on six Species of *Chrysochromulina* from Wild Danish Marine Nanoplankton, including a Description of *C. campanulifera* sp. nov. and a Preliminary Summary of the Nanoplankton as a Whole. 1974 ... 40.–

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