# DISTRIBUTION PATTERNS OF CRYPTOSTIGMATID MITES (Arachnida: Acari) IN SOUTH GEORGIA

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# INTRODUCTION

During the years 1962-64 extensive collections of cryptostigmatid mites were made in South Georgia by H. B. Clagg. A preliminary taxonomic report on some of these collections has already been published (Wallwork 1970) and this, together with an earlier survey (Wallwork 1966) based on material provided by the British Antarctic Survey, allows us to compile a list of 19 species from this locality. The Clagg collections, which have now been examined in detail, comprise just over 300 samples, although not all of these contained cryptostigmatid mites, and some yielded only juvenile specimens which could not be identified to species with any certainty. These samples originate from three different geographical localities, namely the main island of South Georgia, Bird Island and Willis Island, and from a range of microhabitats, so that they provide an opportunity to analyse the effects of geographical and ecological factors on distribution patterns of the mites in this area. All of the species encountered in this latest study have been recorded previously, and this indicates that a representative picture of the faunal composition has been obtained.

The purposes of the present paper are to interpret distribution patterns in terms of geographical and ecological factors, and to discuss the affinities of the South Georgia cryptostigmatid fauna with that of neighbouring areas in the subantarctic, maritime Antarctic and South American regions. The collections were made available through the kindness of Professor J. L. Gressitt and are deposited in Bishop Museum.

# SPECIES COMPOSITION OF THE FAUNA

The 19 species of Cryptostigmata known to occur in South Georgia can be listed as follows:

Family Brachychthoniidae

Liochthonius mollis (Hammer)

Eobrachychthonius oudemansi van der Hammen

Family Camisiidae

Platynothrus skottsbergii Trgdh. expansus Wallw. Camisia segnis (Hermann)

Family Malaconothridae

Trimalaconothrus flagelliformis Wallw.

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Family Oppiidae

Oppia crozetensis (Richters)

scotiae Wallw.

Globoppia intermedia Hammer longiseta Wallw.

Family Podacaridae

Podacarus auberti Grndj. occidentalis Wallw. Alaskozetes antarcticus (Michael) intermedius Wallw. Antarcticola georgiae Wallw. Halozetes marinus (Lohmann) littoralis Wallw. belgicae (Michael)

Family Ceratozetidae

Edwardzetes elongatus Wallw. Magellozetes antarcticus (Michael) Scotiazetes bidens Wallw. Porozetes polygonalis Hammer quadrilobatus Wallw.

Family Parakalummidae

Sandenia georgiae (Oudms.)

# SAMPLING LOCALITIES

On the main island of South Georgia, 16 sampling localities can be identified as follows:

- 1. Royal Bay, Moltke Harbor, 30 samples.
- Grytviken, 28 samples from: Gull Lake (2); Hestesletten (5); Cumberland West Bay (3); Cumberland East Bay (2); Brown Mountain (2); King Edward Point (3); King Edward Cove (1); Maiviken (7); Snowy Coulm (1); Gun Plain (1); Mt Duce (1).
- 3. Stromness Peninsula, 19 samples from: Husvik (14); Leith Harbor (2); Stromness Valley (1); Stromness beach (1); Alert Cove (1).
- 4. Barff Peninsula, 9 samples from: Ocean Harbor (3); Lonneberg Valley (2); Sörling Valley (2); St. Andrews Bay (1); Jorobihaan (1).
- 5. Kelpbugten, 4 samples.
- 6. Busen Peninsula, 5 samples from: The Crutch (2); Olsen Valley (1); Carlita Bay (1); Jason Harbor (1).
- 7. Bay of Isles, 4 samples from: Murphy Wall (2): Collewick Hubs (1); Paul beach (1).
- 8. Welcome Bay, 3 samples.
- 9. Prince Olaf Harbor, 1 sample.
- 10. Hodges Glacier, 1 sample.
- 11. Fortuna Bay, 1 sample.
- 12. Mt. Krokisius, 2 samples.
- 13. Royal Bay, Köppen Point, 1 sample.
- 14. Hope Valley, 1 sample.

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15. Hound Bay, 1 sample.

16. Right Whale Bay, 3 samples.

On Bird Island, 18 localities were sampled as follows:

Freshwater Bay (17): Wanderer Valley (14); North Valley (8); Bandersnatch (7); Landing beach (5); Stinker Cape (4); Iceberg Point (3); Long Ridge (2); Mountain Coulm (1); Molly Hill (1); Cave Crag (1); Flagstone Pond (1); Cobbley Mound (1); Sound Coulm (1); Tonk (1); Macaroni Creek (1); Pieron Inlet (1); Top Meadow (1). On Willis Island, only two localities were sampled, designated "main island" and "Johan Bay, Wilson Harbour" respectively; one sample was taken at each.

## GEOGRAPHICAL DISTRIBUTION OF CRYPTOSTIGMATA

The total number of species recorded from all sites on the main island of South Georgia was 18. These are listed below in order of their frequency of occurrence:

Edwardzetes elongatus	70 %
Globoppia intermedia longiseta	56 %
Sandenia georgiae	56 %
Oppia crozetensis	50 %
Magellozetes antarcticus	50 %
Scotiazetes bidens	50 %
Porozetes polygonalis quadrilobatus	50 %
Antarcticola georgiae	43 %
Podacarus auberti occidentalis	43 %
Platynothrus skottsbergii expansus	31 %
Alaskozetes antarcticus intermedius	25 %
Trimalaconothrus flagelliformis	25 %
Halozetes belgicae	19 %
Halozetes marinus	19 %
Halozetes littoralis	19 %
Oppia scotiae	6 %
Camisia segnis	6 %
Eobrachychthonius oudemansi	6 %

The total number of species recorded from Bird Island (11) is fewer than that from the main island, despite the fact that more localities were sampled here. The frequency distribution is as follows:

Podacarus auberti occidentalis	78 %
Antarcticola georgiae	67 %
Edwardzetes elongatus	56 %
Oppia crozetensis	50 %
Halozetes belgicae	33 %
Alaskozetes antarcticus intermedius	28 %
Magellozetes antarcticus	22 %
Globoppia intermedia longiseta	22 %

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Halozetes littoralis	16 %
Halozetes marinus	11 %
Scotiazetes bidens	5%

The two samples taken on Willis Island contained a total of 8 species, of which 3 (Alaskozetes antarcticus intermedius, Antarcticola georgiae and Podacarus auberti occidentalis) were present in both, and the remainder (Oppia crozetensis, Globoppia intermedia longiseta, Halozetes belgicae, Edwardzetes elongatus and Porozetes polygonalis quadrilobatus) occurred only once.

# DISTRIBUTION IN RELATION TO MICROHABITAT

The samples taken from the main island of South Georgia and from Bird Island originate from several different microhabitats, as the data presented in Table 1 show. The two samples collected on Willis Island came from clumps of moss, and they are not considered further in this section. Table 1 shows that a greater number of habitat samples were taken on the main island than on Bird Island, and that a greater range of microhabitats was sampled in the former than in the latter. Further, although the great majority of samples on both islands were taken from 4 main microhabitats, namely moss, rocks, grass, and the nest material of various sea birds, the proportions differed in some cases. Thus, while a comparable number of samples was taken from moss on both islands, microhabitats under rocks were sampled much more frequently on the main island than on Bird Island, while the reverse was true of samples of nest material.

	South Georgia: main island		Bird Is	land	Willis Island		
	Number	%	Number	%	Number	%	
MOSS	36	30.2	32	32. 0	2	100	
ROCKS	37	31.0	7	7.0	-	-	
GRASS	23	19.3	15	15.0	-	-	
NEST MATERIAL	12	10.0	44	44.0	-	-	
AQUATIC :							
INTER-TIDAL	3	2.5	2	2.0	-	-	
FRESHWATER	2	1.7	-	-	-	-	
CARRION	2	1.7	-	-	-	-	
WOOD	4	3.4	-	-	-	-	
TOTALS	119		100		2		

Table 1. Numbers of microhabitats sampled on the main island, Bird Island and Willis Island.

An analysis of the sampling data was carried out to determine the average number of cryptostigmatid species per sample, for each of the four main microhabitats. This provided the following values:

Moss	Rocks	Grass	Nest material
3.0	1.8	1.3	2.4

	Moss	Rocks	Grass	Nests	Inter- tidal	Fresh- water	Carrion	Wood
Total no. of samples	68	44	38	56	5	2	2	4
P. skottsbergii exp.	14.7	2. 3	-	8.9	-	-	50.0	25.0
C. segnis	1.5	-	-	-	-	-	-	-
E. oudemansi	-	-	-	1.8	-	-	-	<b>–</b> '
T. flagelliformis	16.2	-	-	· -	-	-		_
O. crozetensis	36.8	4.5	2.6	42.8	-	-		-
O. scotiae	2. 9	-	-	-	-	-	-	-
G. intermedia long.	27.9	11.2	5.2	25.0	-	-	-	-
H. marinus	-	-	-	-	100.0	-	-	-
H. littoralis	-	-	_	-	80.0	-	-	-
H. belgicae	22. 0	2. 3	-	3.6	20.0	-		-
A. antarcticus interm.	10.3	2. 3	2.6	7.1	-	100.0	-	-
Ant. georgiae	41.2	13.7	-	26.8	-	-	-	25.0
P. auberti occid.	29.4	9.9	52.6	66.1	-	-	100.0	50.0
E. elongatus	66.2	29.6	2.6	42. 8	- ·	50.0	50.0	50.0
M. antarcticus	7.3	29.6	26.3	10.7	-	-	-	-
S. bidens	17.6	6.9	-	1.8	-	-	-	
P. polygonalis quadril.	8.8	27.3	39.4	8.9	-	-	-	-
Sand. georgiae	4.4	45.4	-	-	-	-	-	-
No. of species	15	12	7	12	3	2	3	4

Table 2. Relative frequency of Cryptostigmata species, expressed as % of total number of samples taken in each microhabitat, on South Georgia main island and Bird Island.

Clearly, clumps of moss and the debris accumulating at nesting sites harbour a richer fauna of Cryptostigmata than do rock crevices and debris beneath grass tussocks. The microhabitats in the intertidal zone, freshwater, wood and carrion are not included in this comparison since the samples taken were too few to provide meaningful estimates.

The species composition of the cryptostigmatid fauna varied from microhabitat to microhabitat, as indicated by the data presented in Table 2. Here, samples from main island and Bird Island are pooled, and the number of occurrences of a particular species in a given microhabitat is expressed as a percentage of the total number of samples taken from that microhabitat. From these frequency values, the faunal characteristics of each of the four main microhabitats can be summarised as follows:

	Moss	Rocks
Constant (Frequency> 40 %)	{ Edwardzetes elongatus Antarcticola georgiae	Sandenia georgiae
Accessory (Frequency 25-40 %)	Oppia crozetensis Podacarus auberti occidentalis Globoppia intermedia longiseta	Edwardzetes elongatus Magellozetes antarcticus Porozetes polygonalis quadri- lobatus

	Grass	Nest material
Constant	Podacarus auberti occidentalis	Podacarus auberti occidentalis Edwardzetes elongatus
(Frequency> 40 %)		Oppia crozetensis
Accessory	Porozetes polygonalis quadrilobatus	Antarcticola georgiae
(Frequency 25-40%)	Magellozetes antarcticus	Globoppia intermedia longiseta

An additional point emerging from Table 2 is that the inter-tidal cryptostigmatid fauna recorded in this study consists, entirely, of 3 species belonging to the podacarid genus *Halozetes*, and two of these species, *H. marinus* and *H. littoralis*, are restricted in their distribution to this microhabitat. This leads on to a consideration of the extent to which other species are restricted to the microhabitats in which they occur. The data given for eight of the commonest species in Table 3 provide a basis for this analysis. It is evident that *Sandenia georgiae* is virtually restricted to rock crevices, a microhabitat also preferred by *Magellozetes antarcticus*. *Porozetes polygonalis quadrilobatus* also evidently favours rock crevices, but attains its greatest frequency in the grass microhabitat where it ranks second only to *Podacarus auberti occidentalis*. Clear preferences for the moss microhabitat are indicated for *Edwardzetes elongatus* and *Antarcticola georgiae*, although the latter, like *Oppia crozetensis* and *Globoppia intermedia longiseta*, is frequent in nest material. *Podacarus auberti occidentalis*, despite the fact that it occurs in about 50 % of the samples taken from grass (Table 2), shows a stronger preference for the nest material microhabitat.

### DISCUSSION

## Distribution patterns in relation to geographical and ecological factors

Only one species, *Liochthonius mollis*, recorded previously from South Georgia did not occur in the collections examined in this study. A comparison of the species lists for the main island and Bird Island reveals that all of the species recorded from the latter also occur on the former. One absentee from Bird Island is *Porozetes polygonalis quadrilobatus*, a species which occurs with a frequency of 50 % on the main island. This species also occurs on the more remote Willis Island, so its absence from Bird Island can hardly be attributed to a geographical barrier. Further, *P. polygonalis* is present in South America and evidently has an efficient method of dispersal.

Apart from *P. polygonalis quadrilobatus*, there are 6 species present on the main island which are absent from Bird Island and Willis. Three of these (*Platynothrus skottsbergii*, *Camisia segnis*, and *Eobrachychthonius oudemansi*) occur in South America (Hammer 1962), so that their restriction to the main island is probably not due to some geographical factor. The remainder (*Trimalaconothrus flagelliformis*, *Oppia scotiae* and *Sandenia georgiae*) are known only from South Georgia. Only *S. georgiae* might be considered frequent enough on the main island to have colonized the other, neighboring, islands, if it could surmount the geographical barrier.

Thus, while it can be established that qualitative differences exist between the cryptostigmatid fauna of the three islands in the South Georgia group, there is no evidence that these differences result from geographical isolation, in the large majority of cases. Similarly, there are quantitative differences. The most frequent species on the main island is Edwardzetes elongatus, occurring in samples with a frequency of 70 %. Occurring in at least half the samples are 6 more species (Globoppia intermedia longiseta, Sandenia georgiae, Oppia crozetensis, Magellozetes antarcticus, Scotiazetes bidens and Porozetes polygonalis quadrilobatus). On Bird Island, the most frequently occurring species are Podacarus auberti occidentalis and Antarcticola georgiae, two species which rank only eighth in the frequency list of the main island fauna. These two, together with Alaskozetes antarcticus intermedius and Halozetes belgicae, are the only species common to both islands which are more frequent on Bird Island. Again, it is difficult to explain these quantitative differences in terms of a limited ability to surmount geographical barriers, for species such as Edwardzetes elongatus, Globoppia intermedia, Oppia crozetensis, Magellozetes antarcticus, Podacarus auberti, Alaskozetes antarcticus and Halozetes belgicae, have been recorded from other parts of Antarctica (Wallwork, 1966; 1967; 1970).

The possibility that ecological factors may have an important influence on the distribution patterns of South Georgia Cryptostigmata is suggested by the data presented in Tables 2 and 3. It may be concluded from these, that when the emphasis in sampling is for moss microhabitats the picture of faunal composition will be dominated by species such as Edwardzetes elongatus and Antarcticola georgiae; where sampling is conducted mainly on rock crevices, Sandenia georgiae and Magellozetes antarcticus will show a high frequency of occurrence, and where emphasis is placed on sampling from nest material Podacarus auberti occidentalis will become prominent. Table 1 shows that about 60 % of the samples (73 out of 119) taken on the main island were from moss and rock crevices. It could be predicted, therefore, that the main island fauna would include among its most frequent members, species such as Edwardzetes elongatus, Antarcticola georgiae, Globoppia intermedia, Sandenia georgiae and Magellozetes antarcticus, which occur more frequently in moss or rock crevices than in other microhabitats (Table 3). This is, in fact, the case for all these species rank in the top 8 of the frequency list for the main island (see p. 617). On Bird Island, the emphasis in sampling shifted from rock crevices to nest material (Table 1), and this may be the reason for Podacarus auberti occidentalis being recorded with a much higher frequency than on the main island, Moss samples still formed an appreciable number of the total on Bird Island, so that

SPECIES	TOTAL NO. OF OCCUR- RENCES	MOSS	ROCK	GRASS	NESTS	OTHER	TOTAL
E. elongatus	87	51.7	14.9	1.1	27.5	4.6	99.8
P. auberti occid.	85	23.5	4.7	23.5	43.5	4.7	99.9
O. crozetensis	52	48.8	3.8	1.9	45.5	-	100.0
Ant. georgiae	50	56.0	12. 0	-	30.0	2. 0	100.0
G. intermedia long.	40	47.5	12. 5	5.0	35.0	-	100.0
P. polygonalis quadril.	38	15.8	31.6	39.5	1 <b>3.</b> 1	-	100.0
M. antarcticus	34	14.7	38.2	29.4	17.7	-	100.0
Sand. georgiae	23	13.0	87.0	-	-	-	100. 0

Table 3.	Frequency	7 of 8	spec	cies of	C	ryptos	tigmata	in e	each	of	the	main
mic	rohabitats,	expre	ssed a	as %	of	total	occurre	nces	s in	all	mic	roha-
bita	ts.											

Edwardzetes elongatus and Antarcticola georgiae continue to rank high on the frequency list.

This kind of evidence seems to point strongly to the conclusion that qualitative and quantitative differences in the species composition of the cryptostigmatid fauna which occur from island to island in the South Georgia group, are reflections of the differential sampling of the various microhabitats, rather than any geographical limitations. If this is so, it underlines the need to look more closely at the distribution patterns of Antarctic microarthropods in relation to the microhabitats available for colonization, and the habitat specificity of the species concerned, and not simply in terms of geographical position.

#### Affinities of the South Georgia Cryptostigmata

Previously (Wallwork, 1966; 1969) it has been suggested that the South Georgia cryptostigmatid fauna is a composite of endemic, South American, circum-subantarctic and maritime Antarctic elements. The present work generally confirms this suggestion, although it is necessary to re-evaluate the contribution of these elements to the total fauna now that more detailed information on the species composition of this fauna is available. The known ranges of distribution of the 19 species recorded from South Georgia are given in Table 4, from which it may be seen that 6 species are endemic (*T. flagelliformis, O. scotiae, Ant. georgiae, H. littoralis, S. bidens* and *S. georgiae*), 7 may

SOUTH GEORGIA	MARITIME ANTARCTIC	SOUTH AMERICA	EASTERN SUB- ANTARCTIC	ANTARCTIC CONTINENT	EUROPE
L. mollis	+	+			
E. oudemansi	?	+		-	+
P. skottsbergii		· · · +	_		—
C. segnis		+			+
T. flagelliformis					
O. crozetensis	+	?	+	—	
O. scotiae	-				
G. intermedia	+	+	+		_
P. auberti	-		+		
A. antarcticus	+	_	+	+	
Ant. georgiae	—	—			
H. marinus	+	<u> </u>	+		
H. belgicae	+		+		
H. littoralis	-	<sup>1</sup>			—
E. elongatus	+	?	—		—
M. antarcticus	+	+	—	-	
S. bidens					
P. polygonalis	· · · ·	+			—
Sand. georgiae	····· · · · · · · · · ·	-		-	

Table 4. Known distribution of the species of Cryptostigmata occurring in South Georgia.

be regarded as South American in origin (*L. mollis*, *E. oudemansi*, *P. skottsbergii*, *C. segnis*, *E. elongatus*, *M. antarcticus* and *P. polygonalis*), while the remaining 6 species have a circum-subantarctic distribution. Thus, these three major elements in the fauna are represented in approximately equal proportions:

Endemic	31 %
South American	<b>3</b> 8 %
Circum-subantarctic	31 %

These three faunal elements are not always clearly defined. For example, the "South American" grouping includes two species, *Eobrachychthonius oudemansi* and *Camisia segnis*, which may have been introduced from Europe. Again, *Globoppia intermedia* could fit equally well into either the South American or the circum-subantarctic groupings. However, these ambiguities cannot obscure the fact that dispersal of Cryptostigmata has occurred latitudinally and longitudinally in the subantarctic. Further, although the South Georgia fauna has some strong links with the South American fauna, the presence of an equally strong endemic element suggests that this part of the subantarctic is now faunistically isolated from South America. This suggestion is supported by the fact that 2 of the 7 South American species on South Georgia are represented by subspecies which are different from those on the mainland. The nature of the isolating mechanism which has separated the South Georgia fauna from that of the nearest land mass in the South Temperate Zone is not known, although from the evidence presented in this paper it is more likely to be ecological than geographical.

This suggestion receives further support when a comparison is made between the South Georgia fauna and that of the maritime Antarctic zone lying directly to the south and east. This zone comprises the Antarctic Peninsula and South Shetland Islands (herein referred to as the Peninsula region), South Sandwich Is., South Orkney Is. and Bouvet I. A total of 12 species of Cryptostigmata has been recorded from this zone (Wallwork, 1967) of which only three, *Oppia loxolineata*, *Halozetes necrophagus* and *Edwardzetes dentifer*, have not been recorded from South Georgia. The distribution of the remaining 9 species in western Antarctica is given in Table 5, from which it may

SUBANTARCTIC	MARITIME ANTARCTIC			
South Georgia	Peninsula	South Orkney	South Sandwich	Bouvet
E oudemansi			?	
L. mollis	+ -	· -	_	· · · · · · · · · · · · · · · · · · ·
O. crozetensis			+	
G. intermedia			+	
A. antarcticus	+	+	.+ .	+
H. marinus		+	_	
H. belgicae	+	+	+	
E. elongatus	_		+	_
M. antarcticus	···· ·+ · · ·	— <u> </u>	· _ ·	—

Table 5. Known distribution of 9 species of Cryptostigmata in the western subantarctic and maritime Antarctic zones.

be noted that although South Georgia has more species in common with its nearest neighbors, South Sandwich Is., than with any of the other maritime localities, there are three species, *L. mollis*, *H. marinus* and *M. antarcticus*, which are absent from South Sandwich but present further away from South Georgia, on South Orkney Is. and the Peninsula. Evidently these species could disperse to South Sandwich Is., and their absence here is not due to geographical factors. Similarly, although *O. crozetensis*, *G. intermedia* and *H. marinus* have not been recorded from the Peninsula region, they occur in the eastern subantarctic in localities such as Heard I., Kerguelen and Macquarie which are geographically remote from, but ecologically similar to, South Georgia.

It seems, therefore, that there is a broad measure of overlap between the cryptostigmatid fauna of South Georgia and that of the maritime zone, and an earlier suggestion (Wallwork 1969) that the maritime fauna is derived from that of the subantarctic is confirmed.

One final point remains to be made. This paper has been concerned with describing and analysing distribution patterns within a restricted area of the western subantarctic and maritime zone, and the evidence seems to point, rather strongly, in favor of ecological rather than geographical influences. However, it would be unwise, at this stage, to interpret all Antarctic zoogeography in these terms. For example, a comparison of the cryptostigmatid fauna of eastern and western subantarctic regions shows that although species such as *Halozetes belgicae*, *H. marinus*, *Podacarus auberti* and *Alaskozetes antarcticus* are circum-subantarctic in distribution, each is represented by a distinct subspecies in the eastern and western parts of the zone. There may be a strong case for arguing that this subspecific differentiation is the result of the geographical remoteness from each other of eastern and western subantarctic regions, and this topic will be considered in more detail in a later paper.

# SUMMARY

1. 19 species of Cryptostigmata are recorded from South Georgia.

2. Records from over 300 samples taken from a range of microhabitats, including moss, rock crevices, grass tussocks and nest material, on the main island of South Georgia, Bird I. and Willis I. show that distribution patterns within the area are influenced more by ecological, rather than geographical, factors.

3. For the affinities of the South Georgia Cryptostigmata, three main faunal elements are defined, namely an endemic element, an element South American in origin, and a circum-subantarctic element. These three elements occur in approximately equal proportions.

4. A comparison between the South Georgia fauna and that of the maritime Antarctic to the east and south indicates that the maritime zone cannot be regarded as a distinct faunal province, as far as the Cryptostigmata are concerned, for there is a broad overlap between the species composition of this zone and that of South Georgia.

## REFERENCES

Hammer, M. 1962. Investigations on the Oribatid fauna of the Andes Mountains. III. Chile. Biol. Skr. Dan. Vid. Selsk. 13 (2): 96 p.

- Wallwork, J. A. 1966. Some Cryptostigmata (Acari) from South Georgia. Br. Antarct. Surv. Bull. 9: 1-20.
  - 1967. Cryptostigmata (Oribatid mites). In Gressitt, J. L. ed. Entomology of Antarctica. Antarctic Research Ser. (Amer. Geophys. U.) 10: 105-22.
  - 1969. The zoogeography of Antarctic Cryptostigmata. Proc. 2nd. Int. Congr. Acarology. Akad. Kiado, Budapest, 17-20.
  - 1970. Acarina: Cryptostigmata of South Georgia. Pacif. Ins. Monogr. 23: 161-78.