TARDIGRADA FROM THE ANTARCTIC PENINSULA AND SCOTIA RIDGE REGION

By PETER G. JENNINGS

ABSTRACT. A survey of 70 sites in the Antarctic Peninsula and Scotia Ridge region yielded 11 species or species-groups of Tardigrada. Samples were collected from sites on South Georgia, the South Sandwich Islands, the South Orkney Islands, the South Shetland Islands and southward along the western coastal fringe of the Antarctic Peninsula to lat. 70°48′S. The distribution and abundance of Tardigrada in these areas are discussed. Tardigrade population densities were highest ($1 \cdot 922 \times 10^6$ m.$^{-2}$) on King George Island, South Shetland Islands. The distribution and density of the terrestrial Rotifera are also briefly mentioned. A survey of literature relating to Antarctic Tardigrada reveals a list of 23 species.

JENNINGS (1976) reported on the distribution and population density of 16 tardigrade species from Signy Island. Results are presented here of a survey of other islands in the South Orkney Islands and other localities in the maritime Antarctic including the South Sandwich Islands, the South Shetland Islands and the western coastal fringe of the Antarctic Peninsula southward to Marguerite Bay. One sub-Antarctic station (South Georgia) and one continental Antarctic station (Alexander Island) have also been included for comparison (Figs. 1 and 2). The soils of some of these areas have been described by Allen and Heal (1970), while Longton (1967) and Gimingham and Smith (1970) have given a detailed account of the vegetation. Tilbrook (1970) has reviewed the invertebrate fauna of the region.

METHODS

Quantitative examination

Population-density estimates of the Tardigrada in each site were made from six cores each 3·5 cm. diameter (surface area approximately 0·001 m.^{2}) and 3·0 cm. depth. Since the sites were rarely homogeneous over their whole area, an attempt was made to reduce the sampling error by taking pairs of cores, each member of the pair being randomly positioned in a representative sub-sampling plot. The extraction procedure followed was the "tray method" (Whitehead and Hemming, 1965) with the modifications of Jennings (1976). Samples for quantitative examination were taken during the 1974 austral summer, between January and April. The samples were stored at −18° to −20° C until they were analysed in the United Kingdom. The period between collection and analysis of these samples was several months and the effects of storage on the extraction efficiency of the various faunal components are unknown. Details of the counting procedure have been given by Jennings (1976).

Semi-quantitative and qualitative examination

Where the substrate was frozen, or less than 3 cm. in depth, coring was not attempted. In other instances, the substrate was not widespread enough to yield six cores, and no statistical treatment has been applied in these cases. Here a variable quantity of material was collected and the fauna extracted and counted in the normal way. These counts have yielded semi-quantitative data.

Preserved material from previous collections for nematodes (Tilbrook, 1967; Spaull, 1973) was found to contain tardigrades. These specimens were mounted in Hoyer's medium and used to extend the present survey.

SITES

The location, vegetation and other prominent features of the 70 sites investigated are given in Table I. Table II lists those sites from which further information was available, including fresh weight, dry weight (at 105° C), index of humidity (where I.H. = water/dry weight) and per cent water by volume (where percentage water = water/core volume × 100). The sites used for the quantitative study are indicated by a letter (A–I) in both tables.

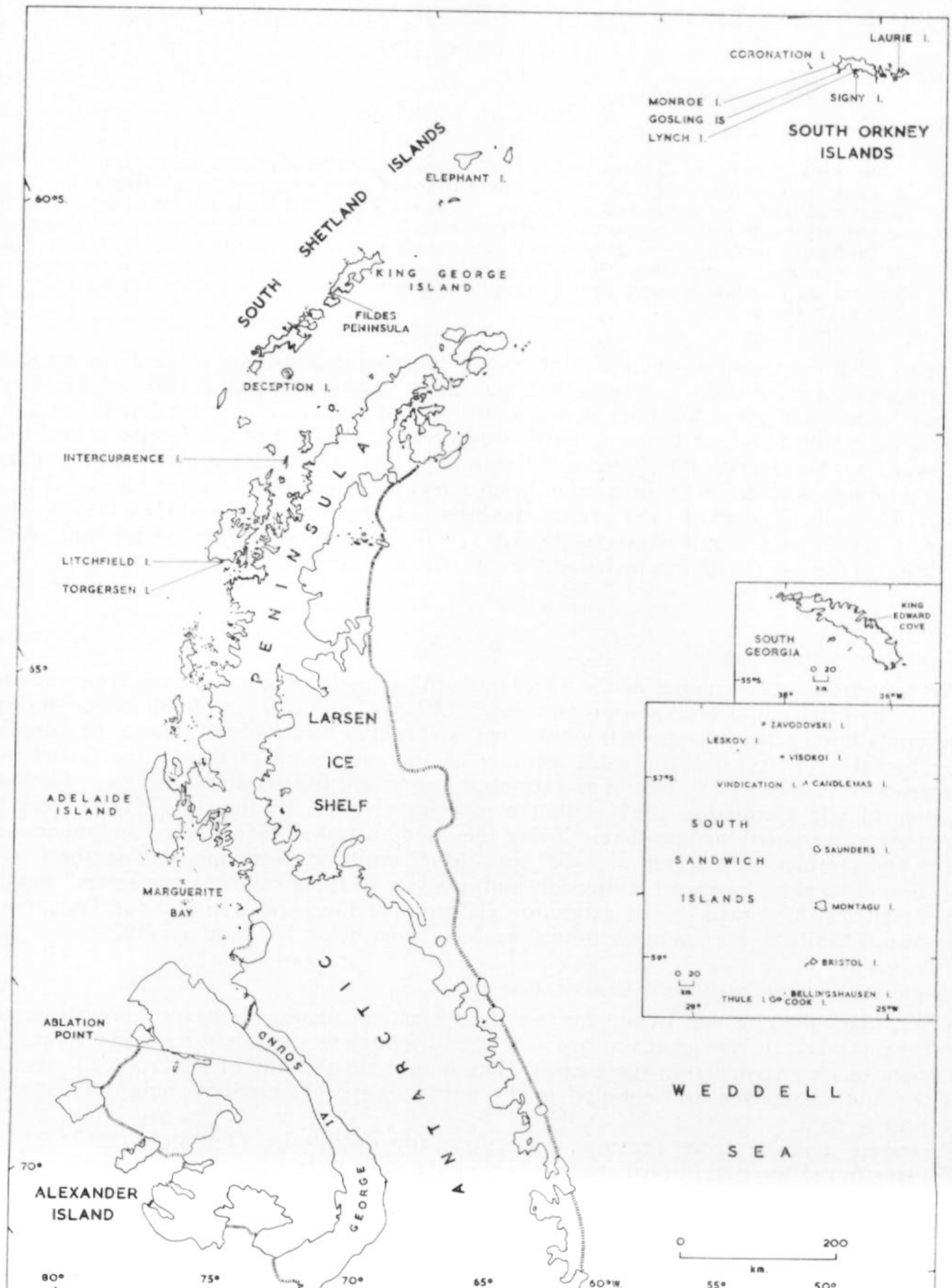

Fig. 1. The Antarctic Peninsula and Scotia Ridge region showing the positions of the sample sites.

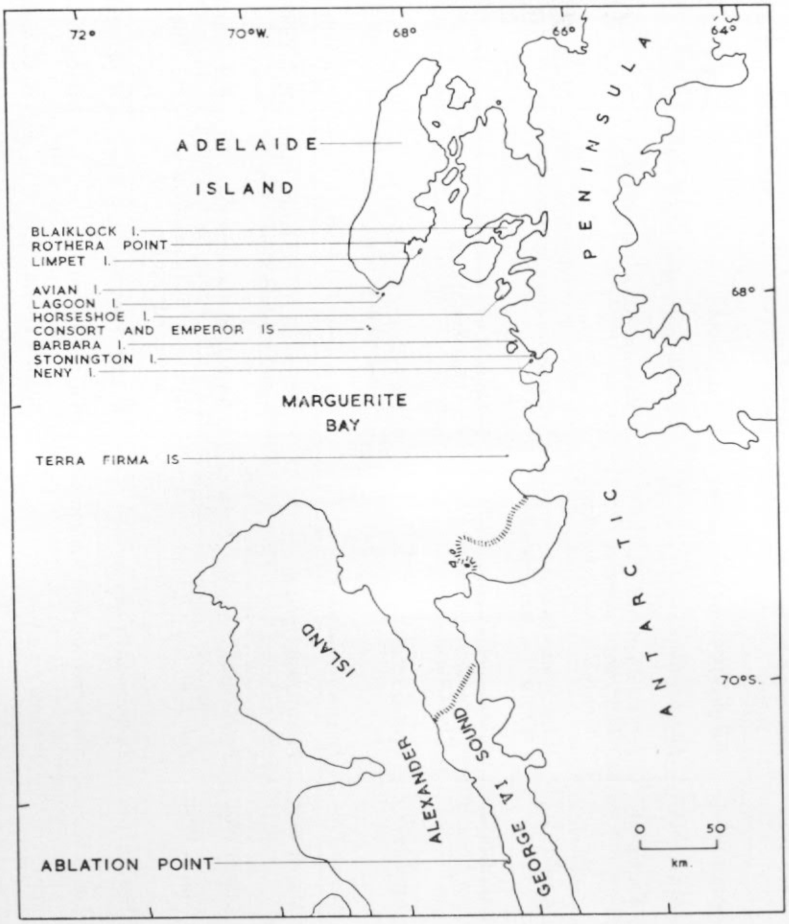

Fig. 2. The Marguerite Bay area of the Antarctic Peninsula showing the positions of sample sites.

Results and Discussion

The 70 sites yielded 11 species or species-groups of Tardigrada (Table III), nine of which have been recorded from Signy Island by Jennings (1976). An estimate of the percentage abundance has been made for all sites where total tardigrade recovery was greater than ten specimens. When these data are grouped according to the vegetation sub-formations recorded by Smith (1972), certain distribution trends become apparent (Table IV).

Three species or species-groups were very widespread. These were *Macrobiotus furciger*, *Hypsibius* (*H.*) *dujardini* and *H.* (*Diphascon*) *alpinus* + *H.* (*D.*) *pinguis*. The distribution patterns of *H.* (*H.*) *dujardini* and *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* are similar to those observed on Signy Island (Jennings, 1976). This species and species-group was found in all eight vegetation sub-formations. However, *M. furciger* does not follow this pattern, and in the present study it was found in only half of the habitat types. The accumulated percentage of these three species or species-groups is very similar to that found on Signy Island for each of the habitat types (Table IV). They also account for 95·3 per cent of the total estimated biomass in the present study, a figure similar to that obtained from Signy Island (95·1 per cent). *H.* (*Isohypsibius*) *renaudi*, however, has a more widespread habitat distribution than was found on Signy Island, although in both studies the percentage occurrence is high only

TABLE I. LOCATION, VEGETATION AND NOTES ON THE SAMPLING SITES

Site	*Location*	*Position* (lat., long.)	*Date*	*Vegetation*	*Notes*	*Collector**
1	South Georgia (King Edward Point)	54°17′S., 36°30′W.	April 1974	*Juncus scheuchzerioides*, *Tortula robusta*	South-facing slope, very wet	
2			April 1974	*Poa flabellata*	Steep slope	
3			April 1974	*Poa flabellata*	Small knolls affected by seals	
4			April 1974	*Festuca contracta*, *Polytrichum alpestre*, *Chorisodontium aciphyllum*	Well-drained grassland area	
5			April 1974	*Polytrichum alpestre*, *Chorisodontium aciphyllum*	Large stand on level ground	
6			April 1974	*Polytrichum alpestre*, *Cladonia rangiferina*, *Barbilophozia* sp.	Understorey to *Rostkovia magellanica* bog	
7			April 1974	*Tortula robusta*	Understorey to *Acaena magellanica*. Dry	
8	Candlemas Island	57°03′S., 26°40′W.	March 1964	*Polytrichum alpinum*	Away from fumaroles	P. J. Tilbrook
9			March 1964	*Polytrichum alpinum*	Influenced by fumarolic heat and condensation	P. J. Tilbrook
10			March 1964	*Pohlia* sp.	Away from fumaroles	P. J. Tilbrook
11			March 1964	*Pohlia* sp.	Influenced by fumarolic heat and condensation	P. J. Tilbrook
12	Monroe Island	60°36′S., 46°03′W.	Feb. 1971	*Drepanocladus uncinatus*	Site not known	H. G. Smith
13	Lynch Island	60°39′S., 45°36′W.	Feb. 1971	*Brachythecium austro-salebrosum*	Site not known	H. G. Smith
14			Feb. 1971	*Prasiola crispa*	Site not known	H. G. Smith
15	Gosling Islands	60°39′S., 45°55′W.	Feb. 1971	*Drepanocladus uncinatus*	Site not known	H. G. Smith
16	Laurie Island	60°44′S., 44°37′W.	Feb. 1971	*Drepanocladus uncinatus*	Site not known	H. G. Smith
17	Elephant Island	61°10′S., 55°14′W.	March 1971	*Deschampsia antarctica*	Soil from level ground	V. W. Spaull†

18			March 1971	*Deschampsia antarctica*	North-facing slope on moraine	V. W. Spaull†
19			March 1971	*Deschampsia antarctica*	East-facing slope	V. W. Spaull†
20			March 1971	*Deschampsia antarctica*	Level ground	V. W. Spaull†
21			Feb. 1971	*Drepanocladus uncinatus*	Site not known	V. W. Spaull†
22	King George Island (Fildes Peninsula)	62°12′S., 58°58′W.	April 1974	*Polytrichum alpinum*	West-facing slope	
A			April 1974	*Drepanocladus uncinatus*	Level ground	
23			April 1974	*Prasiola crispa*	Near giant petrel nest	
24	Deception Island	62°57′S., 60°38′W.	April 1974	*Prasiola crispa*	On boulder	
25	Intercurrence Island	63°55′S., 61°24′W.	Jan. 1969	*Brachythecium austro-salebrosum*, *Bryum algens*, *Drepanocladus uncinatus*	North-facing slope	V. W. Spaull†
B	Torgersen Island	64°46′S., 64°05′W.	March 1974	*Deschampsia antarctica*	North-facing slope. Penguin rookery nearby	
C	Litchfield Island	64°46′S., 64°06′W.	March 1974	*Chorisodontium aciphyllum*, *Pohlia nutans*	North-facing slope	
D			March 1974	*Calliergidium* cf. *austro-stramineum*	Level ground	
E			April 1974	*Polytrichum alpestre*	North-west facing slope	
27			March 1969	*Drepanocladus uncinatus*, *Pohlia nutans*	In slight hollow. North-facing slope	V. W. Spaull†
F			April 1974	*Calliergidium* cf. *austro-stramineum*	North-facing slope	
28	Blaiklock Island	67°33′S., 67°04′W.	March 1974	*Deschampsia antarctica*	West- to north-west-facing slope	
29			Feb. 1969	*Polytrichum alpinum*, *Pohlia nutans*, *Cephaloziella* sp.	Near melt stream	V. W. Spaull†
30			March 1974	*Polytrichum alpinum*	Under old dog spans on level ground	
31			March 1974	*Bryum algens* *Drepanocladus uncinatus*	West- to north-west-facing slope	

TABLE I—*continued*

Site	*Location*	*Position* (lat., long.)	*Date*	*Vegetation*	*Notes*	*Collector**
32	Adelaide Island (Rothera Point)	67°34′S., 68°08′W.	April 1974	*Drepanocladus uncinatus*	North-facing rock clefts	
33	Lagoon Island	67°35′S., 68°16′W.	April 1974	*Deschampsia antarctica*	North-facing slope	
34			April 1974	*Andreaea depressinervis*	South-facing slope	
35	Limpet Island	67°38′S., 68°18′W.	Feb. 1969	*Brachythecium austro-salebrosum*	South-east-facing rock terrace	V. W. Spaull†
36			Feb. 1969	*Drepanocladus uncinatus*	As 35	V. W. Spaull†
37	Avian Island	67°46′S., 68°54′W.	Feb. 1969	*Drepanocladus uncinatus*, *Bryum algens*	North-east-facing slope	V. W. Spaull†
G			April 1974	*Drepanocladus uncinatus*	North-facing crevices. Penguin rookery nearby	
H			April 1974	*Drepanocladus uncinatus*	Level ground near pond	
39			April 1974	*Prasiola crispa*	North-facing crevices. Penguin rookery nearby	
40			April 1974	*Lecania brialmontii*	North-facing crevices. Penguin rookery nearby	
41	Horseshoe Island	67°51′S., 67°12′W.			Site not known	
42			March 1974	Bare soil	From lakeside	
43			March 1974	*Usnea* sp.	North rock faces	
44			March 1974	*Lecania brialmontii*	North rock faces	
45	Consort Islands	67°52′S., 68°42′W.			Site not known	
46	Emperor Island	67°52′S., 68°43′W.	Feb. 1969	*Drepanocladus uncinatus*, *Bryum algens*	Exposed rock ledge	V. W. Spaull†
47	Barbara Island	68°08′S., 67°06′W.	March 1974	*Ceratodon* sp.	North-west-facing slope of rock outcrop	
48			March 1974	*Prasiola crispa*	As 47	

49			March 1974	*Alectoria minuscula*	As 47	
50			March 1974	*Physcia* sp.	As 47	
51	Stonington Island	68°11′S., 67°00′W.	March 1974	*Prasiola crispa*	Rock crevices in station area	
52	Neny Island	68°12′S., 67°03′W.	March 1974	*Colobanthus quitensis*	North-west-facing slope of knoll. Dominican gull nest nearby	
53			March 1974	*Deschampsia antarctica*	As 52	
54			March 1971	*Grimmia* sp.	Site not known	
55			March 1974	*Ceratodon* sp.	As 52	
56			March 1974	*Prasiola crispa*	As 52	
58	Terra Firma Islands	68°42′S., 67°32′W.	Feb. 1969	*Cephaloziella* sp., *Pohlia nutans*	On bare granite. West-facing slope	V. W. Spaull†
I	Alexander Island (Ablation Point)	70°48′S., 68°22′W.	Feb. 1974	*Bryum* sp., *Campylium* cf. *polygamum*	Wet. North-facing slope	R. B. Heywood
59			Feb. 1974	*Bryum* sp., *Campylium* cf. *polygamum*	As I	R. B. Heywood
60			Feb. 1974	*Bryum* sp., *Lepraria neglecta*	Wet. North-facing slope. Moribund appearance	R. B. Heywood
61			Feb. 1974	*Bryum* sp., *Didymodon gelidus*, *Encalypta procera*, *Distichium capillaceum*	Wet. Level ground. Near skua nest	R. B. Heywood

* Collected by I. B. Collinge unless otherwise stated.
† Samples collected for V. W. Spaull.

TABLE II. PHYSICAL CHARACTERISTICS OF SAMPLE

Number	*Location*	*Wet weight* (g.)	*Dry weight* (g.)	*Index of humidity*	*Per cent water by volume*
1	South Georgia	12·62	1·27	8·92	39
2	South Georgia	11·12	3·48	5·12	26
3	South Georgia	25·87	6·50	3·02	67
4	South Georgia	19·99	7·90	2·63	41
5	South Georgia	11·87	2·45	3·92	33
6	South Georgia	6·58	1·45	3·53	17
7	South Georgia	18·11	3·01	5·24	53
22	King George Island	9·64	3·06	2·15	23
A	King George Island	12·55	1·74	6·24	38
23	King George Island	13·99	8·66	0·75	–
24	Deception Island	4·75	3·90	0·22	–
B	Torgersen Island	12·61	2·84	3·59	34
C	Litchfield Island	10·53	3·16	2·32	25
D	Litchfield Island	16·86	0·81	21·01	58
26	Galindez Island	14·93	3·93	2·80	–
E	Galindez Island	18·06	5·43	2·40	44
F	Galindez Island	14·61	1·58	8·35	47
28	Blaiklock Island	30·82	20·05	0·54	–
30	Blaiklock Island	14·82	11·67	0·27	–
31	Blaiklock Island	32·31	15·39	1·10	–
32	Adelaide Island	15·76	2·06	6·65	–
33	Lagoon Island	34·16	8·00	3·27	–
34	Lagoon Island	7·70	2·00	2·82	–
G	Avian Island	10·33	1·03	8·17	33
H	Avian Island	13·59	1·55	7·86	44
39	Avian Island	2·68	1·16	1·31	–
40	Avian Island	5·97	4·23	0·41	–
42	Horseshoe Island	30·13	27·58	0·09	–
43	Horseshoe Island	2·55	2·29	0·12	–
44	Horseshoe Island	7·38	5·43	0·37	–
47	Barbara Island	11·87	9·12	0·30	–

TABLE II—*continued*

Number	Location	Wet weight (g.)	Dry weight (g.)	Index of humidity	Per cent water by volume
48	Barbara Island	6·32	2·33	1·71	–
49	Barbara Island	0·87	0·86	0·01	–
50	Barbara Island	2·50	2·27	0·10	–
52	Neny Island	16·06	10·55	0·52	–
53	Neny Island	9·09	5·34	0·70	–
55	Neny Island	62·75	41·91	0·50	–
56	Neny Island	23·67	19·25	0·23	–
57	Neny Island	8·89	7·97	0·11	–
59	Alexander Island	32·60	5·17	5·33	95
60	Alexander Island	20·87	12·62	0·64	28
61	Alexander Island	26·93	4·88	4·51	76
I	Alexander Island	24·80	6·00	3·77	65

on sites of the foliose alga *Prasiola crispa* which invariably benefit from nutrient enrichment from bird or seal concentrations. It was noted on Signy Island that *H.* (*D.*) *scoticus* showed some preference for the relatively rich organic soils rather than moss and peat substrates. Similarly, in the present study, this species was recorded in high proportions only in the nutrient-rich brown-earth soils under the Antarctic phanerogams. Other tardigrade species were not found in sufficient numbers to determine any general distribution trends.

Few of the sites examined were directly affected by vertebrates but sites B and G, which were enriched from this source, do not support the earlier view (Jennings, 1976) that enrichment leads to higher tardigrade densities (Table V). However, the present results do support the data for the moss turves of Signy Island, where tardigrade population densities were relatively low ($0\cdot011 \times 10^6$ tardigrades $m.^{-2}$). A *Chorisodontium* moss turf (site C) from Litchfield Island yielded only $0\cdot002 \times 10^6$ tardigrades $m.^{-2}$, while no Tardigrada were extracted from six cores of a *Polytrichum* moss turf (site E) from Galindez Island. The range of population densities found at other sites was from $0\cdot025 \times 10^6$ $m.^{-2}$ in a *Calliergidium* moss carpet from Galindez Island to $1\cdot922 \times 10^6$ $m.^{-2}$ in a *Drepanocladus* moss carpet from King George Island.

Rotifera were found in all samples collected in the austral summer of 1974. Adinetids were present in 84 per cent of the samples, while other bdelloid rotifers were recovered from 98 per cent of the samples. Although monogonont Rotifera were never abundant, they were found in 30 per cent of the samples. Total rotifer densities ranged from $0\cdot005 \times 10^6$ $m.^{-2}$ in a mat of *Drepanocladus* on level ground to $0\cdot223 \times 10^6$ $m.^{-2}$ in a mat of *Drepanocladus* near a penguin rookery. Both of these samples were taken from Avian Island (sites G and H).

As at Signy Island (Jennings, 1976), no clear correlation existed between rotifer or tardigrade population density and either moisture content or pH of the substrate. Although subjective grouping of the sites into "wet" and "dry" sites (where this was possible) indicated that higher numbers of tardigrades (Table III) were extracted from the "wet" substrates ($t = 2\cdot02$ with 32 degrees of freedom). However, this analysis cannot be accepted as completely reliable, since it does not take a varying sample size into account. Also, many of the

TABLE III. PERCENTAGE OCCURRENCE OF TARDIGRADE SPECIES OR SPECIES-GROUPS AND TOTAL NUMBERS OF TARDIGRADES AND ROTIFERS RECOVERED FROM 70 SAMPLE SITES

	Location	*Number of replicates*	*Echiniscus* sp.	*Macrobiotus furciger*	*Hypsibius (H.) antarcticus*	*H. (H.) dujardini*	*H. (H.) oberhaeuseri*	*H. (Isohypsibius) asper*	*H. (I.) renaudi*	*H. (Diphascon) alpinus + H. (D.) pinguis*	*H. (D.) chilenensis*	*H. (D.) scoticus*	*Milnesium tardigradum*	*Total number of tardigrades recovered*	*Total number of rotifers recovered*
South Georgia	1. King Edward Point	2	–	–	–	–	–	+	–	+	–	–	–	2	14
	2. King Edward Point	2	–	–	–	–	–	–	–	+	–	+	–	2	92
	3. King Edward Point	2	–	–	+	–	–	–	–	–	–	–	–	1	66
	4. King Edward Point	2	–	+	–	–	–	–	–	+	–	–	–	5	45
	5. King Edward Point	2	–	70	–	–	–	–	–	30	–	–	–	17	488
	6. King Edward Point	2	–	+	–	–	–	–	–	–	–	–	–	7	9
	7. King Edward Point	6	–	99	1	–	–	–	–	–	–	–	–	158	89
South Sandwich Islands	8. Candlemas Island	2	–	–	–	81	–	–	19	–	–	–	–	16	–
	9. Candlemas Island	1	–	–	–	–	–	–	–	–	–	–	–	0	–
	10. Candlemas Island	2	–	–	–	100	–	–	+	–	–	–	–	117	–
	11. Candlemas Island	2	–	–	–	–	–	–	–	–	–	–	–	0	–
South Orkney Islands	12. Monroe Island	1	–	54	–	–	–	–	5	36	–	5	–	22	–
	13. Lynch Island	1	–	–	–	23	–	–	–	67	–	–	–	16	–
	14. Lynch Island	1	–	–	–	92	–	4	–	4	–	–	–	27	–
	15. Gosling Islands	1	–	100	–	–	–	–	–	–	–	–	–	30	–
	16. Laurie Island	1	–	92	–	–	–	–	–	8	–	–	–	25	–
South Shetland Islands	17. Elephant Island	1	–	100	–	–	–	–	–	–	–	–	–	17	–
	18. Elephant Island	1	–	5	–	–	–	–	–	40	2	53	–	55	–
	19. Elephant Island	1	–	2	–	–	–	–	–	34	–	64	–	103	–
	20. Elephant Island	1	–	8	–	1	–	–	–	18	–	73	–	115	–
	21. Elephant Island	1	–	99	–	–	–	–	–	1	+	+	–	316	–
	22. King George Island	1	–	–	–	–	–	–	–	–	–	–	–	0	7
	A. King George Island	6	–	+	–	–	–	–	–	100	–	–	–	1,922	248
	23. King George Island	2	–	–	–	–	–	–	97	3	–	–	–	69	25
	24. Deception Island	2	–	–	–	–	–	–	100	–	–	–	–	300	1,494

TABLE III—*continued*

Region	Location	*Number of replicates*	*Echiniscus* sp.	*Macrobiotus furciger*	*Hypsibius (H.) antarcticus*	*H. (H.) dujardini*	*H. (H.) oberhaeuseri*	*H. (Isohypsibius) asper*	*H. (I.) renaudi*	*H. (Diphascon) alpinus* + *H. (D.) pinguis*	*H. (D.) chilenensis*	*H. (D.) scoticus*	*Milnesium tardigradum*	*Total number of tardigrades recovered*	*Total number of rotifers recovered*
Northern Antarctic Peninsula	25. Intercurrence Island	1	–	5	–	–	–	–	–	95	–	–	–	19	–
	B. Torgersen Island	6	6	–	–	82	–	–	6	6	–	–	–	17	201
	C. Litchfield Island	6	–	–	–	–	–	–	–	+	–	–	–	2	197
	D. Litchfield Island	6	–	78	–	–	–	–	–	22	–	–	–	65	393
	26. Galindez Island	1	–	–	–	+	–	–	–	–	–	–	–	1	115
	E. Galindez Island	6	–	–	–	–	–	–	–	–	–	–	–	0	70
	27. Galindez Island	1	–	100	–	–	–	–	–	–	–	–	–	40	–
	F. Galindez Island	6	–	32	–	–	–	–	–	68	–	–	–	25	38
Marguerite Bay	28. Blaiklock Island	1	–	–	–	–	–	–	–	100	–	–	–	14	11
	29. Blaiklock Island	1	–	–	–	100	–	–	–	–	–	–	–	14	–
	30. Blaiklock Island	1	–	–	–	+	–	–	–	–	–	–	–	9	21
	31. Blaiklock Island	1	–	–	–	+	–	–	–	–	–	–	–	4	27
	32. Adelaide Island	1	2	91	–	–	–	–	–	7	–	–	–	33	–
	33. Lagoon Island	2	–	19	–	81	–	–	–	–	–	–	–	21	53
	34. Lagoon Island	1	–	+	–	–	–	–	–	–	–	–	–	3	9
	35. Limpet Island	1	–	67	–	–	–	–	–	33	–	–	–	69	–
	36. Limpet Island	1	–	94	–	4	–	–	–	2	–	–	–	103	–
	37. Avian Island	1	–	68	–	32	–	–	–	–	–	–	–	28	–
	G. Avian Island	6	–	72	–	1	–	–	–	27	–	–	–	181	1,285
	H. Avian Island	6	–	93	–	–	–	–	–	6	–	1	–	264	27
	38. Avian Island	1	–	72	–	28	–	–	–	–	–	–	–	65	–
	39. Avian Island	1	–	–	–	–	–	–	+	–	–	–	–	2	76
	40. Avian Island	1	–	–	–	–	–	–	–	+	–	+	–	9	71
	41. Horseshoe Island	1	–	–	–	100	–	–	–	–	–	–	–	24	–
	42. Horseshoe Island	1	–	–	–	+	–	–	–	–	–	–	–	7	18
	43. Horseshoe Island	2	–	–	–	+	–	–	+	–	–	–	–	2	32
	44. Horseshoe Island	2	+	–	–	+	–	–	–	–	–	–	–	7	20

TABLE III—*continued*

	Location	Number of replicates	*Echiniscus* sp.	*Macrobiotus furciger*	*Hypsibius (H.) antarcticus*	*H. (H.) dujardini*	*H. (H.) oberhaeuseri*	*H. (Isohypsibius) asper*	*H. (I.) renaudi*	*H. (Diphascon) alpinus* + *H. (D.) pinguis*	*H. (D.) chilenensis*	*H. (D.) scoticus*	*Milnesium tardigradum*	*Total number of tardigrades recovered*	*Total number of rotifers recovered*
Marguerite Bay—continued	45. Consort Island	1	–	–	–	–	–	–	+	–	–	–	–	9	–
	46. Emperor Island	1	–	85	–	14	–	–	–	1	–	–	–	87	–
	47. Barbara Island	1	–	–	–	–	–	–	–	–	–	–	–	0	48
	48. Barbara Island	1	–	–	–	55	–	–	45	–	–	–	–	168	502
	49. Barbara Island	2	+	–	–	–	–	–	+	–	–	–	–	2	10
	50. Barbara Island	1	–	–	–	+	–	–	–	–	–	–	–	1	15
	51. Stonington Island	2	–	–	–	+	–	–	+	–	–	–	–	6	33
	52. Neny Island	1	–	–	–	89	–	–	–	11	–	–	–	53	84
	53. Neny Island	1	–	–	–	+	–	–	–	+	–	–	–	9	16
	54. Neny Island	1	–	–	–	38	–	–	–	62	–	–	–	13	–
	55. Neny Island	1	–	–	–	+	–	–	–	+	–	–	–	2	65
	56. Neny Island	1	–	–	–	98	–	–	–	2	–	–	–	81	4
	57. Neny Island	1	–	–	–	17	–	–	–	83	–	–	–	12	3
	58. Terra Firma Islands	1	–	–	–	–	–	–	–	+	–	–	–	2	–
Alexander Island	I. Ablation Point	6	1	40	–	33	1	–	2	20	–	–	3	228	233
	59. Ablation Point	2	–	14	–	11	–	24	–	49	–	–	2	71	38
	60. Ablation Point	2	–	–	–	–	–	–	–	+	–	+	–	2	92
	61. Ablation Point	2	10	13	–	13	–	5	–	58	–	–	1	39	45
	Number of sites where each species or species-group occurred		6	30	2	31	1	4	13	38	2	9	3		

\+ <1 per cent occurrence or presence only where total recovery was less than ten individuals.

TABLE IV. THE DISTRIBUTION AND MEAN PERCENTAGE OCCURRENCE OF EIGHT TARDIGRADE SPECIES OR SPECIES-GROUPS IN EIGHT BROAD HABITAT TYPES IN THE MARITIME ANTARCTIC (i.e. EXCLUDING SOUTH GEORGIA AND ALEXANDER ISLAND

Site	*Habitat type and site numbers*							
	Crustose lichen (40, 44, 49)	*Alga (14, 23, 24, 39, 48, 51, 56)*	*Moss cushion (34, 43, 54)*	*Moss carpet (12, 15, 16, 21, A, B, D, 27, F, 32, 36, G, H, 58)*	*Herbs (17, 18, 19, 20, 28, 33, 52, 53)*	*Moss turf (8, 9, 22, C, E, 29, 30)*	*Moss hummock (13, 25, 31, 35, 37, 46)*	*Lichen-encrusted moss (47, 55)*
Sites giving percentage abundance	0	5	1	14	8	3	4	1
Echiniscus (E.) capillatus + *E. (E.) meridionalis*	+	–	–	+	1	–	–	–
Macrobiotus furciger	–	–	+	70	17	–	56	–
Hypsibius (H.) dujardini	+	49	17	4	32	60	12	100
H. (Isohypsibius) asper	–	1	–	–	–	–	–	–
H. (I.) renaudi	+	48	+	+	1	7	–	+
H. (Diphascon) alpinus + *H. (D.) pinguis*	+	2	83	25	25	33	32	+
H. (D.) scoticus	+	–	–	+	24	–	–	–
H. (D.) chilenensis	–	–	–	+	+	–	–	–
Number of species found in this study	5	4	4	7	7	3	3	3
Number of species found on Signy Island	5	10	8	8	7	3	–	–
Accumulate percentage of *M. furciger*, *H. (D.) alpinus* + *H. (D.) pinguis* and *H. (H.) dujardini*	–	51	100	99	74	93	100	100
Accumulate percentage of three species as found on Signy Island	45	54	96	98	98	100	–	–

+ 1 per cent occurrence or presence only where total recovery was less than ten individuals.

TABLE V. MEAN TARDIGRADE DENSITY $m.^{-2}$ WITH 95 PER CENT CONFIDENCE LIMITS (ITALICIZED). SITES AFFECTED BY VERTEBRATES ARE INDICATED BY AN ASTERISK

Site and habitat	*Echiniscus (E.) capillatus* + *E. (E.) meridionalis*	*Macrobiotus furciger*	*Hypsibius (H.) dujardini*	*H. (H.) oberhaeuseri*	*H. (Isohypsibius) renaudi*	*H. (Diphascon) alpinus* + *H. (D.) pinguis*	*H. (D.) scoticus*	*Milnesium tardigradum*	*Total Tardigrada*
A. King George Island *Drepanocladus*	–	1,802 *5,733*	–	–	–	1,920,496 *1,292,439*	–	–	1,922,297 *1,296,817*
B.* Torgersen Island *Deschampsia*	901 *2,866*	–	14,413 *11,465*	–	901 *2,866*	901 *2,866*	–	–	17,115 *11,818*
C. Litchfield Island *Chorisodontium*	–	–	–	–	–	1,802 *0*	–	–	1,802 *0*
D. Litchfield Island *Calliergidium*	–	51,345 *137,614*	–	–	–	13,512 *42,995*	–	–	64,857 *180,602*
E. Galindez Island *Polytrichum*			No tardigrades recovered						
F. Galindez Island *Calliergidium*	–	8,107 *20,064*	–	–	–	17,115 *37,262*	–	–	25,222 *57,327*
G.* Avian Island *Drepanocladus*	–	129,715 *63,189*	1,802 *5,733*	–	–	49,544 *34,515*	–	–	204,030 *148,338*
H. Avian Island *Drepanocladus*	–	245,016 *367,763*	–	–	–	15,314 *22,017*	3,603 *4,054*	–	264,834 *386,370*
I. Alexander Island *Bryum*	1,802 *4,054*	90,980 *144,202*	75,667 *21,829*	901 *2,866*	5,405 *17,198*	45,941 *45,951*	–	7,206 *5,733*	227,901 *211,196*

samples classified as "dry" consist of *Polytrichum* and/or *Chorisodontium*, a substrate which supports few tardigrades regardless of its overall moisture content.

Little pattern was apparent when densities were considered in relation to climate. Fig. 3 illustrates a number of climatic factors as well as tardigrade density and biomass for a single moss type over the geographical range studied. Both population density and biomass decreased markedly southward along the Antarctic Peninsula from the South Shetland Islands, but increased again at sites in Marguerite Bay. This pattern is also reflected in Table IV even though a variety of moss types is considered. This apparent paradox may relate to micro-environmental factors which, although not measured, may be deduced from Fig. 3. Tardigrades are only active when the moss is not frozen and free water is available. This active period can occur only during the brief Antarctic summer when the insulating snow-cover melts or ablates. Temperatures at plant level in the maritime Antarctic often show little correlation with those measured in Stevenson screens. The characteristic summer pattern is one of wide diurnal fluctuations (Greene and Longton, 1970). Daytime surface temperatures in the moss communities are closely linked to site aspect and radiation receipt and can exceed air temperature by up to 20° C (Longton, 1972). On Signy Island, temperatures in the upper 3 cm. of a moss carpet have reached 20° C, whilst 28° C has been recorded in a moss turf (personal communication from E. P. Wright). The high tardigrade densities of the South Orkney Islands and the South Shetland Islands with a higher air temperature but fairly low radiation receipt contrast with the low densities of the colder, cloudier north Antarctic Peninsula. The direct micro-climate effect of increased solar energy might be expected to reverse this trend (Marguerite Bay and Alexander Island) even though the latitude is higher and the mean air temperature lower. The effects of a favourable micro-environment appear also to affect the species diversity (Table V). Although the pattern is complicated by the results from South Georgia (where competition with organisms not present at higher latitudes presumably accounts for the low species diversity) and the South Sandwich Islands (where replication was very low), a trend of decreasing species diversity to Marguerite Bay followed by a large increase at Alexander Island is apparent.

Only two specimens of *H.* (*H.*) *antarcticus* were recovered from South Georgia, and it has been suggested by Dastych (1973) that this species represents specimens of *H.* (*H.*) *dujardini* in the simplex stage (i.e. that period before the moult when the entire buccal apparatus has been lost and before it has fully reformed). However, in this instance no specimens of *H.* (*H.*) *dujardini* were recovered from South Georgia, but with such a small sample this suggestion can be neither refuted nor confirmed. Table VI shows that *M. furciger*, *H.* (*I.*) *asper*, *H.* (*D.*) *alpinus* + *H.* (*D.*) *pinguis* and *H.* (*D.*) *scoticus* were present in a wide geographical range of habitats, from the sub-Antarctic (South Georgia) to the continental Antarctic (Alexander Island). Any comments on the zoogeographical distribution of individual tardigrade species are at present of limited value, since the samples used are too small and too few to support more general conclusions for this very large area.

Previous information on the composition and distribution of the tardigrade fauna of the Antarctic has been given by Richters (1904, 1908, 1909), Murray (1906, 1910), Morikawa (1962), Sudzuki (1964) and Jennings (1976). Omitting those species which have not been sufficiently described, 23 tardigrade species have been reported from the Antarctic as a whole (Table VII). Only 11 of these have been found by two or more investigators, and only *E.* (*E.*) *meridionalis*, *M. furciger*, *H.* (*I.*) *asper*, *H.* (*D.*) *alpinus*, *H.* (*D.*) *chilenensis* and *Miln. tardigradum* have been recorded by three or more investigators. It is, however, very difficult to distinguish the small members of the sub-genus *Diphascon* (Petersen, 1951; Jennings, 1976) and for this reason some or all of the species in the group *D. alpinus*, *D. chilenensis*, *D. ongulensis*, *D. pinguis*, *D. puniceus* and *D. scoticus* may have been confused in this and other investigations. From the studies of Murray (1906), Richters (1908) and Jennings (1976, present paper) the total recorded tardigrade fauna from the Scotia Ridge–Antarctic Peninsula region numbers 17 species, eight of which have been found by more than one investigator. 13 species have not been recorded from the Antarctic outside localities in the Antarctic Peninsula and Scotia Ridge region, but this may reflect the intensity of the investigations and the taxonomic progress made in this group in recent years.

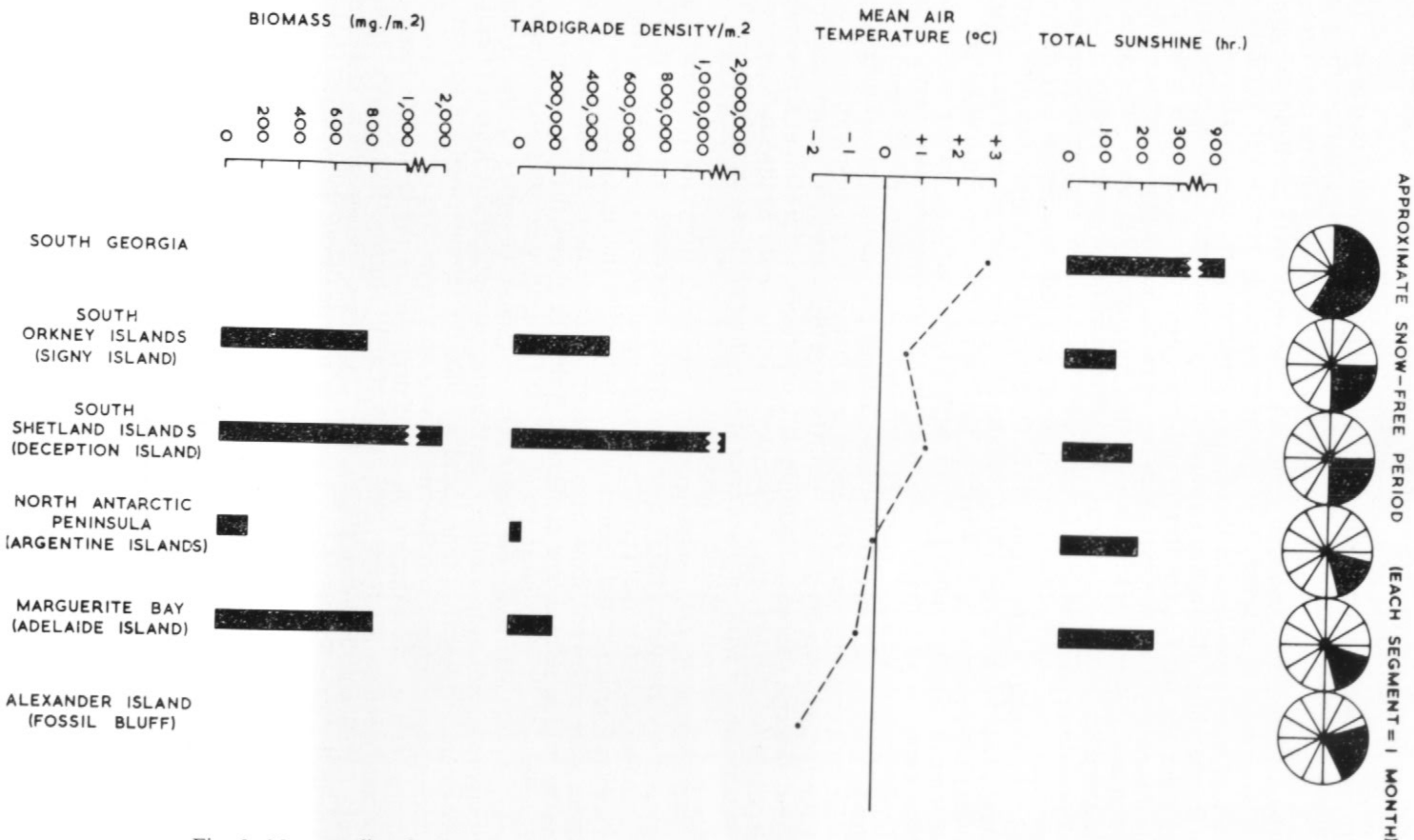

Fig. 3. Mean tardigrade densities and biomass in the moss-carpet sub-formation are given with meteorological data for the areas considered in this study. Meteorological data obtained for the *snow-free period* of the 10 years 1963–72 (unpublished data of the British Antarctic Survey Atmospheric Sciences Division).

Table VI. Relative abundance (per cent) of each terrestrial tardigrade species or species-group by zones of latitude

Location	*Sites*	*Lat. S.*	*Oreella mollis*	*Echiniscus* sp.	*Macrobiotus furciger*	*Hypsibius (H.) antarcticus*	*H. (H.) dujardini*	*H. (H.) oberhaeuseri*	*H. (Isohypsibius) asper*	*H. (I.) renaudi*	*H. (Diphascon) alpinus* + *H. (D.) pinguis*	*H. (D.) chilenensis*	*H. (D.) scoticus*	*H. (D.) puniceus*	*H. (D.)* sp.	*Milnesium tardigradum*	*Mean number of species/site*
South Georgia	1–7	54°	–	–	84	+	–	–	+	–	15	–	+	–	–	–	1·7
South Sandwich Islands	8–11	57°	–	–	–	–	90	–	–	10	–	–	–	–	–	–	1·0
South Orkney Islands	12–16*	60–61°	+	+	18	–	20	–	3	9	38	+	6	+	+	4	3·5
South Shetland Islands	17–24, A	61–62°	–	–	32	–	+	–	–	23	23	+	22	–	–	–	2·3
Northern part of Antarctic Peninsula	25–27, B–F	63–66°	–	1	36	–	13	–	–	1	48	–	–	–	–	–	1·6
Marguerite Bay	28–58, G–H	67–69°	–	+	39	–	39	–	–	3	20	–	+	–	–	–	1·8
Alexander Island	59–61, I	70°	–	3	22	–	19	+	9	+	42	–	+	–	–	2	5·0

* Includes data from all terrestrial sites examined on Signy Island (Jennings, 1976).

TABLE VII. COMPARISON OF THE FAUNISTIC LISTS OF ANTARCTIC AND SUB-ANTARCTIC TARDIGRADA FROM VARIOUS AUTHORS. SYNONYMS ARE GIVEN WHERE THESE HAVE APPEARED IN PREVIOUS ANTARCTIC LITERATURE

Species and authority	*Richters (1904, 1908, 1909)*			*Murray (1906, 1910)*		*Sudzuki (1964)*	*Morikawa (1962)*	*Jennings (1976, this paper)*	*Synonym*
Oreella mollis J. Murr. 1910	–	–	–	–	–	–	–	▲	
Echiniscus (*Echiniscus*) *arctomys* Ehrbg. 1853	–	▲	–	–	–	–	–	–	
capillatus Ramazzotti 1956	–	–	–	–	–	–	–	▲	
meridionalis J. Murr. 1906	–	▲	–	▲	–	–	–	▲	
wendti Richters 1903	–	▲	–	–	–	–	–	–	
Macrobiotus furciger J. Murr. 1907	–	▲	–	▲	–	–	–	▲	*M. furcatus*
meridionalis Richters 1909	–	–	●	–	–	–	–	–	
polaris J. Murr. 1910	–	–	–	–	●	–	–	–	
Hysibius (*Hypsibius*) *antarcticus* (Richters 1904)	●	–	–	–	–	●	–	–	
arcticus (J. Murr. 1907)	–	–	–	–	●	–	●	–	
dujardini (Doy. 1840)	–	▲	–	–	–	–	–	▲	*M. murrayi*
mertoni simoizumi Sudzuki 1964	–	–	–	–	–	●	–	–	
oberhaeuseri (Doy. 1840)	–	–	–	–	●	–	–	▲	
(*Isohypsibius*) *asper* (J. Murr. 1906)	–	▲	–	▲	–	–	–	▲	*M. asperus*
papillifer (J. Murr. 1905)	–	–	–	–	–	–	–	▲	
renaudi Ramazzotti 1972	–	–	–	–	–	–	–	▲	
(*Diphascon*) *alpinus* (J. Murr. 1906)	–	▲	–	▲	●	–	–	▲	*D. alpinum*
chilenensis (Plate 1888)	–	▲	–	▲	–	*	–	▲	
ongulensis Morikawa 1962	–	–	–	–	–	–	●	–	
pinguis Marcus 1936	–	–	–	–	–	–	–	▲	
puniceus Jennings 1975	–	–	–	–	–	–	–	▲	
scoticus (J. Murr. 1905)	–	▲	–	–	–	–	–	▲	
Milnesium tardigradum Doy. 1840	–	▲	–	–	–	●	–	▲	

– Not found.
● Found in the Antarctic.
▲ Found in the Antarctic Peninsula.
* Variety found (Sudzuki (1962) listed one species as *H.* (*D.*) *Chilenensis langhovdensis* Sudzuki 1962, which differs slightly from *H.* (*D.*) *chilenensis*).

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