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27

A Systematic Survey of Tardigrada from Iceland

CLIVE I. MORGAN

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A Systematic Survey of Tardigrada from Iceland

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Abstract. Collections of terrestial and aquatic mosses lichen, soil, littoral and sub-littoral marine sand, from localities in northern and eastern Iceland were examined for tardigrades. Over 150 samples from 28 localities were analysed. Tardigrada were found in 55% of all samples, representing 24 localities. Thirty-two species were recorded, of which 22 species, two varieties, one genus (*Milnesium*) and one sub-genus (*Diphascon*) represent new additions to the Icelandic fauna. No marine tardigrades were observed despite extensive collecting in marine habitats. Morphological, ecological, and biogeographical notes are provided on selected species, together with a key for the identification of the 42 species of Tardigrada known to occur in Iceland.

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INTRODUCTION

The Tardigrada are a common component of the interstitial fauna of mosses, lichens, liverworts, and some angiosperms. In addition, they occur also in soil, and marine sand and sediments. Recorded estimates of population density vary considerably, but can exceed 2×10^6 per m^2 in moss (Morgan 1977). A characteristic of many of the habitats colonized by tardigrades is a tendency to dry up temporarily, with potentially detrimental effects on the interstitial fauna. At the onset of unfavourable conditions, however, tardigrades and other interstitial forms are able to enter a drought resistant cryptobiotic state in which they can survive a wide range of environmental extremes. Normal activity recommences on rehydration of the substrate. During drying periods the interstitial fauna of mosses is confined to the green functional parts of the stems (Hallas 1975), the region which will retain the very last water in leaf exils prior to complete dehydration.

Iceland, because of its flora, climate, and topography would appear to be an ideal environment for tardigrades. Lush moss and lichen growth, which in many areas may never dry out, presents optimum conditions for population growth, although fungal depredations could be limiting (Morgan 1977). The phylum Tardigrada has attracted considerable attention in recent years, particularly by European workers. However knowledge of Icelandic tardigrades is sparse.

The Tardigrada of Iceland have been the subject of three previous investigations (Fig. 1). Richters (1904) recorded seven species including *Pseudechiniscus islandicus* (Richters) and *Macrobiotus islandicus* Richters both new to science, in moss samples (principally *Rhacomitrium* species) from east Iceland. De Coninck (1939) analyzed samples of terrestrial and aquatic mosses from south-west Iceland recording ten species of tardigrade, nine of which were new additions to the Icelandic fauna. The synopsis of Icelandic Tardigrada produced by Tuxen (1941) includes two species, *Macrobiotus hastatus* Murray and *Macrobiotus macronyx* Dujardin, identified from material preserved in the collections of the Zoological Museum, Copenhagen. There would appear to be only one other direct reference to Icelandic tardigrades, Ramazzotti (1972) gives Reykjavik as one of the two localities from which *Pseudechiniscus tridentifer* Bartos has been recorded. These authors have recorded nineteen species, representing four genera: *Echiniscus* (two species); *Pseudechiniscus* (three species); *Macrobiotus* (ten species); *Hypsibius* (four species) (Table 1). The specimens obtained in each survey were extracted from material collected in a variety of habitats. Significantly, each of the major lists has a quite different species composition, which suggests that the Icelandic tardigrade fauna has still to be completely investigated. Other European countries for which accurate faunal lists are available include: Ireland, 40 species (Morgan 1975); mainland Britain, 74 species (Morgan 1976); Greenland, 40 species (Petersen 1951); Finland, 48 species (Hallas 1977).

MATERIALS AND METHODS

The data presented in this paper were drawn from collections of terrestrial and aquatic mosses, lichen, soil, littoral, and sub-littoral marine sand. Samples were obtained by the author during the summers of 1969 and 1975 as a member of University College of Swansea Expeditions to Northern Iceland. In addition, eight localities in Eastern Iceland were sampled in 1977 by W. Baxter, a member of the University of Aberdeen Expedition.

Samples of moss and lichen collected by the author in 1969 were air dried and stored in open

polythene bags prior to transit to Britain, where the tardigrade component was extracted using the Boisseau apparatus (Morgan & King 1976). Terrestrial and freshwater samples obtained by the author in 1975 were extracted at Katla Field Station, located at Víkurbakki, Eyjafjördur, using the following modification of the washing technique outlined by Morgan & King (1976). Plant material was soaked overnight in a known quantity of water, after which an equal volume of 4% acetic acid was added and the mixture allowed to stand for 15 minutes to narcotize the interstitial fauna. After vigorous stirring to get all solids into suspension the mixture was decanted through coarse (500 μ mesh) and fine (60 μ mesh) nylon filters. The solid debris was resuspended in water, agitated, and again decanted; this process was repeated several times for each sample. Any interstitial fauna, plus minute particulate debris, collected on the fine nylon filter and could be readily washed of and preserved in 10% alcohol with the addition of a few drops of 10% formalin. This method is not quantitative but is admirable for use in the field since the bulk of extracted sample for transport is usually much less than the complete plant sample which gave rise to it. The danger of damaging mould growth is removed, and if a reasonable dissecting microscope is available, negative samples can be discarded on the spot. Marine samples collected in 1975 were treated similarly, although 10% alcohol was substituted as a narcotizing agent. Material obtained by W. Baxter (1977, Aberdeen University Eastern

Fig. 1.
Distribution of collecting-sites within Iceland. Letters refer to previous investigations:
D De Coninck,
R Ramazzotti,
r Richters,
T Tuxen.
Numbers refer to sites sampled during the present study.

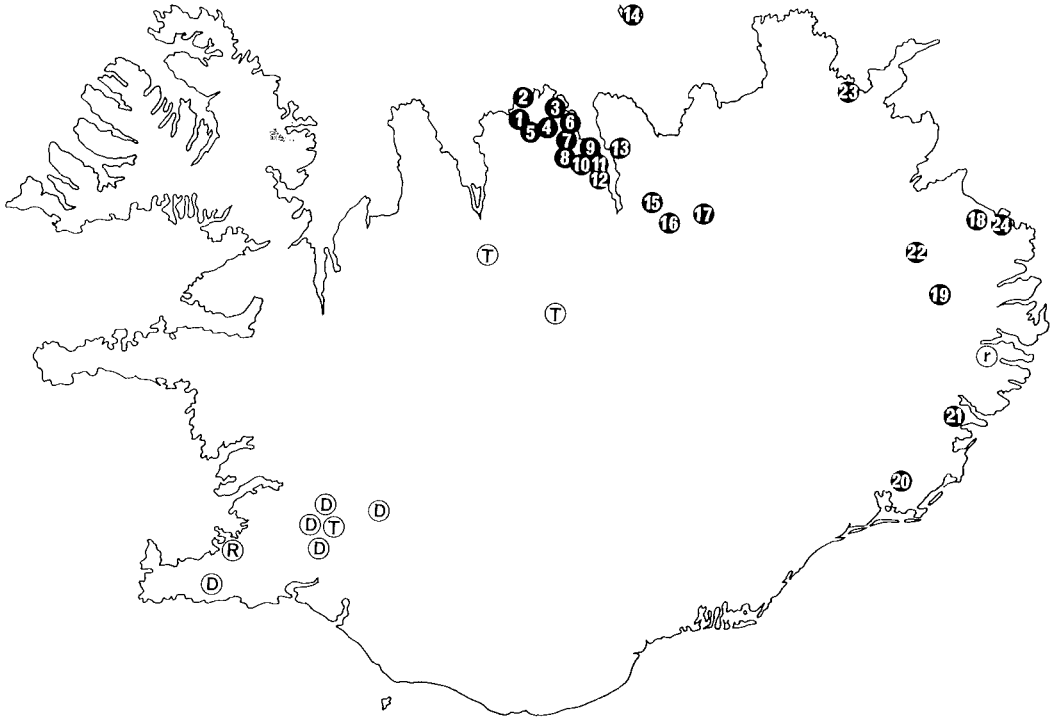

Table 1
A survey of records of Icelandic Tardigrada, including new additions to the fauna.

	Richters (1904)	De Coninck (1939)	Tuxen (1941)	Ramazzotti (1972)	The present study
Echiniscus (Echiniscus) blumi					M
Echiniscus (Echiniscus) granulatus	r				M
Echiniscus (Echiniscus) merokensis					M
var. suecicus					M
Echiniscus (Echiniscus) spitsbergensis		D			
Echiniscus (Echiniscus) wendti					M
Echiniscus (Bryodelphax) parvulus					M
Pseudechiniscus islandicus	r	D			M
Pseudechiniscus suillus	r				
Pseudechiniscus tridentifer				R	M
Macrobiotus ambiguus		D	T		
Macrobiotus areolatus					M
Macrobiotus dispar					M
Macrobiotus echinogenitus	r				
Macrobiotus furciger		D			M
Macrobiotus harmsworthi	r				M
Macrobiotus hastatus			T		M
Macrobiotus hufelandii	r				M
Macrobiotus intermedius	r				
Macrobiotus islandicus	r				M
Macrobiotus macronyx			T		
Macrobiotus occidentalis		D			
Macrobiotus pullari		D			M
Macrobiotus richtersi					M
Hypsibius (Diphascon) alpinus					M
Hypsibius (Diphascon) arduifrons					M
Hypsibius (Diphascon) belgicae					M
Hypsibius (Diphascon) chilenensis					M
Hypsibius (Diphascon) oculatus					M
Hypsibius (Diphascon) pinguis					M
Hypsibius (Diphascon) scoticus					M
Hypsibius (Diphascon) spitzbergensis					M
Hypsibius (Hypsibius) conjungens					M
Hypsibius (Hypsibius) convergens		D			
Hypsibius (Hypsibius) dujardini		D	T		M
Hypsibius (Hypsibius) oberhaeuseri					M
Hypsibius (Hypsibius) zetlandicus					M
Hypsibius (Isohypsibius) augusti		D			
Hypsibius (Isohypsibius) granulifer					M
Hypsibius (Isohypsibius) prosostomus					M
var. cambrensis					M
Hypsibius (Isohypsibius) sattleri					M
Hypsibius (Isohypsibius) schaudinni		D			M
Milnesium tardigradum					M

Iceland Expedition) was also extracted in the field.

Tardigrades were mounted for microscopy as semi-permanent preparations in Gurrs ACS mountant (marketed by Searle Diagnostic, High Wycombe, Buckinghamshire, England). Hairs were used to support the coverslip and prevent undue specimen distortion. The coverslip was ringed with stiff Canada Balsam, to give the slide a degree of permanence. All observations were made on prepared material.

More than 150 samples from 28 localities were examined (Fig. 1). Tardigrades were recorded in 55% of all samples, representing 24 localities, and yielding 32 species, of these, three are included by Richters (1904), four are listed by De Coninck (1939), and 22 species, two varieties, one genus (*Milnesium*) and one subgenus (*Diphascon*) are recorded for the first time from Iceland (Table 1). In Tables 2, 3, and 4 the distribution of each species is provided on the basis of localities indicated in Fig. 1. Morphological and ecological notes are provided, together with a key for the identification of the 42 known Icelandic tardigrade species.

SYSTEMATIC ACCOUNTS

This section includes those species recorded for the first time from Iceland, together with others of particular interest. A complete synonomy is not provided for each species; references cited include those of the original author, the latest relevant sources of information, and previous Icelandic records (if appropriate).

Echiniscus (Echiniscus) blumi Richters

Echiniscus Blumi Richters, 1903:172
Echiniscus (Echiniscus) blumi Richters; Ramazzotti 1972:270

An abundant population of this species was found in moss from a waterfall (Mígandifoss, Eyjafjördur).

E. (E.) blumi is a morphologically diverse species with a wide distribution. Recorded from the British Isles and Greenland, but absent from parts of Scandinavia.

Echiniscus (Echiniscus) granulatus (Doyère)

Emydium granulatum Doyère, 1840:282.
Echiniscus crassus Richters, 1904:374.
Echiniscus (Echiniscus)? granulatus (Doyère); Tuxen 1941:2.
Echiniscus (Echiniscus) granulatus (Doyère); Ramazzotti 1972:290.

Richters (1904) provided an incomplete description of *E. crassus*, recorded in moss from Fáskrúdsfjördur; this species is now widely regarded as being synonymous with *E. (E.) granulatus*. During the present survey *granulatus* was recorded from Kötlufjall (964m) and around Mývatn.

Echiniscus (Echiniscus) merokensis Richters

Echiniscus merokensis Richters, 1904:500.
Echiniscus (Echiniscus) merokensis Richters; Ramazzotti 1972:312.

The commonest *Echiniscus* species throughout the study area. Occasionally found in large numbers, e.g. in moss from thufur crests (Mígandifoss, Eyjafjördur). The variety *suecicus* Thulin, 1911 was found once, sharing a sample with the typical form (lacking lateral filament B).

E. (E.) merokensis has a widespread distribution and has been recorded in the Arctic and Scandinavia.

Key to localities given in Table 2. The dates in brackets refer to the years when collections were made.

1 Knappsstadir, Fljót (1975).
2 Almenningsnöf, near Siglufjördur (1975).
3 Ólafsfjördur (1975).
4 Ólafsfjardarvatn (1975).
5 Lágheidi, Ólafsfjördur (1975).
6 Mígandifoss, Eyjafjördur (1975).
7 Dalvík, Eyjafjördur (1975).
8 Thorvaldsdalur, Staerri-Árskógur, Eyjafjördur (1969, 1975).

Table 2

The tardigrade fauna of eight localities in northern Iceland.

	1	2	3	4	5	6	7	8
Echiniscus (Echiniscus) blumi						X		
Echiniscus (Echiniscus) granulatus								
Echiniscus (Echiniscus) merokensis		X				X		
var. suecicus						X		
Echiniscus (Echiniscus) spitsbergensis								
Echiniscus (Echiniscus) wendti		X	X			X		
Echiniscus (Bryodelphax) parvulus								
Pseudechiniscus islandicus		X						
Pseudechiniscus suillus								
Pseudechiniscus tridentifer								X
Macrobiotus ambiguus								
Macrobiotus areolatus								
Macrobiotus dispar				X	X			X
Macrobiotus echinogenitus								
Macrobiotus furciger								X
Macrobiotus harmsworthi		X	X		X	X	X	X
Macrobiotus hastatus				X				
Macrobiotus hufelandii			X			X		
Macrobiotus intermedius								
Macrobiotus islandicus		X				X		X
Macrobiotus macronyx								
Macrobiotus occidentalis								
Macrobiotus pullari					X			
Macrobiotus richtersi								
Hypsibius (Diphascon) alpinus								X
Hypsibius (Diphascon) arduifrons								
Hypsibius (Diphascon) belgicae			X					
Hypsibius (Diphascon) chilenensis								
Hypsibius (Diphascon) oculatus						X		X
Hypsibius (Diphascon) pinguis								X
Hypsibius (Diphascon) scoticus							X	X
Hypsibius (Diphascon) spitzbergensis								
Hypsibius (Hypsibius) conjungens			X					
Hypsibius (Hypsibius) convergens								X
Hypsibius (Hypsibius) dujardini	X			X			X	X
Hypsibius (Hypsibius) oberhaeuseri			X					
Hypsibius (Hypsibius) zetlandicus								
Hypsibius (Isohypsibius) augusti								
Hypsibius (Isohypsibius) granulifer							X	X
Hypsibius (Isohypsibius) prosostomus	X			X				X
var. cambrensis				X				X
Hypsibius (Isohypsibius) sattleri								
Hypsibius (Isohypsibius) schaudinni								
Milnesium tardigradum			X	X			X	

Echiniscus (Echiniscus) wendti Richters

Echiniscus Wendti Richters, 1903:172.
Echiniscus (Echiniscus) wendti Richters; Ramazzotti 1972:375.

A tardigrade with characteristic cuticular sculpturing and lateral cirri A which usually measure 55—70% of the length of the body. Distribution within area restricted: in moss from boulders high (60m) on a sea cliff at Almenningsnöf; in moss and lichens from the splash zone at Ólafsfjördur; from a waterfall over a sea cliff (Mígandifoss) on Eyjafjördur. Often present in abundant populations.

E. (E.) wendti has a wide distribution, from the Arctic to the Antarctic. It is not noted as a colonizer of permanently wet habitats; the splash zone of the sea shore is utilized by few tardigrade species. In southern Europe it is more frequent at high altitude.

Echiniscus (Bryodelphax) parvulus (Thulin)

Echiniscus intermedius Murray, 1910:161.
Bryodelphax parvulus Thulin, 1928:221.
Echiniscus (Bryodelphax) parvulus (Thulin); Ramazzotti 1972:258.

Found in a moss mixture (*Rhacomitrium, Polytrichum*, and *Dicranum* species) on wet rock surfaces at Egilsstadir.

A small species, rarely exceeding 175 μm in length, which is easily overlooked, being colourless or greyish or only faintly reddish. The cuticular plates are often faintly delineated, making observation of the transversally divided 1st and 2nd median plates and the characteristically shaped third median plate difficult.

E. (B.) parvulus has a widespread, though spartan, distribution and can probably be regarded as a more southern species.

Pseudechiniscus islandicus Richters

Echiniscus islandicus Richters, 1904: 374.
Pseudechiniscus islandicus (Richters); Marcus 1928:111.
Pseudechiniscus islandicus (Richters); De Coninck 1939:197.
Pseudechiniscus islandicus (Richters); Tuxen 1941:2.
Pseudechiniscus islandicus (Richters); Ramazzotti 1972:638.

Since the description of this species by Richters (1904) it has only been recorded from Switzerland, Scotland, Shetland, and the Faeroes, and by De Coninck (1939). Ramazzotti (1972) describes *P. islandicus* as montane, yet all Icelandic specimens in the present survey derived from material collected at or near sea level, in moss from amongst grasses and sedges or on boulders. This highly characteristic species with prominently reticulate, cuticular sculpturing, massive lateral and pseudosegmental spines, and grand dimensions (often exceeding 500 μm body length), is not easily overlooked. Consequently its restricted distribution must indicate a narrow microhabitat range, possibly reflected in the northern aspect of all Icelandic collection sites.

Pseudechiniscus tridentifer Bartos

Pseudechiniscus tridentifer Bartos, 1935:140.
Pseudechiniscus tridentifer Bartos; Ramazzotti 1972:658.

Ramazzotti (1972) cites Reykjavik as one of only two localities where this species was known to occur; the other being the High Tatra, Carpathian Mountains (Czechoslovakia) at 1800—2300 m altitude. In northern Iceland *P. tridentifer* was found in two quite different habitats: in moss, subject to immersion along stream edges in Thorvaldsdalur, and from scree

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Key to localities given in Table 3. The dates in brackets refer to the years when collections were made.

9 Víkurbakki, Eyjafjördur (1969, 1975).
10 Kötlufjall, Staerri-Árskógur, Eyjafjördur (1969—1975).
11 Gáseyri, Eyjafjördur (1975).
12 River Hörgá, Eyjafjördur (1975).
13 Grenivík, Eyjafjördur (1975).
14 Grímsey (1975).
15 Ljósavatn (1975).
16 Godafoss (1975).

Table 3
The tardigrade fauna of eight localities in northern Iceland.

	9	10	11	12	13	14	15	16
Echiniscus (Echiniscus) blumi			X					
Echiniscus (Echiniscus) granulatus		X						
Echiniscus (Echiniscus) merokensis var. suecicus	X	X						
Echiniscus (Echiniscus) spitsbergensis								
Echiniscus (Echiniscus) wendti								
Echiniscus (Bryodelphax) parvulus								
Pseudechiniscus islandicus								
Pseudechiniscus suillus								
Pseudechiniscus tridentifer		X						
Macrobiotus ambiguus								
Macrobiotus areolatus	X							
Macrobiotus dispar	X	X						
Macrobiotus echinogenitus								
Macrobiotus furciger	X	X						
Macrobiotus harmsworthi	X		X					X
Macrobiotus hastatus								
Macrobiotus hufelandii	X							
Macrobiotus intermedius								
Macrobiotus islandicus		X						
Macrobiotus macronyx								
Macrobiotus occidentalis								
Macrobiotus pullari								
Macrobiotus richtersi								
Hypsibius (Diphascon) alpinus								
Hypsibius (Diphascon) arduifrons		X						
Hypsibius (Diphascon) belgicae						X		
Hypsibius (Diphascon) chilenensis								
Hypsibius (Diphascon) oculatus		X		X				
Hypsibius (Diphascon) pinguis		X						
Hypsibius (Diphascon) scoticus	X	X			X			
Hypsibius (Diphascon) spitzbergensis	X							
Hypsibius (Hypsibius) conjungens	X							
Hypsibius (Hypsibius) convergens								
Hypsibius (Hypsibius) dujardini	X	X	X	X	X		X	
Hypsibius (Hypsibius) oberhaeuseri	X		X					
Hypsibius (Hypsibius) zetlandicus		X						
Hypsibius (Isohypsibius) augusti								
Hypsibius (Isohypsibius) granulifer		X		X				
Hypsibius (Isohypsibius) prosostomus var. cambrensis			X					
Hypsibius (Isohypsibius) sattleri								
Hypsibius (Isohypsibius) schaudinni								
Milnesium tardigradum								

slopes on Kötlufjall. It is generally considered to be a waterloving species.

Macrobiotus areolatus Murray

Macrobiotus echinogenitus (form A) Richters, 1904:503 part.
Macrobiotus areolatus Murray, 1910:167.
Macrobiotus areolatus Murray; Morgan 1976:612.

Individual tardigrades and eggs corresponding to *M. areolatus* were found in only one locality, Víkurbakki, Eyjafjördur.

Macrobiotus dispar Murray

Macrobiotus dispar Murray, 1907:6.
Macrobiotus dispar Murray; Ramazzotti 1972:546.

An aquatic species, with a cosmopolitan distribution (Ramazzotti 1972). Found in seven localities in northern and eastern Iceland. *M.dispar* is very similar to *Macrobiotus macronyx* Dujardin and early workers separated the two species on the basis of the eggs which, typically, are smooth and laid in the moulted cuticle in *macronyx*, but spiny and laid freely in *dispar*. Tuxen (1941) did not have eggs available to aid with his identification of *macronyx*, utilizing instead proportional lengths of the pharyngeal rods for determination; this latter character is not generally accepted. Typically, the cuticle of *macronyx* is smooth, while all or part of the dorsal cuticle of *dispar* is granulate, a feature readily observed using oil immersion. Adults of *dispar* may have two dorso-caudal humps. Without the benefit of additional specimens or checking the material on which Tuxen based his identification, *macronyx* must stand as a member of the Icelandic fauna, though there must be some doubt as to its status.

Macrobiotus furciger Murray

Macrobiotus furciger Murray, 1907:852.
Macrobiotus furciger Murray; De Coninck 1939:201.
Macrobiotus furciger Murray; Tuxen 1941:3.
Macrobiotus furciger Murray; Ramazzotti 1972:-552.

A species with a widespread, if spartan, distribution. *M. furciger* prefers moss subject to periodic desiccation and is rarely found in permanently wet habitats. In northern Iceland the species figured prominently in an intensive survey of thufur. Moss samples were taken from the top of thufur mounds and the hollows. Without exception, no moss sample from a hollow yielded *M. furciger*, all specimens obtained came from the tops of thufur hummocks. This same pattern of distribution was displayed by *E. (E.) merokensis* while *M. dispar* and *Hypsibius (Diphascon) scoticus* (Murray) were confined to the hollows (Table 5). Conditions at the top of hummocks are likely to be more severe than in the hollows. During the winter months needle ice formation, coupled with strong winds, could result in the removal of frozen or small freeze-dried particles from the mound. Disintegration of thufur mounds in this way could provide cryptobiosed tardigrades with an active wind dispersal mechanism.

Macrobiotus harmsworthi Murray

Macrobiotus echinogenitus (form A) Richters, 1904:503 part.
Macrobiotus echinogenitus Richters, 1904:375.
Macrobiotus harmsworthi Murray, 1907:677.
Macrobiotus harmsworthi Murray; Marcus 1936:-169.
Macrobiotus harmsworthi Murray; Tuxen 1941:4.
Macrobiotus harmsworthi Murray; Morgan 1976:-614.

Key to localities given in Table 4. Dates in brackets refer to the years when collections were made.

17 Mývatn (1969, 1975).
18 Miklavatn (1977).
19 Egilsstadir (1977).
20 Höfn (1977).
21 Djúpivogur (1977).
22 Jökulsárhlíd gorge (1977).
23 Thistilfjördur (1977).
24 Dyrfjöll (1977).

Table 4
The tardigrade fauna of eight localities in northern and eastern Iceland

	17	18	19	20	21	22	23	24
Echiniscus (Echiniscus) blumi	X							
Echiniscus (Echiniscus) granulatus	X							
Echiniscus (Echiniscus) merokensis var. suecicus			X					
Echiniscus (Echiniscus) spitsbergensis								
Echiniscus (Echiniscus) wendti								
Echiniscus (Bryodelphax) parvulus			X					
Pseudechiniscus islandicus				X				
Pseudechiniscus suillus								
Pseudechiniscus tridentifer								
Macrobiotus ambiguus								
Macrobiotus areolatus								
Macrobiotus dispar		X						X
Macrobiotus echinogenitus								
Macrobiotus furciger								
Macrobiotus harmsworthi	X							X
Macrobiotus hastatus								
Macrobiotus hufelandii	X	X	X	X		X		
Macrobiotus intermedius								
Macrobiotus islandicus								X
Macrobiotus macronyx								
Macrobiotus occidentalis								
Macrobiotus pullari								
Macrobiotus richtersi		X	X	X	X	X	X	X
Hypsibius (Diphascon) alpinus								
Hypsibius (Diphascon) arduifrons		X						
Hypsibius (Diphascon) belgicae								
Hypsibius (Diphascon) chilenensis		X						
Hypsibius (Diphascon) oculatus								
Hypsibius (Diphascon) pinguis								
Hypsibius (Diphascon) scoticus		X	X		X			
Hypsibius (Diphascon) spitzbergensis								
Hypsibius (Hypsibius) conjungens			X					
Hypsibius (Hypsibius) convergens								
Hypsibius (Hypsibius) dujardini		X				X	X	X
Hypsibius (Hypsibius) oberhaeuseri	X							
Hypsibius (Hypsibius) zetlandicus								
Hypsibius (Isohypsibius) augusti								
Hypsibius (Isohypsibius) granulifer								X
Hypsibius (Isohypsibius) prosostomus var. cambrensis	X		X					
Hypsibius (Isohypsibius) sattleri			X					
Hypsibius (Isohypsibius) schaudinni		X						
Milnesium tardigradum								

Adults and eggs of this controversial species were common in mosses and lichens sampled during the present survey.

Richters does not give a comprehensive description of his specimens yet Marcus supposed that at least a part of the former's Icelandic material answered the description of *harmsworthi*. Recently, a great deal of attention has been devoted to the structure of the eggs of *harmsworthi* and the morphologically similar *M. areolatus* and *M. richtersi* (Hallas 1972, Morgan 1976). This investigation provided no new information on whether the three species should be united as one, or maintained as distinct. It is likely that only controlled culturing experiments from isolated eggs will resolve this issue.

Macrobiotus hastatus Murray

Macrobiotus hastatus Murray, 1907:663.
Macrobiotus hastatus Murray; Tuxen 1941:7.
Macrobiotus hastatus Murray; Ramazzotti 1972:-560.

A single adult specimen with six eggs visible inside it, several displaying the characteristic projections, from moss subject to immersion at the edge of Ólafsfjardarvatn. Tuxen (1941) recorded adults of this species but did not observe eggs.

Macrobiotus hufelandii Schultze

Macrobiotus Hufelandii Schultze, 1834:5—7.
Macrobiotus hufelandii Schultze; Tuxen 1941:6.
Macrobiotus hufelandii Schultze; Ramazzotti 1972:563.

M. hufelandii is generally accepted to be the most common tardigrade, occurring everywhere. However, while records of the species in Iceland are widespread numbers are low; *Hypsibius (Hypsibius) dujardini* (Doyère) is far more abundant. Hallas (1977) detailed considerable variation in the egg structure, which is also a feature of Icelandic material.

Macrobiotus islandicus Richters

Macrobiotus islandicus Richters, 1904:376.
Macrobiotus islandicus Richters; Ramazzotti 1972:571.

M. islandicus is a species which can attain a size of 500 μm and more. The pharyngeal bulb and the rods it contains, often appears disproportionately large for the size of the body. This species is often confused with *Macrobiotus coronifer* Richters, not yet found in Iceland, which has a toothed depression at the base of each claw. During the present survey small numbers of *islandicus* were recovered from moss and lichen collected from sea level up to 964m, including permanently wet habitats.

Confined in its distribution to the Northern Hemisphere, *islandicus* may only occur on mountain tops in more southern latitudes.

Macrobiotus pullari Murray

Macrobiotus pullari Murray, 1907:663.
Macrobiotus pullari Murray; De Coninck 1939:-206.
Macrobiotus pullari Murray; Tuxen 1941:6.
Macrobiotus pullari Murray; Ramazzotti 1972:-592.

An aquatic species, probably cosmopolitan in distribution. Recorded from only one location during this survey, in moss from a stream near Ólafsfjördur. Several eggs present, but these are virtually indistinguishable from those of *M. dispar*.

Macrobiotus richtersi Murray

Macrobiotus richtersi Murray, 1911:7.
Macrobiotus richtersi Murray; Ramazzotti 1972:-595.
Macrobiotus richtersi Murray; Morgan 1976:615.

In mosses and lichens collected from localities in eastern Iceland. This restricted distribution of adults and eggs corresponding to *M. richtersi* could be significant with regard to the controversy over the status of *areolatus*, *harmsworthi*, and *richtersi*.

Hypsibius (Diphascon) alpinus (Murray)

Diphascon alpinum Murray, 1906:29.

Hypsibius (Diphascon) alpinus (Murray); Morgan & King 1976:95.

A cosmopolitan species, recorded here for the first time from Iceland. In moss from the flood plain of the river Thorvaldsdalsá at the point where it enters Eyjafjördur.

Hypsibius (Diphascon) arduifrons Thulin

Diphascon arduifrons Thulin, 1928:257.
Hypsibius (Diphascon) arduifrons (Thulin); Ramazzotti 1972:410.

H. (D.) arduifrons has been recorded in mosses from relatively few European localities, although these include Swedish Lapland. Its distribution in Iceland is confined to two areas, Mývatn and Víkurbakki, Eyjafjördur. The species may be confused with *Hypsibius (Diphason) scoticus* Murray, the most common Icelandic member of the sub-genus *Diphascon.*

Hypsibius (Diphascon) belgicae (Richters)

Diphascon belgicae Richters, 1911: 17
Hypsibius (Diphascon) belgicae (Richters); Ramazzotti 1972:411.

An uncommon species, which has been recorded previously from northern latitudes (Bear Island, and Spitsbergen). All Icelandic specimens derived from lichen collections made in the splash zone of the sea shore near Ólafsfjördur, and on Grímsey.

Hypsibius (Diphascon) chilenensis (Plate)

Diphascon chilenense Plate, 1889:537.

Hypsibius (Diphascon) chilenensis (Plate); Morgan & King 1976:102.

Found in *Polytrichum* species, near Miklavatn, eastern Iceland. This cosmopolitan species can be confused with *H. (D.) alpinus*; *chilenensis* has macroplacoids of equal length and a short oval pharyngeal bulb.

Hypsibius (Diphascon) oculatus (Murray)

Diphascon oculatum Murray, 1906:216.
Hypsibius (Diphascon) oculatus (Murray); Morgan & King 1976:110.

One of the commoner Icelandic *Diphascon* species recorded in four localities, in freshwater and terrestrial situations, at altitudes ranging from just above sea level to 964m.

H. (D.) oculatus is found extensively throughout the Northern Hemisphere, including Scandinavia.

Hypsibius (Diphascon) pinguis Marcus

Hypsibius (Diphascon) pinguis Marcus, 1936:308.
Hypsibius (Diphascon) pinguis Marcus; Morgan & King 1976:113.

This species was only recovered from

Table 5
The distribution of tardigrade species in thufur

	HUMMOCKS	HOLLOWS
M. furciger	+	—
E. (E.) merokensis	+	—
H. (H.) oberhaeuseri	+	+
H. (H.) dujardini	+	+
M. harmsworthi	+	+
M. hufelandii	+	+
M. dispar	—	+
H. (D.) scoticus	—	+

material collected in Eyjafjördur: in moss from the edge of snow and ice patches at 800m on Kötlufjall; from aquatic mosses along river Thorvaldsdalsá. In several samples *pinguis* co-occurred with *H. (D.) oculatus* and *H. (D.) scoticus* and is readily confused with the latter; *pinguis* has shorter, more angular macroplacoids and a short, oval-shaped pharyngeal bulb.

Hypsibius (Diphascon) scoticus (Murray)

Diphascon scoticum Murray, 1905:162.
Hypsibius (Diphascon) scoticus (Murray); Morgan & King 1976:118.

The commonest *Diphascon* species found in Iceland (see tables 2, 3, and 4) occurring in a wide range of microhabitats and not confined to the soil as in Denmark (Hallas & Yeates 1972). This cosmopolitan species can display great variability with regard to the size, shape and arrangement of the pharyngeal bulb.

Hypsibius (Diphascon) spitzbergensis (Richters)

Diphascon spitzbergense Richters, 1903:172.
Hypsibius (Diphascon) spitzbergensis (Richters); Morgan & King 1976:119.

An abundant population extracted from soil and moss collected in late snow hollows at Víkurbakki, Eyjafjördur.

This species has a widespread distribution throughout the Northern Hemisphere.

Hypsibius (Hypsibius) conjungens Thulin

Hypsibius conjungens Thulin, 1911:37.
Hypsibius (Hypsibius) conjungens Thulin; Morgan & King 1976:103.

H. (H.) conjungens is an uncommon species with a widespread distribution throughout the Northern Hemisphere. Recorded in three localities in Iceland, although numbers were low. Principal characteristic of the species is the length of the buccal tube between the stylet supports and the pharyngeal bulb, which in *conjungens* is about half the length of the bulb. Thus *H. (H.) conjungens* is intermediate between the normal *Hypsibius* and *Diphascon* conditions.

Hypsibius (Hypsibius) dujardini (Doyère)

Macrobiotus Dujardin Doyère, 1840:288.
Hypsibius (Hypsibius) dujardini (Doyère); Morgan & King 1976:104.

H. (H.) dujardini, a new Icelandic record, was recorded extensively during this survey. One of the commonest Icelandic tardigrades, found in a wide range of microhabitats, its absence from the collections of previous workers is surprising. Hallas (1977) regards *Hypsibius (Hypsibius) convergens* (Urbanowicz), a species with a spartan distribution which includes Iceland, as a synonym of *dujardini*.

Hypsibius (Hypsibius) oberhaeuseri (Doyère).

Macrobiotus Oberhaeuser Doyère, 1840:286.
Hypsibius (Hypsibius) oberhaeuseri (Doyère); Ramazzotti 1972:468.

Species found in only a few localities, in both fresh water and terrestrial situations. The characteristic cuticular granulation readily visible but most individuals lacked any traces of cuticular pigmentation. Largest specimens only 300μm, the remainder much smaller.

H. (H.) oberhaeuseri is a cosmopolitan species with an unusual distribution in northern latitudes: common in southern Britain (Morgan 1976), southern Sweden (Thulin 1911), and southern Finland (Hallas 1977) but rare in the northern parts of these countries. The Icelandic records do not conflict seriously with these previous reports; diminished size and lack of pigmentation could reflect curtailed growth and development under sub-optimal conditions.

Hypsibius (Hypsibius) zetlandicus (Murray)

Macrobiotus zetlandicus Murray, 1907:659.
Hypsibius (Hypsibius) zetlandicus (Murray); Ramazzotti 1972:475.

A single specimen of this highly characteristic species in moss from 250 m on Kötlufjall, Eyjafjördur. The deep indentation on the exterior surface of each macroplacoid does not permit confusion with other species.

H. (H.) zetlandicus has been found in Greenland, Spitsbergen, Shetland, Finland and the British Isles, suggesting a restricted northern distribution.

Hypsibius (Isohypsibius) granulifer (Thulin)

Isohypsibius granulifer Thulin, 1928:251.
Hypsibius (Isohypsibius) granulifer (Thulin); Ramazzotti 1972:494.

Common in freshwater mosses in a few restricted localities. Characteristic cuticular granulations often complemented by a dark brown pigmentation. *H. (I.) granulifer* is probably cosmopolitan in distribution, although rarely recorded in northern latitudes.

Hypsibius (Isohypsibius) prosostomus (Thulin)

Hypsibius tetradactylus (Greef); Thulin 1911:32.
Isohypsibius prosostomus Thulin, 1928: 240, 250.
Hypsibius (Isohypsibius) prosostomus (Thulin); Ramazzotti 1972:512.

H. (I.) prosostomus, common in freshwater mosses in northern Iceland, has been widely recorded throughout Scandinavia. Many Icelandic individuals failed to show a complete complement of chitinous bars on the legs, an important diagnostic feature. A few mixed populations with the normal form and the variety *cambrensis*, recorded here for the first time outside the British Isles.

Hypsibius (Isohypsibius) sattleri (Richters)

Macrobiotus Sattleri Richters, 1902:12.
Hypsibius (Isohypsibius) sattleri (Richters); Ramazzotti 1972:515.

A single specimen in moss from dwarf birch woodland (*Betula nana*) near Egilsstadir. There is some confusion regarding morphological variability displayed by this species. The Icelandic individual possessed characteristic swellings and spines and faint traces of reticulate cuticular sculpturing. The species has been recorded throughout Scandinavia.

Milnesium tardigradum Doyère

Milnesium tardigradum Doyère, 1840: 282—284.
Milnesium tardigradum Doyère; Ramazzotti 1972:608.

A large species which may attain 1200 μm in length, although Icelandic material did not exceed 870μm. Specimens obtained during this survey were found mainly in lichens, rarely in moss, from Ólafsfjördur and Eyjafjördur. Such restricted habitat and location indicate how such a characteristic species could have been overlooked in previous surveys.

M. tardigradum has often been noted in association with *H. (H.) oberhaeuseri* (Morgan 1976) and Icelandic specimens occurred variously with *E. (E.) wendti*, *H. (H.) oberhaeuseri*, and *H. (H.) conjungens*.

A KEY TO THE SPECIES OF ICELANDIC TARDIGRADA

1 Cephalic cirrus A and clavus present; body with characteristic dorsal plating (Fig. 2A) 2
— Without cirrus A and clavus; no dorsal plating (Fig. 3A) 11
2(1) With a pseudosegmental plate inserted between the terminal plate and the second paired plates or third median plate (GENUS *PSEUDECHINISCUS*, Fig. 2D) 3
— Pseudosegmental plate absent; the second paired plates or the third median plate are followed by the terminal plate 5
3(2) With lateral appendages B, C, D (spines), and E (filament) 4
— Without lateral appendages B, C, D, E. Legs long with a punctate region, near the base, on the upper surface of each ..... *Pseudechiniscus suillus.*
4(3) A pair of long (ca 55μm), robust dorsal spines at the posterior margin of the pseudosegmental plate .... *Pseudechiniscus islandicus.*
— A pair of long spines at positions Cd and

Dd, with short spines or small teeth sometimes present on the pseudosegmental plate. A large triangular tooth, with a much enlarged base in place of the dentate collar on the fourth pair of legs ..... *Pseudechiniscus tridentifer.*

5(2) Median plates undivided (SUBGENUS *ECHINISCUS*) 6

— Median plates 1 and 2 divided transversally, the third undivided and frequently well-developed. (SUBGENUS *BRYODELPHAX*) .... *Echiniscus (B.) parvulus.*

6(5) With one or more lateral appendages B, C, D, E 7

— Body without lateral appendages B, C, D, E. Lateral cirri A long (over half body length). Cuticular sculpturing of small, round, finely granulate areas outlined by larger granular elements . ..... *Echiniscus (E.) wendti.*

7(6) With lateral appendages at three positions 8

— With lateral appendages all filamentous, at four positions. Cd a filament or short spine which is not inserted exactly at the posterior angle of the first paired plates but a little nearer the mid-line of the animal. Dd is a short spine or a triangular tooth .... *Echiniscus (E.) merokensis* var. *suecius.*

8(7) With lateral filament B 9

— Without lateral filament B 10

9(8) Median plate 3 is present. Lateral appendages B, C, D are filaments. Cd is usually a long filament whilst Dd is a medium length to short spine .... *Echiniscus (E.) blumi.*

— Median plate 3 is absent. Lateral appendages B, C, D are filaments, increasing in size from B to D. Cd is typically a long spine, Dd a short recurved spine .... *Echiniscus (E.) spitsbergensis.*

10(8) All lateral appendages, C, D, and E, are filaments. Terminal plate always, though often indistinctly, facetted. Cd and Dd are usually long and short spines respectively, but either can be a filament or occasionally absent .... *Echiniscus (E.) merokensis.*

— Lateral appendages C and D are filaments whilst E is a short spine. The terminal plate is not facetted. Cd and Dd are spines of about equal length; exceptionally Dd may be missing ... . *Echiniscus (E.) granulatus.*

11(1) Animal with six rostral papillae around the buccal aperture and two other papillae laterally, or rostrolaterally. The pharyngeal bulb is pear-shaped and lacks placoids .. *Milnesium tardigradum.*

— Without papillae around the buccal aperture. Pharyngeal bulb with placoids 12

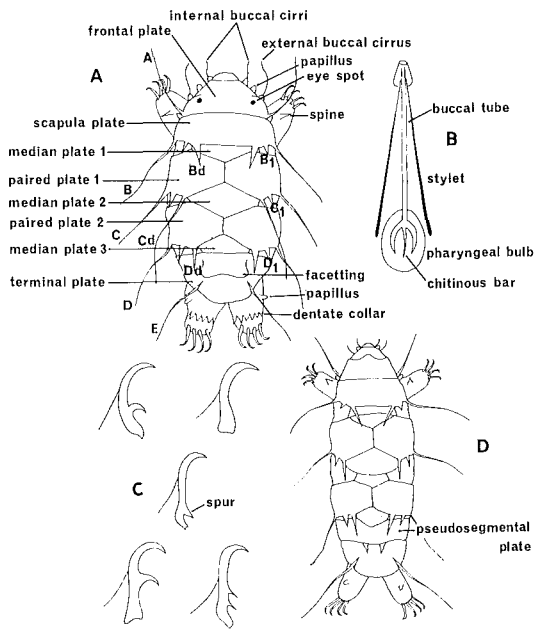

Fig. 2.
A GENERALIZED *ECHINISCUS.*
B *ECHINISCUS* PHARYNGEAL APPARATUS
C *ECHINISCUS* CLAWS
D GENERALIZED *PSEUDECHINISCUS*

12(12) The two double claws on each leg are of equal size and similar; they are symmetrical about the median plane of the foot (GENUS *MACROBIOTUS*, Fig. 3 F, G, H) 13

— The two double claws of each leg are more or less dissimilar in size and shape and always asymmetrical with respect to the median plane of the foot (GENUS *HYPSIBIUS*, Fig. 3 I, J,K) 39

13(12) Cuticle wholly or partly granulate or punctate, and/or with swellings, or with dark irregularly shaped pigment granules in the hypodermis 14

— Cuticle smooth and featureless, or appearing so, at the most ornamented with small, spherical or oval highly refractive points or "pearls" 18

14(13) The two arms of each double claw diverge at their common base, i.e. form a V (*echinogenitus* type, Fig. 3 F) or else the principal arm of each double claw is longer than the secondary and is at about right angles to it, a *macronyx* type claw (Fig. 3 H) 15

— The two arms of each double claw are united as one from the base to about the middle of their maximum height and then diverge, i.e. form a Y (*hufelandii* type, Fig. 3 G) 16

15(14) Cuticular sculpturing confined to a swelling, or granule, or papillus on each of the legs. Pharyngeal bulb with two macroplacoids and a microplacoid. Claws of the *echinogenitus* type, i.e. a V ..... *Macrobiotus echinogenitus.*

— Cuticle finely granulate and with two dorsal or dorsolateral swellings between

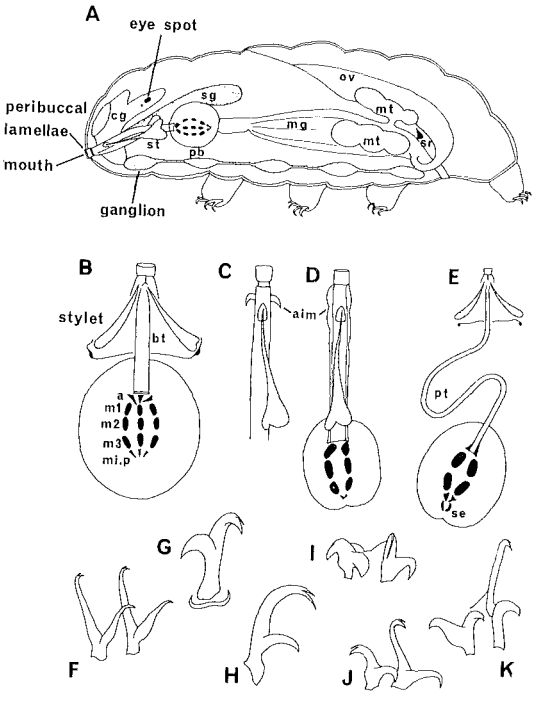

Fig. 3.

A GENERALIZED *MACROBIOTUS*
cg — cerebral ganglion
mg — midgut
mt — Malpighian tubule
ov — ovary
pb — pharyngeal bulb
sg — salivary gland
sr — seminal receptacle
st — stylet

B *MACROBIOTUS* PHARYNGEAL APPARATUS
a — apophysis
bt — buccal tube
m1, m2, m3 — macroplacoids
mi.p — microplacoid

C, D *HYPSIBIUS* PHARYNGEAL APPARATUS
aim — appendages for insertion of muscles

E *DIPHASCON* PHARYNGEAL APPARATUS
pt — pharyngeal tube
se — septulum

F *ECHINOGENITUS* TYPE CLAW

G *HUFELANDII* TYPE CLAW

H *MACRONYX* TYPE CLAW

I *CALOHYPSIBIUS* TYPE CLAW

J *ISOHYPSIBIUS* TYPE CLAW

K *HYPSIBIUS* TYPE CLAW

legs 3 and 4. Pharyngeal bulb with two macroplacoids but no microplacoid. Claws of the *macronyx* type .... *Macrobiotus dispar.*

16(14) Sculpturing of the cuticle comprising of small variously arranged round or oval points or pearls 17

— Sculpturing consists of dark brown or black pigment granules scattered irregularly in the hypodermis and found most densely at the caudal end of the body. Pharyngeal bulb a short oval shape, with apophysis and two rod-like macroplacoids, the first of which is longer than the second and may be throttled so that it appears divided in two or is actually so. Microplacoid present. Projections of the egg are shaped like inverted egg cups .... *Macrobiotus hufelandii.*

17(16) The pharyngeal bulb contains two club-shaped macroplacoids, the first up to twice the length of the second and having a slight median constriction. There may or may not be a microplacoid. The cuticle is scattered with small round or oval points, more or less regularly dispersed. The eggs are covered with small, delicate, isolated aculei, which have normal conical bases, but are bent and undivided at their apices ..... *Macrobiotus occidentalis.*

— The pharyngeal bulb contains two rod-shaped macroplacoids, the first longer than the second but rarely with a median constriction. Microplacoid absent. The cuticle is strewn with minute points or circles, well spaced out and which may be irregularly arranged in transverse bands over the dorsal and lateral surfaces. The projections of the egg are narrow based cones their apices often bearing 2—6 accessory points ..... *Macrobiotus islandicus.*

18(13) With two macroplacoids in the pharyngeal bulb 19

— With three macroplacoids in the pharyngeal bulb 28

19(18) The principal arm of each double claw is longer than the secondary and is at about right angles to it, i.e. a *macronyx* type claw (Fig. 3 H). Generally aquatic tardigrades 20

— The principal and secondary arms of each double claw are of about equal length, i.e. *hufelandii* and *echinogenitus* type claws (Fig. 3 F, G) 22

20(19) The eggs are smooth, oval (greatest diameter up to 60μm) and from 15 to 17 are deposited in the old cuticle .... *Macrobiotus macronyx.*

— The eggs are spherical, have a sculpted surface, and are laid free 21

21(20) The projections of the egg are either pointed tubercles with polygonal bases or mammary-shaped structures; they are in close contact at their bases. Egg diameter from 115—150μm including the projections .. *Macrobiotus ambiguus.*

— The projections of the egg are cone-like and well spaced out so that a region of the shell remains visible between them. Egg diameter about 90μm including projections ..... *Macrobiotus dispar.*

22(19) The two arms of each double claw diverge at their common base, i.e. form a V (*echinogenitus* type, Fig. 3 F) ... 23

— The two arms of each double claw are united as one from the base to about the middle of their maximum height and then diverge, i.e. form a Y (*hufelandii* type, Fig. 3 G) 25

23(22) Microplacoid present. The pharyngeal bulb contains two macroplacoids of about equal length though the first may be slightly longer and with a median constriction. Exceptionally each of the legs may bear a swelling, or granule, or papillus. Projections of the egg shaped like onion bulbs, often thread-like distally and rather sparsely distributed; alternatively they may be hemispherical ..... *Macrobiotus echinogenitus.*

— Microplacoid absent. Legs without a

swelling, granule or papillus. Projections of egg not as above 24

24(23) Projections of the egg in the shape of rods, calyxes, or Fleur-de-Lys, which are always partially immersed in a hyaline, external zone of the shell. Pharyngeal bulb with two rod-like macroplacoids, the first of which may or may not have a median constriction. *Macrobiotus hastatus.*

— Projections of the egg in the shape of small conical tubercles or mammary-like structures, well spaced out so that the shell surface is visible between them. There may be a coronet of points at the base of each projection. Pharyngeal bulb with two macroplacoids, as elongate granules or rods, the first often with a median constriction ..... *Macrobiotus pullari.*

25(22) Microplacoid present 26

— Microplacoid absent 27

26(25) The macroplacoids are narrow rods, the first double the length of the second and usually with a median constriction. The cuticle is smooth and older individuals may be pigmented with brown or brown/black pigment granules may be scattered in the hypodermis at the caudal end. The projections of the egg are shaped like inverted egg cups, i.e. a truncate cone or hemispherical base, with or without a ring of small points, and a distal extremity enlarged as a flat or concave disc which may be notched at its margin ... *Macrobiotus hufelandii.*

— The macroplacoids are club-shaped, the first longer than the second and frequently with a slight median constriction. The cuticle is smooth or more or less regularly scattered with small round or oval points. Animal colourless, yellow or orange. The eggs are yellow to red-orange in colour and are covered with small, delicate aculei which are spaced apart and have normal conical bases but are bent and wrinkled at their apices ..... *Macrobiotus occidentalis.*

27(25) Macroplacoids broad rods, the first longer than the second and only rarely with a slight median constriction. Lunule at base of each double claw usually smooth but may be weakly dentate. Eggs 90—100μm in diameter excluding ornamentation, which consists of slender, upright cones, 11—13μm in height and often with 2—6 secondary points at their apices ..... *Macrobiotus islandicus.*

— Macroplacoids club-shaped; the first, up to twice the length of the second, is very close to the apophyses and may have a median constriction. There is a small, smooth lunule at the base of each double claw. The eggs (58—68μm in diameter) are yellow to red-orange in colour and are covered with small delicate aculei which are spaced apart and have normal conical bases but are bent and wrinkled at their apices ..... *Macrobiotus occidentalis.*

28(18) The two arms of each double claw split at their common base, i.e. form a V (*echinogenitus* type, Fig. 3 F) 29

— The two arms of each double claw remain united for about half the length of the principal arm and then diverge, i.e. form a Y (*hufelandii* type, Fig. 3 G) 31

29(28) Microplacoid present. The macroplacoids are rods and the third is the longest. Cuticle smooth but there may be a swelling, or granule, or papillus on each of the legs. Diameter of eggs from 65—160μm including the projections (from 14—32 in the optical section and 12—38μm in height), which are conical or onion-shaped structures, punctate or strewn with small papillae and frequently bent at the apex ..... *Macrobiotus echinogenitus.*

— Microplacoid absent. Without swelling, or granule, or papillus on each leg. Structure of egg not as above 30

30(29) The macroplacoids are short rods; the

first and second are of equal length and close together whilst the third is separate and usually shorter. The eggs possess a transparent external zone in which are immersed, either completely or in part, projections in the form of goblets, calyxes, or Fleur-de-Lys .... *Macrobiotus hastatus.*

— The macroplacoids are short, almost granular, rods and all three are equal in length. The eggs are without an external transparent zone and have projections in the shape of small conical tubercles or mammary-like structures, which are spaced out so that the shell is visible between them. There may be a ring of points at the base of each projection . ..... *Macrobiotus pullari.*

31(28) Body with a steep forehead, as in *Hypsibius* species, when viewed in profile. The pharyngeal bulb is almost spherical; the buccal tube is narrow (about 1μm) and bends at the entrance to the bulb. The projections of the egg resemble screws with large heads and may or may not be individually embedded in a hyaline capsule external to the shell ..... *Macrobiotus intermedius.*

— Body with a normal receding forehead, as in most *Macrobiotus* species, when seen in profile. The projections of the egg are goblet-shaped, mammary-like or conical 32

32(31) The third macroplacoid terminates caudally with a small spheroidal enlargement, or knob, or is lightly or otherwise constricted 33

— The third macroplacoid does not terminate with a small sphere or knob, and is not constricted 34

33(32) Eyespots present (rarely absent). Third macroplacoid generally longer than the two preceding ones though the first and third are often equal in length and the second is shorter. Microplacoid present and normal, at the most one third of the length of the third macroplacoid. Buccal tube ratio (that is the external diameter of the buccal tube divided by the length of the buccal tube) 0.10 to 0.145. Projections of the egg roughened bulbous cones, often truncated and with the shell between their bases appearing punctate ..... *Macrobiotus harmsworthi.*

— Eyespots absent (rarely present). The three macroplacoids sometimes equal in length, or the first and third the longest, or the third longest with the first and second shorter and equal in length. Microplacoid large and well developed, half the length of the third macroplacoid. Buccal tube ratio 0.167 to 0.2375. Projections of the egg roughened, blunt cones, the surface of the shell between the ornamentation showing a "plating" into small round or polygonal areas . ..... *Macrobiotus richtersi.*

34(32) All three macroplacoids are of approximately equal length 35

— The three macroplacoids are of unequal length with the third the longest and second the shortest 37

35(34) Eyespots absent (rarely present). Microplacoid large and well developed, half the length of the third macroplacoid. Projections of the egg roughened, blunt cones, the surface of the shell between the ornamentation showing a " plating" into small round or polygonal areas ..... *Macrobiotus richtersi.*

— Eyespots present. Microplacoid normal, less than half of the length of the third macroplacoid. Projections of the egg not blunt cones 36

36(35) The macroplacoids are rods or short oval granules. The principal arm of each double claw bears very robust accessory points. Projections of the egg cone-like, dichotomously branched and denticulate at the apex .... *Macrobiotus furciger.*

— The macroplacoids are rods. The principal arm of each double claw with normal, almost insignificant, accessory

points. Projections of the egg in the shape of inverted egg cups, i.e. with a hemispherical base and the distal extremity capped by a large disc, flat or concave, and which may be notched at the margin ..... *Macrobiotus hufelandii.*

37(34) Microplacoid absent or minute. Projections of the egg smooth, incurved, broad-based cones, pointed distally, giving the egg a stellate appearance. The shell between projections is " plated" ..... *Macrobiotus areolatus.*

— Microplacoid present and often exceptionally well developed. Projections of the egg roughened, truncated cones, with the shell between them sometimes "plated" 38

38(37) Eyespots present (rarely absent). Microplacoid normal, at the most one third of the length of the third macroplacoid. Buccal tube ratio (that is the external diameter of the buccal tube divided by the length of the buccal tube) 0.10 to 0.145. Projections of the egg roughened bulbous cones, often truncated, with the shell between their bases appearing punctate .... *Macrobiotus harmsworthi.*

— Eyespots absent (rarely present). Microplacoid large and well developed, half the length of the third macroplacoid. Buccal tube ratio 0.167 to 0.2375. Projections of the egg roughened blunt cones, the surface of the shell between the ornamentation showing a "plating" into small round or polygonal areas . ..... *Macrobiotus richtersi.*

39(12) The buccal tube between the stylet supports and the bulb is flexible (the so-called pharyngeal tube portion) and ıt least equal in length to that of the bulb, rarely smaller. (SUB-GENUS *DIPHASCON*, Fig. 3 E) 40

— The buccal tube between the stylet supports and the bulb is rigid and its maximum length is equal to about half that of the bulb or slightly more (SUB-GENERA *HYPSIBIUS* AND *ISOHYPSIBIUS,* Fig. 3 C, D) 48

40(39) Cuticle with a dense, fine granulation in the caudal region of the body .... *Hypsibius (Diphascon) oculatus.*

— The cuticle is smooth and unsculptured 41

41(40) The flexible portion of the buccal tube is wide (minimum diameter 3μm). The pharyngeal bulb has two rod-like macroplacoids, the second x2 to x3 the length of the first. Microplacoid present, septulum absent. Length of animal up to 450μm; body slender and elongate .. *Hypsibius (Diphascon) spitsbergensis.*

— The flexible portion of the buccal tube is narrow (maximum diameter 2.5μm). Two or three macroplacoids in pharyngeal bulb 42

42(41) With two macroplacoids in pharyngeal bulb 43

— With three macroplacoids in pharyngeal bulb 44

43(42) Macroplacoids short rounded rods or granules; the first often equal to the length of the second or longer (up to x2). Flexible portion of the pharyngeal tube narrow and about twice the length of the bulb (which has a ratio of length to breadth of 1.3:1), frequently undulating or looping. Cuticle generally smooth, but there may be a finely granulate caudal region (often indistinct) ..... *Hypsibius (Diphascon) oculatus.*

— Macroplacoids long, slender rods, the first about half the length of the second. The pharyngeal bulb is ovoidcylindrical, its length more than double its breadth . *Hypsibius (Diphascon) belgicae.*

44(42) Pharyngeal bulb containing microplacoid and septulum 45

— Pharyngeal bulb lacking microplacoid and septulum. A row of three macroplacoids takes up 50—55% of the length of the bulb, which has a ratio of length to breadth of 1.8:1. The body is broad

posteriorly and tapers sharply towards the head from the 2nd pair of legs. Length of animal up to 285μm .... *Hypsibius (Diphascon) arduifrons.*

45(44) Three macroplacoids short, rounded rods or granules of about equal dimensions and often almost touching. Pharyngeal tube about x1½ the length of the oval bulb (ratio of length: breadth of 1.5:1 or less). Double claws slender and short with little notable difference between them .... *Hypsibius (Diphascon) chilenensis.*

— Macroplacoids of different lengths and double claws of each leg markedly dissimilar 46

46(45) The macroplacoids are elongate granules or short rods. The flexible section of the pharyngeal tube is much greater in length than the oval bulb, and may be looped .. *Hypsibius (Diphascon) alpinus.*

— The macroplacoids are rods. The flexible section of the pharyngeal tube is about equal in length to that of the bulb, or may be a little more 47

47(46) The pharyngeal bulb is an elongate oval (ratio of length to breadth of 2:1) and often wider caudally. Length of animal up to 462μm, body thin and slender . ..... *Hypsibius (Diphascon) scoticus.*

— The pharyngeal bulb is a short oval (ratio of length to breadth of 1.2—1.3:1). Length of animal up to 407μm, body broad and stumpy, with short legs ..... *Hypsibius (Diphascon) pinguis.*

48(39) Cuticle of the body, but not always that of the legs, smooth 49

— Cuticle of the body at least partially sculptured, with humps and/or various types of granulation 57

49(48) Two macroplacoids in pharyngeal bulb 50

— Three macroplacoids in pharyngeal bulb 54

50(49) The length of the buccal tube between the stylet supports and the bulb is a little more than half the length of the bulb. Eggs laid free, ovoid (26—30μm × 57μm), covered with flexible, not very sharp aculei. Animals up to 265μm in length; older individuals with brown pigment bands or spots .... *Hypsibius (Hypsibius) conjungens.*

— The length of the buccal tube between the stylets and the bulb is only half the length of the pharyngeal bulb, or less 51

51(50) Both macroplacoids have a deep indentation at about the middle of their exterior side .... *Hypsibius (Hypsibius) zetlandicus.*

— Both macroplacoids are smooth, or may be the first has a slight throttling, but never both with an indentation on their exterior side 52

52(51) The double claws of each leg are of about equal dimensions, at the most there only being a slight difference between them. Length of animal up to 900μm, although usually much less. An aquatic species which may occur in terrestrial situations .... *Hypsibius (Isohypsibius) augusti.*

— The double claws of any given leg have very different dimensions 53

53(52) Macroplacoids are slender rods of about equal length, or the first frequently with a throttling — a little longer than the second. Buccal tube 2μm in diameter. Microplacoid present. Two to nineteen smooth, oval eggs (51—73μm × 42—62μm) laid in the exuvium .... *Hypsibius (Hypsibius) dujardini.*

— The macroplacoids are wide rods, the first x1½ the length of the second. Buccal tube 1—1.7μm in diameter. Microplacoid absent. Lays 1—7 smooth eggs, oval or spherical (45—54μm in diameter), in the exuvium .... *Hypsibius (Hypsibius) convergens.*

54(49) The two double claws of each leg have similar or only slightly differing dimensions. Macroplacoids usually slender

rods, the first and third of equal length whilst the second may be shorter or longer. Cuticle smooth but there is often a blunt projection on each of the first three pairs of legs ..... *Hypsibius (Isohypsibius) augusti.*

— The two double claws of each leg have notably different dimensions 55

55(54) Buccal tube straight and the buccal aperture is terminal (as in *Macrobiotus* species). The first two macroplacoids are of about equal length whilst the third is shorter or longer. Microplacoid present. The first three pairs of legs bear a cuticular structure in the form of an oblique bar occurring near the base of the minor claw 56

— Buccal aperture positioned more ventrally, as is usual in the genus *Hypsibius.* Macroplacoids increase in length from the first to the third. Microplacoid may or may not be present. No chitinous bar on each of the first three pairs of legs ..... *Hypsibius (Isohypsibius) schaudinni.*

56(55) Cuticle smooth and featureless, no irregular dark brown pigment granules in hypodermis.... *Hypsibius (Isohypsibius) prosostomus.*

— Cuticle appearing smooth, but under oil immersion seen to be finely granulate. There are usually dark brown pigment granules in the hypodermis, which may be arranged in two irregular lines along the dorsal mid-line and strewn over the head and along the flanks ..... *Hypsibius (Isohypsibius) prosostomus* var. *cambrensis.*

57(48) With dorsal humps or swellings, irregularly dispersed or else in 8—9 transverse rows of four ..... *Hypsibius (Isohypsibius) sattleri.*

— Without dorsal humps or swellings as above 58

58(57) With two macroplacoids. Cuticle with a dense granulation and nine transverse and five longitudinal bands of chestnut brown pigment ..... *Hypsibius (Hypsibius) oberhaeuseri.*

— With three macroplacoids 59

59(58) Microplacoid present. A chitinous bar at the base of the minor claw on each of the first three pairs of legs. Cuticle finely granulate, with or without pigment granules in the hypodermis ..... *Hypsibius (Isohypsibius) prosostomus* var. *cambrensis.*

— Microplacoid absent. Cuticle covered in a regular pattern with granules which are larger on the dorsal and lateral surfaces. Double claws of each leg massive with a slender basal portion; principal and secondary arms of the external double claw very strongly curved ..... *Hypsibius (Isohypsibius) granulifer.*

CONCLUDING REMARKS

Tuxen (1941) stated that "18 species of Tardigrada are known from Iceland, but this is no doubt far from the actual number of species present" (p. 8). As a result of the present survey the Icelandic tardigrade fauna now comprises some 42 species, comparing favourably with other northern European countries. However, the restricted nature of sampling to date must mean that still more species await discovery. There are still no records of marine Tardigrada around the coast of Iceland; all marine sand samples collected from Eyjafjördur proved negative.

Details of substrate, host plant, and macrohabitat have traditionally been included with species descriptions in faunal surveys. As more records have become available many species with supposedly narrow ranges of tolerance have been shown to colonize a wide range of habitat types. Similarly, species with very local distributions have had their ranges extended, and eventually recognized as truly cosmopolitan; there are many such cosmopolitan species included amongst the Icelandic tardigrade fauna. Others, despite extensive collecting, continue to display restricted distributions

which are not readily explained in terms of climate, altitude, and host plant specificity. In view of the lifestyle of tardigrades and their probable dependance on wind dispersal mechanisms it is surprising that not all species are cosmopolitan.

Recently Hallas (1977) has suggested that the microhabitat could dictate the presence or absence of species. Successional changes in the state of development of host plants may result in corresponding increases or decreases in the range of microhabitats available, which will be reflected in diversity of tardigrade species present. This theory readily accounts for the often haphazard local distribution of tardigrades in mosses and lichens, and could explain the relative paucity of tardigrades in Icelandic lichens. In future it is envisaged that greater attention will be paid to the microhabitat requirements of tardigrades.

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