

Redescription of *Hypsibius antarcticus* (Richters, 1904), with some notes on *Hypsibius arcticus* (Murray, 1907) (Tardigrada)

(With 41 figures)

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Abstract: The tardigrade *Hypsibius antarcticus* (Richters, 1904) is redescribed based on type-material. Taxonomic confusion surrounding that species has resulted from inadequate original description and misleading additions (Richters 1904a, 1908a). All records of *H. antarcticus* from the Northern Hemisphere were verified and proved to be misidentifications. All records of another polar tardigrade, *Hypsibius arcticus* (Murray, 1907) from the Antarctic, have to be considered now as those of *H. antarcticus*. The taxonomic status of *H. arcticus* and its possible synonymy with *H. antarcticus* are discussed, but the question remains unsettled.

Keywords: Tardigrada, Antarctica, *Hypsibius antarcticus*, redescription.

Introduction

A considerable amount of confusion surrounds two polar tardigrades, *Hypsibius antarcticus* (Richters, 1904) and *Hypsibius arcticus* (Murray, 1907). The dispersal pattern of the two species is rather peculiar. *H. antarcticus* has been described from the Antarctic, but the majority of literature records refer to individuals in Europe. *H. arcticus* has been described from Arctic islands and belongs to the most often recorded tardigrades in Antarctica. By contrast, its records in the Northern Hemisphere are relatively rare.

Original descriptions of both these species, particularly that of *H. antarcticus*, are inadequate. The two taxa are morphologically similar and one cannot exclude the possibility that they are conspecific (Dougherty 1964, McInnes & Ellis-Evans 1987). However, a lack of data on whereabouts of their type-materials has been a major obstacle to solving that question. The Richters' collection was believed to had been destroyed during World War II (Dalenius & Wilson 1958: p. 403), at last as the mites are concerned. That suggested the loss of his other materials, including tardigrades. The only known limited tardigrade collection of Murray does not contain any slides of *H. arcticus* (Van der Land 1966,

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Morgan 1977) and the repository of his Antarctic material could not be traced (Ms. S. McInnes, in litt. 1988).

Recently, the remnants of the Richters' collection has been located (Dastych, 1990), including type-material of *H. antarcticus*. This finding sheds new light on the character-states of *H. antarcticus* and its relation to *H. arcticus*. The present paper re-describes *H. antarcticus*, discusses its distribution and taxonomic status of *H. arcticus*.

Materials and methods

Type-material of *Hypsibius antarcticus* comes from the Richters' collection deposited at the Senckenberg Museum, Frankfurt a. M. (Germany). Other tardigrades and their eggs examined were obtained on loan from several institutions: the Zoological Institute and Zoological Museum, University of Hamburg (material from the maritime and East Antarctica), the Zoological Museum, Copenhagen (Greenland, Sweden, West Spitsbergen, East Antarctica), British Antarctic Survey, Cambridge (the maritime Antarctic). Additionally, I examined material from my own collection (the maritime and Continental Antarctica) and one specimen from Norway, identified as *H. antarcticus* (the Maucci's collection in the Civic Museum of Natural History, Verona). Unfortunately I failed to trace the materials identified as *H. antarcticus* by Carlzon (1909), Weglarska (1959), Rudescu (1964), and Robotti (1972). The Sudzuki's material (1964, 1979) has been lost recently (Dr. Sudzuki, in litt. 1988).

Tardigrades and their eggs housed in the above collections are in various stages of preservation. They are mounted on slides in one of the following media: formalin, glycero-gelatine, Aqualite, polyvinyl-lactophenol, Hoyer's or Faure's mountant. All observations were carried out and illustration were made under phase and Nomarski contrast.

Historical perspective

Macrobotus antarcticus was described by Richters (1904a) from Gaussberg in East Antarctica. It is the first tardigrade recorded from the Antarctic. The original description is very short and lacks illustrations. Richters suggested the absence of processes on the egg shell and a sticky surface as important specific characters. He pointed out (op. cit.) that the eggs either were adhered to the moss leaves or were covered with detritus or (Richters 1904b) mineral particles. Richters gave a more exact description of the taxon along with the first figures in another paper (1908a). Then he recorded the occurrence of macroplacoids in the anterior part of pharynx (op. cit., tab. 19, Fig. 30; Fig. 37, this paper) and recognized this feature as one more specific character. Moreover, he noted the presence of many small pores on the egg shell. The species was listed in his other papers as well (1907, 1908b, 1909). In the last of these papers the eggs were described as "smooth". Richters & Krumbach (1926: Figs. 44, 52) gave drawings of an embrionate egg and a hatched juvenile. Those figures were re-drawn from already published photographs (Richters 1908a: tab. 20, Figs. 10, 11). The macroplacoids are located in the median part of pharynx in all of these juveniles.

In the Northern Hemisphere the species was recorded by Carlzon (1909). Thulin (1911) transferred it to the genus *Hypsibius* Ehrenberg, 1848. Until the publication of major tardigrade monographs by Marcus (1928, 1929, 1936), *H. antarcticus* was listed several times but without any new information on its morphology or distribution (Murray 1906, 1911c, Richters 1913, Urbanowiczowna 1924, Urbanowicz 1925, Rahm 1928, Thulin 1928).

Marcus (1928) summarized all data on *H. antarcticus* and compiled a diagnosis. He identified as key characters: the presence of macroplacoids in the anterior part of pharynx and freely laid, smooth and sticky eggs with a shell perforated by small pores. However, the adult form depicted as *H. antarcticus* (op. cit., Fig. 256 A; Marcus 1929: Fig. 342) represents another species. Its pharynx has three (!) pairs of macroplacoids placed in the middle of the organ. Marcus corrected partly that mistake in his last monograph (1936) depicting only two pairs of macroplacoids. Nevertheless, he placed them in the middle of pharynx, in conflict with the diagnosis, identification keys, and some figures redrawn from Richters (1908a) and Richters & Krumbach (1926).

Marcus' diagnosis of *H. antarcticus* was repeated in subsequent monographs or identification keys (Cuènot 1932, Ramazzotti 1945, 1958, 1962, 1972, Ramazzotti & Maucci 1983, Rudescu 1964, Bartoš 1967, Maucci 1986, Dastych 1988). Original records about the species, others than those of Richters (1904a) and Carlzon (1909) were presented from Greenland (Petersen 1951), Norway (Durante Pasa & Maucci 1979), Poland (Weglarska 1959, Dastych 1970), Romania (Rudescu 1964) and Antarctica (Sudzuki 1964, Jennings 1976a, 1976b, McInnes & Ellis-Evans 1987).

Dastych (1970) reported *H. antarcticus* from Tatra Mts, recognizing it later (Dastych 1973) as a "simplex"-form of *H. convergens* (Urbanowicz) and *H. dujardini* (Doyère), and as a junior synonym of the latter taxon. Jennings (1976a) found two specimens of *H. antarcticus* in South Georgia. Curiously, he excluded that information from the table summarizing the distribution of tardigrades in Antarctica (op. cit., p. 94). He also presented no data on morphology of these two specimens. McInnes & Ellis-Evans (1987) reported *H. antarcticus* from Signy Island and suggested that the taxon „may simply be a variation of *H. arcticus*". This was earlier suggested by Dougherty (1964) and repeated by Crisp & Kristensen (1983).

Almost paralelly to the description of *H. antarcticus* by Richters (1904a), Murray (1907a) described other polar tardigrade, *Macrobiotus arcticus*. The material came from Prince Charles Foreland (Archipelago Svalbard) and Franz Joseph Land in the Arctic. In absence of adults, he based a short description of the species only on morphology of two available eggs and one embryo. The embryo had two pairs of macroplacoids located in the median part of pharynx (op. cit., Fig. 5a). He viewed "spiny eggs with rod-like blunt processes embedded in hyaline matrix... spines subclavate, slightly expanded and blunt at tips" as another specific character. He reported similar egg but with shorter processes and a hatched juvenile from Scotland (Murray 1907b) and egg with thicker processes from South Africa (1907c).

Murray (1910) found numerous specimens and eggs of an Antarctic tardigrade which he identified as *Macrobiotus arcticus*. His description of those individuals was insufficient. He described eggs as "...thick-shelled, studded with short rods which are embedded in a hyaline substance". He mentioned the thickness of the shells ("...about 5 or 6 μ , but varies considerably...") and noted that the eggs "...often appear to be viscous and have much adherent material; some are quite clean and don't seem viscous".

Murray (1911a) pointed out that his earlier data on *M. oberhaeuseri* from Scotland (1907b) referred, in fact, to *M. arcticus*. He recorded *M. arcticus* from Irland (1911b), Uganda (1913a), Australia, New Zealand, Canada and Bolivia (1913b). However, he found separately either individuals or eggs in those collections. Thus, he considered that "...there is a certain doubt about the

identification" (Murray, 1910). Heinis (1914) reported *H. arcticus* from Columbia and Thulin (1911) transferred it to the genus *Hypsibius*.

Richters (1911) listed *H. arcticus* from Spitsbergen and Greenland. He commented briefly on the size of an individual and its cuticle and provided photographs of the adult and egg. However, the poorly visible buccal apparatus of the individual bears resemblance to that of *Macrobiotus*-type, and the egg processes are similar to those of *Macrobiotus hastatus* Murray (op. cit., Figs. 10, 11). Richters also described the new taxon, *Macrobiotus heinisi* in that paper. The chorion structure of *M. heinisi* resembles that of *H. arcticus*. Marcus (1930) recognized *M. heinisi* as a junior synonym of *H. arcticus*, reported the latter taxon from Switzerland but provided no morphological information.

The description and illustrations of *H. arcticus* presented in the monographs by Marcus (1928, 1929, 1936) are principally a repetition of Murray's (1910) redescription, based until then, however, on the Antarctic material. The only original figure is that of a claw, drawn by Thulin (Marcus 1929: Fig. 343 G; 1936: Fig. 261 E). This compilation has been repeated in subsequent monographs of tardigrades (Cuènot 1932, Ramazzotti 1945, 1958, 1962, 1972, Ramazzotti & Maucci 1983). *H. arcticus* is recognized as a cosmopolitan species, despite Murray's (1910) doubts about the correctness of some of his own identifications.

Data on distribution of *H. arcticus* accumulated after World War II come almost exclusively from the Antarctic region. The only exception are those from Romania (Rudescu 1964) on *H. arcticus* (and *H. antarcticus*). *H. arcticus* has been reported from the Antarctic by Morikawa (1962), Dougherty & Harris (1963), Dougherty (1964), Everitt (1981), Dastych (1984), McInnes & Ellis-Evans (1987), Usher & Dastych (1987), and Dastych (1989). McInnes & Ellis-Evans (op. cit.) thought that one of the most abundant tardigrades in the maritime Antarctic, identified by Jennings (1976a, 1976b) as *H. dujardini* (Doyère), represents probably *H. arcticus*.

Species descriptions

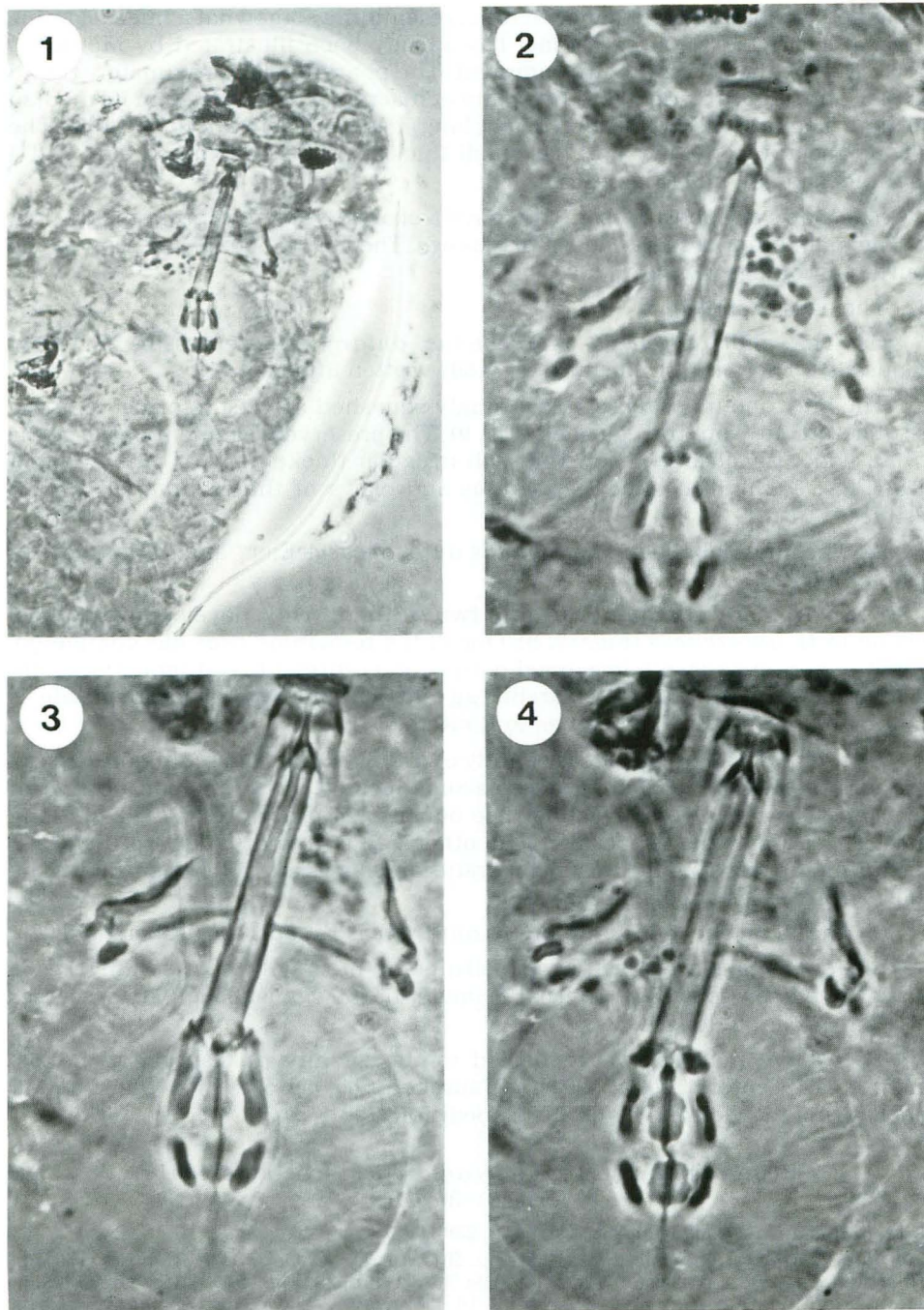
Description of the type-material of *Hypsibius antarcticus* (Richters, 1904) (Figs. 1–15)

Richters' collection of *H. antarcticus* comprises one adult individual and four eggs on four slides. The slides are non-standard 47 × 22 mm with cover slips 18 × 18 mm, and framed with Canada balsam. The specimens are mounted in formalin, as judged from the presence of a small number of characteristic cristals. Such a preparation was often used at the turn of century (Marcus 1928). Some air has penetrated the mountant but has not destroyed the objects.

A) The adult (one slide labelled "*Macrobiotus antarcticus*" and "Gaussbg", written in a black ink)

The animal is mounted in latero-ventral position, flattened and surrounded by a small amount of mountant (Fig. 1). The length of the body is 294 µm. The cuticle is slightly wrinkled but without trace of granulation. The eye dots are relatively large and composed of numerous dark-brown pigment granules.

The posterior edge of mouth cavity is surrounded by a ring of small oval structures which are well visible on the ventral side only. One side of the ventral transversal ridges has three small granules (Fig. 15). The mouth tube is relatively wide and its outer diameter measures 4.4 µm. The length of mouth tube measured from the mouth opening and including apophyses is 39.6 µm. There is an



Figs. 1-4 - *Hypsibius antarcticus* (Richters): 1 - anterior part of the body; 2 - buccal apparatus, dorsal view; 3 - buccal apparatus; 4 - buccal apparatus, ventral view (type-material).

elongated artifact inside the mouth tube, resembling somewhat a buccal lamina (Figs. 1–4, 13, 15). Such an artifact has already been illustrated by Morikawa (1962: Fig. 2), then without any comment. The pharynx is approximately round ($38 \times 37 \mu\text{m}$) and provided with two pairs of macroplacoids located in its median portion. The first macroplacoid ($7.7 \mu\text{m}$ long) has an incision in the middle. The second macroplacoid ($4.7 \mu\text{m}$) has small thickening on its external side and a slight incision as well (Figs. 4, 13).

The claws are poorly visible but have a characteristic sculpture inside (Fig. 5). The main branches have accessory spines. The length of external claw on the fourth pair of legs is $22 \mu\text{m}$.

B) The eggs (3 slides)

(1) The slide labelled "*Macrobotus antarcticus* gepresstes Ei" and "Gaussbg". There is also the number "180" written in pencil.

The only one mounted egg is strongly squashed and its deformed embryo is squeezed out from the egg shell (Fig. 9). The preserved fragment of the egg is $77 \mu\text{m}$ wide. Its surface is covered with irregular thickenings of differentiated size (Figs. 9, 10). The buccal apparatus and claws of the embryo are poorly visible.

(2) The slide labelled "*Macrobotus antarcticus* 4 Eier" and "Gaussbg". In pencil: "178".

Four eggs are mounted but only two of them (with developed embryos) belong to *H. antarcticus* (Figs. 7, 8). One of the remaining eggs has completely smooth chorion and well developed mastax and represents Rotifera. The origin of another, smooth and transparent egg but without any structure inside is unknown. Possibly it also belongs to Rotifera.

One of the tardigrade eggs is slightly oval ($95 \times 83 \mu\text{m}$, excluding processes). The embryo has two pair of macroplacoids located in the median portion of pharynx. Claws are poorly visible. The majority of processes (0.8 – $2.2 \mu\text{m}$ long and 0.8 – $1.1 \mu\text{m}$ wide) is rod-like. The other egg is round ($80 \mu\text{m}$ in diameter, excluding processes). The buccal apparatus and claws are not recognizable. The chorion processes are 0.8 – $1.7 \mu\text{m}$ long.

(3) The slide labelled "*Macrobotus antarcticus* Ei" and "Gaussberg Mai 02".

The only egg is preserved in a small amount of cristallized medium (Fig. 6). No embryo is present. The external diameter of the egg is $85 \mu\text{m}$, its processes are up to $1.1 \mu\text{m}$ in length.

The above material was collected in the vicinity of Gaussberg in East Antarctica (Richters 1904a, 1904b: "Gaussberg, $65^\circ 50' 5''\text{s}$. Br."; "leg. Vanhöfen") during the German Antarctic Expedition (1901–1903).

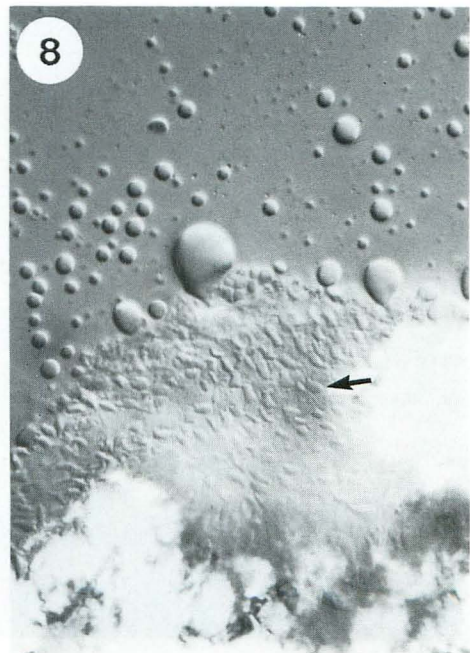
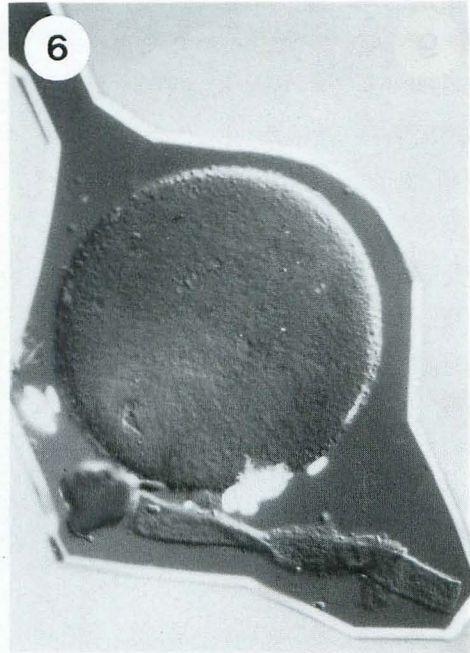
Redescription of *Hypsibius antarcticus* (Richters, 1904)
(Figs. 1–36, 41)

Macrobotus antarcticus Richters, 1904 a. p. 239

Macrobotus antarcticus: Richters (1904b, p. 59), Murray (1906, p. 333), Richters (1907, p. 916), Richters (1908a, p. 296–297, tab. 19, Figs. 30–31, tab. 20, Figs. 9–11), Carlzon (1909, p. 141: misidentification), Murray (1910, p. 103–105), Murray (1911c, p. 194), Urbanowiczowna (1924, p. 12), Urbanowicz (1925, p. 139), Richters & Krumbach (1926, p. 49, Figs. 44, 52), Rahm (1928, p. 15: in part);

Makrobotus (sic!) *antarcticus*: Richters (1908a, p. 55), Richters (1909, p. 604) Richters (1913, p. 1019);

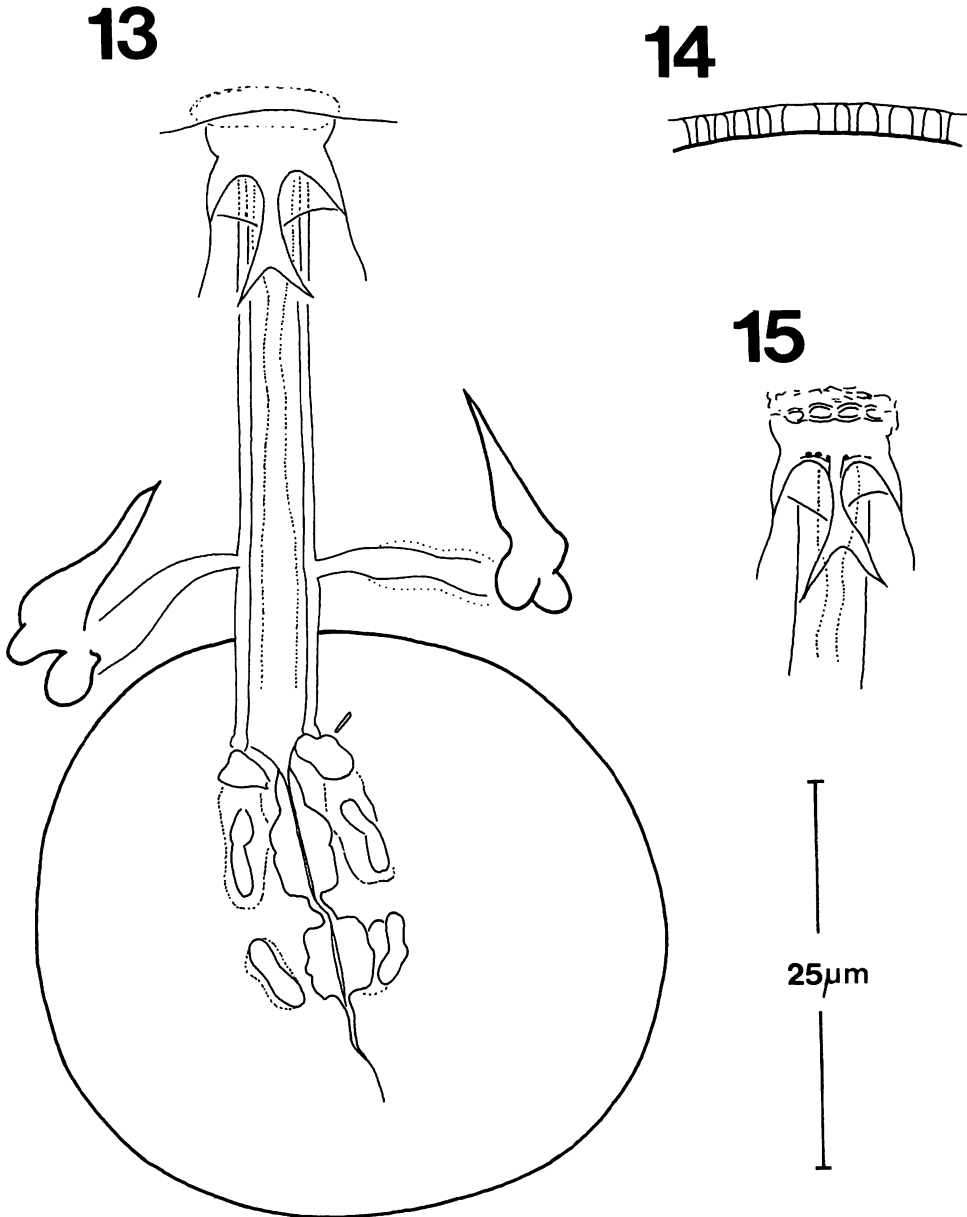
Hypsibius antarcticus: Thulin (1911, p. 27), Thulin (1928, p. 241), Marcus (1928, p. 207–208, Fig. 254 a-e: in part), Cuènot (1932, p. 88), Petersen (1951, p. 77, Fig. 31: misidentification), Robotti (1972, p. 159–160, Fig. 12: misidentification), Ramazzotti & Maucci (1983, p.



Figs. 5-8 - *Hypsibius antarcticus* (Richters): 5 - external claw of the IVth pair of leg; 6 - egg; 7, 8 - fragment of egg (type-material) (arrows: processes of egg).



Figs. 9–12 – *Hypsibius antarcticus* (Richters): 9 – squashed egg; 10–12 – egg and its processes (arrows) (type-material).

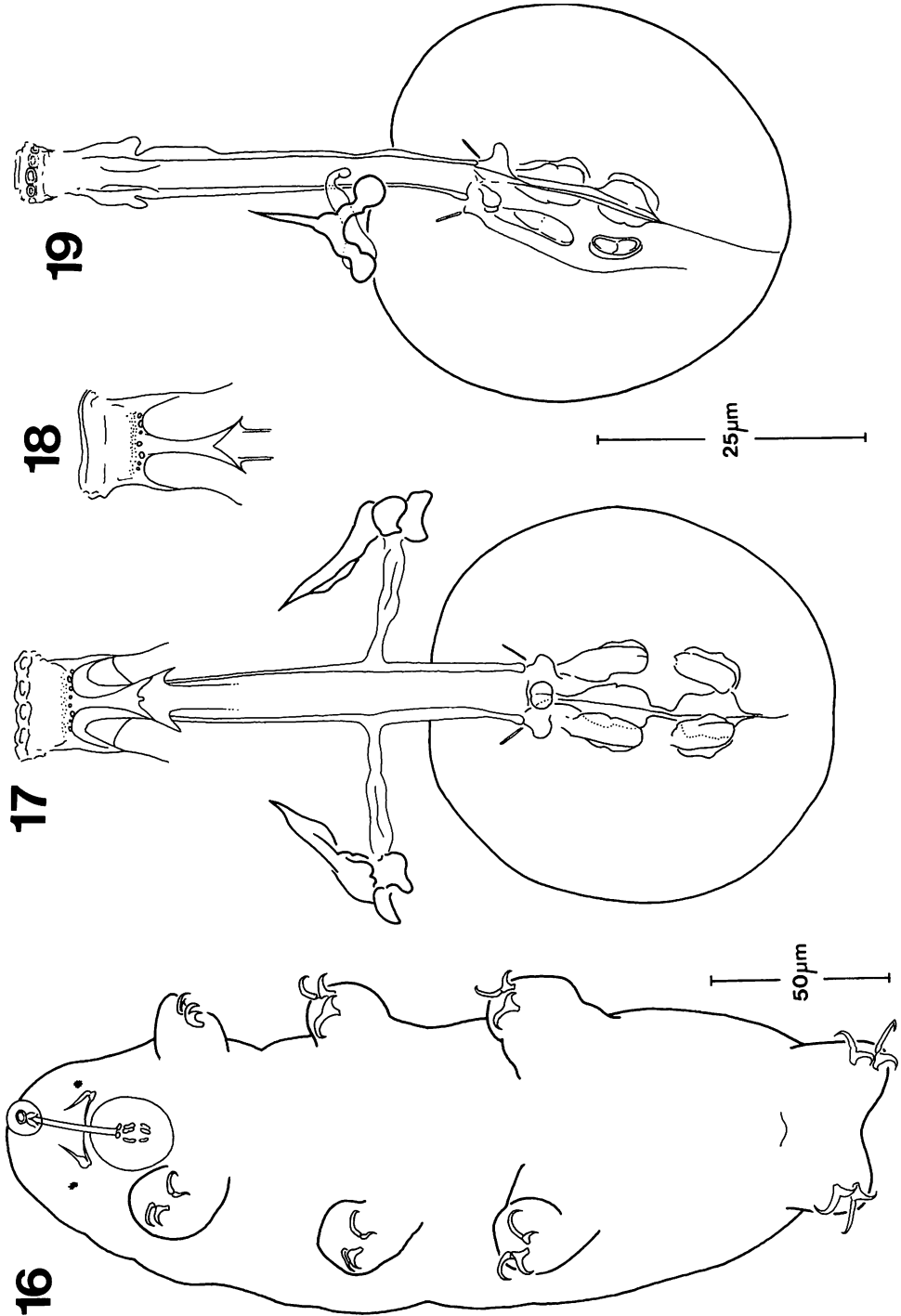


Figs. 13–15 – *Hypsibius antarcticus* (Richters): 13 – buccal apparatus, ventral view; 14 – processes of egg, lateral view; 15 – mouth cavity, dorsal view (type-material).

540–541, Fig. 319: in part), Maucci (1986, p. 268–269, Fig. 181; misidentification), McInnes & Ellis-Evans (1987, p. 116, 120), Dastyh (1988, p. 155, Fig. 103 D, E: in part);

Hypsibius (s. str.) *antarcticus*: Marcus (1929, p. 504–505, Fig. 342: in part), Marcus (1936, p. 270–271, Fig. 260: in part), Weglarska (1959, p. 356: misidentification);

Hypsibius (*H.*) *antarcticus*: Ramazzotti (1945, p. 159), Ramazzotti (1958, p. 110), Ramazzotti (1962, p. 241–242, Fig. 47: in part), Rudescu (1964, p. 270–272, Fig. 211: misidentification), Sudzuki (1964, p. 14–15, pl. 8, Figs. 13–15), Bartoš (1967, p. 158, Fig. 39 A, B, D, CH: in part), Dastyh (1970, p. 77: misidentification), Ramazzotti (1972, p. 448–449, Fig. 235: in part), Dastyh (1973, p. 81–85, Figs. 14–17: synonymy with *H. dujardini*), Jennings (1976a, p. 86–89, 91, 94), Durante Pasa & Maucci (1979, p. 66: misidentification);



Figs. 16–19 – *Hysibius antarcticus* (Richters): 16 – habitus, ventral view; 17 – buccal apparatus, dorsal view; 18 – mouth cavity, ventral view; 19 – buccal apparatus, lateral view (Fig. 16 – specimen from King George Island; Figs. 17, 18 – the Vestfold Hills; Fig. 19 – the Casey Station).

Macrobiotus arcticus Murray, 1910, p. 96–98, 101–103, tab. 14, Fig. 2 a–e

Hypsibius arcticus: Marcus (1928, p. 211–212, Fig. 258: in part), Morikawa (1962, p. 3–4, Figs. 1–4), Dougherty & Harris (1963, p. 498), Dougherty (1964, p. 7–11), Everitt (1981, p. 232), Ramazzotti & Maucci (1983, p. 541–542, Fig. 320: in part), Dastych (1984, p. 407–409, Figs. 18, 28, 29, tab. 1), McInnes & Ellis-Evans (1987, p. 116, 118, 120), Usher & Dastych (1987, p. 164), Dastych (1989, p. 253);

Hypsibius (s. str.) *arcticus*: Marcus (1929, p. 505–507, Fig. 343: in part), Marcus (1936, p. 271–273, Fig. 261: in part);

Hypsibius (*H.*) *arcticus*: Ramazzotti (1945, p. 159: in part), Ramazzotti (1962, p. 243–244, Fig. 49: in part), Rudescu (1964, p. 360–361, Fig. 205: in part), Ramazzotti (1972, p. 449–450, Fig. 236: in part);

Hypsibius (*H.*) *mertoni simoizumii* Sudzuki, 1964, p. 15, pl. 7, Figs. 1–10, **new synonym**, Ramazzotti (1965, p. 160–162, Fig. 25), Janetschek (1967, p. 243), Ramazzotti (1972, p. 464–466, Fig. 251);

Hypsibius simoizumii: Ramazzotti & Maucci (1983, p. 565–567, Fig. 342);

Hypsibius mertoni: Opalinski (1972, p. 388, 390: misidentification);

Hypsibius (*H.*) *convergens*: Janetschek (1962, p. 243)?;

Hypsibius (*H.*) *dujardini*: Jennings (1976a, p. 79, 91, tab 3–6), Jennings (1976b, p. 4, 11–12, 21, tab. 6–8);

Hypsibius convergens cf. Ramazzotti (1968): Sudzuki (1979, p. 106)?;

Hypsibius (*Hypsibius*) sp. 2: Sudzuki (1964, p. 16).

Diagnosis: *Hypsibius* with two pairs of macroplacoids located in the median part of the pharynx. Freely layed eggs, often in cluster, are covered with numerous, short and rod-like processes of variable size. The eggs are sometimes deposited into exuviae. Type locality: East Antarctica, vicinity of Gaussberg.

Description: Body white, 146–460 μm long; intestine often green; legs short (Figs. 16); eye spots usually large, and composed of dark brown pigment granules; cuticle smooth.

The mouth opening has no lamelles, presence of lobes is unknown. The anterior edge of the mouth cavity is surrounded by a ring of small oval structures (Figs. 15, 17, 19, 20, 24). In dorsal or ventral view, they are visible as 4–5 connected thickenings. The dorsal and ventral transversal ridges have several granules which are particularly well developed in large specimens (Figs. 15, 17, 18, 23, 24). In small individuals the granules are minute or missing. The mouth tube ist relatively wide (external diameter: 2.0–6.6 μm) and has an elongated thickening on its externo-dorsal wall, just below the mouth cavity (Fig. 19).

The pharynx is usually round, with large apophyses and two pairs of macroplacoids (Figs. 1–4, 13, 16, 17, 19, 20, 22). A septulum and a macroplacoid are lacking. The placoids are located in the median part of pharynx. The first macroplacoid is longer than the second and constricted in the middle. The second macroplacoid is usually granular and most often with well pronounced incisions on both sides, slightly below the middle. The size of macroplacoids and their shape, including the degree of incision, are highly variable, even among the specimens from the same sample.

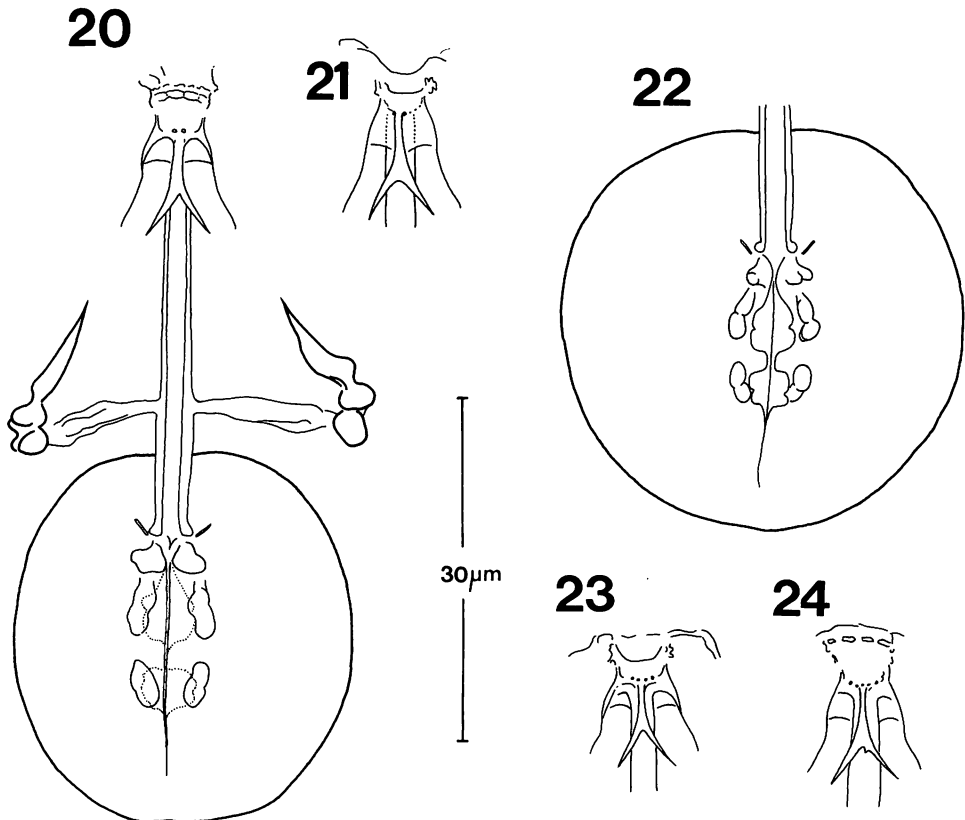
The claws have usually well pronounced sculpture inside (Figs. 5, 25–28). No lunules. The claws are slightly thickened at the base which is most often rolled-up and poorly visible. No cuticular longitudinal bars occur at the bases from the first to the third pair of claws and no bars are developed between the claws. The thickness and shape of the claws varies within and among populations.

The following measurements were taken on a single specimen 278 μm long: Length of the mouth tube from mouth opening and including apophyses 40 μm ; tube external diameter 3.3 μm . The pharynx measures 32 \times 30 μm . The first

macroplacoid is 6.0 μm long, the second 4.4 μm , both 2.2 μm wide. The external claws of the fourth pair of legs are 16.5 μm long, with the main branches 11 μm long.

The eggs are white and usually round, rarely short-oval. They are freely layed, mainly in clusters and only seldom into exuviae. In the examined material 1–2 eggs were found in 4 exuviae. The freely layed eggs are often covered with detritus, mineral particles or diatoms. Numerous and small processes are developed on the egg chorion (Figs. 6–12, 29–36). Usually the processes form elongated tiny rods with slightly thickened bases. Their distal extremities touch a thin transparent sheath that surrounds the egg (Figs. 14, 29–35). The sheath and processes form a „shell“, well visible on the circumference of egg. This shell resembles, to some degree, the gemmule shells of fresh-water sponges. The shape and size of the processes are highly variable. Rods may range from elongated with narrow or wide tips (Figs. 29–33, 36) to short irregular thickenings with tips wide relative to bases (Figs. 14, 34, 35). The length of processes determines the thickness of the egg shell. The egg processes observed at low magnification resemble more or less regular granulation or perforation. The diameter of eggs including processes is 66–103 μm and without processes 62–94 μm . The processes are 0.8–5.0 μm long and 0.3–1.5 μm wide.

Material. Continental Antarctic: Gaussberg (type-material: 1 adult individual, designed here as lectotype; 4 eggs [housed in the Senckenberg Museum, Frankfurt a. M.]);



Figs. 20–24 – *Hypsibius antarcticus* (Richters): 20 – buccal apparatus, dorsal view; 21 – mouth cavity, ventral view; 22 – pharynx, ventral view; 23 – mouth cavity, dorsal view; 24 – mouth cavity, ventral view (all specimens from the Casey Station).

Casey Station (38 specimens, 3 eggs: the Zoological Institute and Zoological Museum, University of Hamburg); Vestfold Hills (41 specimens, 31 eggs: collection of the author: the sample sent by Everitt (1981) for identification; 2 specimens and 3 eggs: the Zoological Museum, Copenhagen). Maritime Antarctic: South Shetland Islands (77 specimens, 7 eggs), South Georgia (2 eggs) (collection of the author); South Shetland Islands and the Antarctic Peninsula (27 specimens: see Usher & Dastych 1987); South Orkney Islands (Signy Island) and the Antarctic Peninsula (Alexander Island): 22 specimens identified as *H. antarcticus*, *H. arcticus* or *H. dujardini* (collection of the British Antarctic Survey: see Jennings 1976a, 1976b, McInnes & Ellis-Evans 1987). Other comparative materials. Greenland: Zackenberg, 1 specimen of "*H. antarcticus*", det. Petersen (1951); Disco Island, 6 eggs and 1 specimen of "*H. arcticus*?", det. R. M. Kristensen; West Spitsbergen: Kung Karl, 4 eggs of "*H. arcticus*", det. R. M. Kristensen; Atomfjella, 4 specimens of "*H. ?arcticus*", det. Dastych (1985). Sweden, Gotland: 1 specimen of "*H. arcticus*?", det. G. Thulin. Norway, Bodo: 1 specimen of "*H. antarcticus*", det. Durante Pasa & Maucci (1979).

Locus typicus. Vicinity of Gaussberg, East Antarctica ("Gaussberg, 65° 50' 5" s. Br": Richters 1904a, 1908a). The outcrop (371 m) exact location is 66° 48' 08" S + 89° 19' 27" E (Brunk et al. 1988). It should be noted that Sudzuki (1979) described the locality of his "*Hypsibius convergens* cf Ramazzotti (1968)" as "Gaussberg (87° E, 67° S)".

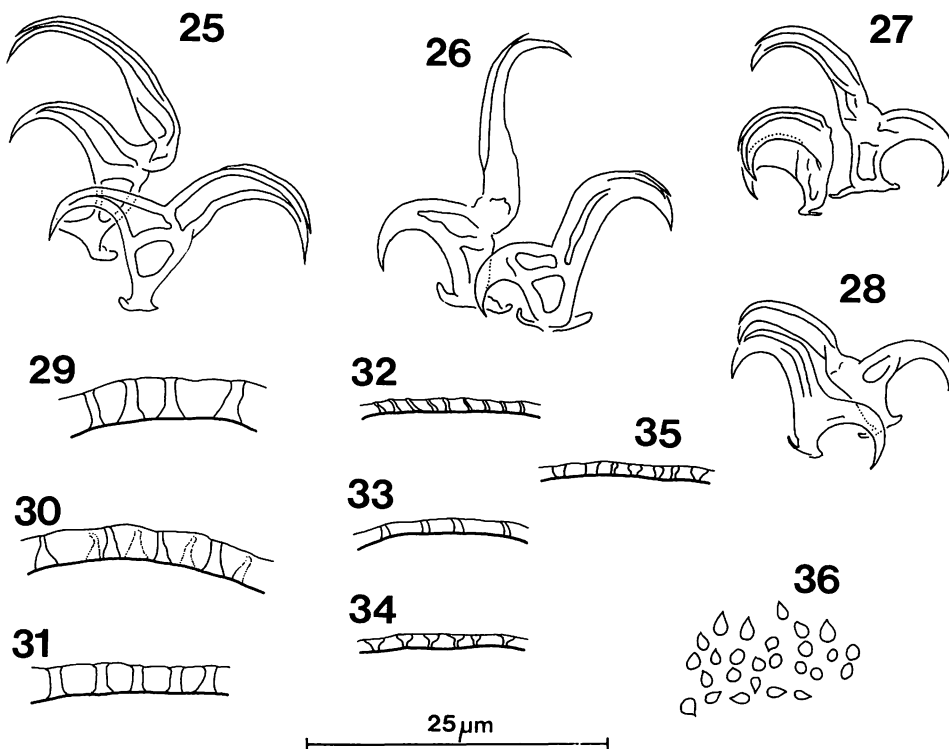
Habitat. *H. antarcticus* lives in mosses, lichens, grasses, algae, soil and cyanophytan mats in terrestrial and freshwater ecosystems of the Antarctic. It belongs to the most abundant and common tardigrades in that region, occurring sometimes in great densities. Additional, though limited data on biology and ecology of *H. antarcticus* (under the names: *H. arcticus* and *H. dujardini*) are in Dougherty (1964), Jennings (1976a, 1976b, Everitt (1981) and McInnes & Ellis-Evans (1987).

Distribution. The species has continuous distribution in non-glaciated areas around Antarctica (Fig. 41). It is also known from South Shetlands, South Orkneys, South Sandwich Islands and South Georgia.

Discussion

Taxonomic confusion involving *H. antarcticus* results from inaccuracies of the original description and the misleading additions to that description (Richters 1904a, 1908a). Richters (1908a) recognized two key characters of the species. One is unique position of macroplacoids, i. e. in the anterior part of pharynx. However, Richters' assessment is contradicted by his own photographic records (op. cit.) as well as by his type material. In both cases the macroplacoids are located "normally", that is they occur in the median part of pharynx (comp. Figs. 1-4, 13, 17, 19, 20, 22, 37, and Richters 1908a: tab. 20, Figs. 9-11). The reasons why Richters' description is inaccurate are far from clear. In so-called "simplex"-form (Eutardigrada) one can sometimes observe posterior dislocation of the pharynx within buccal apparatus. It may happen under the impact of the mounting medium as well. Such an aberrant displacement of the pharynx can give a misleading impression of macroplacoids being situated anteriorly. However, that position of pharynx (and macroplacoids) is inconsistent with its normal function.

The second key-character of *H. antarcticus* is the type of oviposition and structure of the egg chorion. Richters (1904a, 1904b, 1908a) described the eggs as freely laid, smooth and having their surface covered with small perforation. However, in the type-material the chorion is covered with numerous small processes (Figs. 6-12) which were misinterpreted by Richters as pores.



Figs. 25–36 – *Hypsibius antarcticus* (Richters): 25–27 – claws of the IVth pair of legs, ventral view; 28 – claws of the IIInd pair of legs, ventral view; 29–35 – processes of egg, lateral view; 36 – processes of egg, dorsal view (Figs. 25, 30, 33, 36 – specimens from the Vestfold Hills; Figs. 26–28, 34, 35 – the Casey Station; Figs. 31, 32 – King George Island; Fig. 29 – South Georgia).

As a result of these errors, several aberrant tardigrades, mainly from the "*H. convergens*"-complex, have been misidentified as *H. antarcticus* and subsequently reported from the Northern Hemisphere.

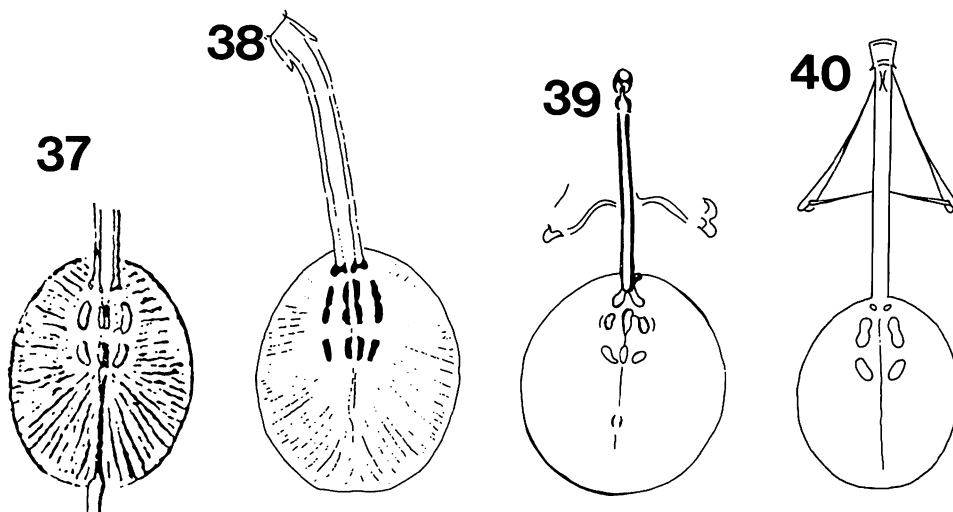
Carlzon (1909) listed *H. antarcticus* from Sweden and described its eggs as "smooth and viscous". At present it is even difficult to assign that species to a genus.

Petersen (1951) reported *H. antarcticus* from Greenland. However, the only specimen found (Fig. 38) has evident buccal lamina, a character overlooked by him. In fact, it represents an aberrant individual of the genus *Doryphoribius* Pilato, 1969, presumably *D. macrodon* Binda, Pilato & Dastych, 1980.

Weglarska (1959) listed *H. antarcticus* from Pieniny Mts in Poland, without providing any information about its eggs. The site lies close to the Czechoslovakian border. Bartoš (1967) listed *H. antarcticus* from Czechoslovakia but gave no data on its locality, probably adopting Weglarska's determination as correct.

Rudescu (1964) recorded *H. antarcticus* from Romania but found no eggs. He re-published uncritically Marcus' (1928, 1929) incorrect illustration of that species with three (!) macroplocoids (op. cit., 1964: Fig. 211 A).

Robotti (1972) identified the individuals and eggs found in Piedmont, Italy, as *H. antarcticus*. He presented an original illustration of the pharynx (Fig. 39) with relatively small macroplocoids. That fact and his remark about eggs layed



Figs. 37–40 – Pharynx or buccal apparatus of *Hypsibius antarcticus* (Richters), after various authors: 37 – Richters (1908a); 38 – Petersen (1951); 39 – Robotti (1972); 40 – Maucci (1986).

into exuvium indicates that he probably had a species from "*H. pallidus-microps*" group.

Durante Pasa & Maucci (1979) reported one individual of *H. antarcticus* from Norway. Possibly, the pharynx of that specimen has been depicted in Maucci (1986) (Fig. 40). Presented an almost extreme dislocation of that organ was probably caused by the mounting medium, i. e. polyvinyl-lactophenol. This mountant is known to frequently deform pharynx in slide preparations.

The type-material of *H. antarcticus* corresponds perfectly with the description of individuals and eggs found by Murray (1910) in South Victoria Land (Antarctica), however, identified by him as *H. arcticus*. There is no doubt that the material from both Antarctic localities (Gaussberg and South Victoria Land) represents the same species, i. e. *H. antarcticus*. Also the morphological characteristics found in type-material agree entirely with material from eastern and western parts of the Antarctic. Specimens from the latter sites have been identified by various authors either as *H. arcticus* (Morikawa 1962, Dougherty & Harris 1963, Dougherty 1964, Everitt 1981, Dastyh 1984, McInnes & Ellis Evans 1987, Usher & Dastyh 1987, Dastyh 1989) or as *H. dujardini* (Jennings 1976a, 1976b). Thus, all these records represent in fact erroneously defined *H. antarcticus*.

H. antarcticus has been listed from the Antarctic under other names as well. In my opinion, it was misidentified as *H. convergens* by Janetschek (1967), as "*H. convergens* cf. *Ramazzotti* (1968)" by Sudzuki (1979), as *H. mertoni simoizumii* by Sudzuki (1964) and Janetschek (1967) and as *H. mertoni* by Opalinski (1972). *H. mertoni simoizumii* Sudzuki, 1964, the taxon described from East Antarctica, is recognized here as a junior synonym of *H. antarcticus*. Indication for this is its original description and illustration (Sudzuki 1964: p. 15, pl. 7, Figs. 1–10) which strikingly resemble the latter species. Recently, this subspecies has been even elevated to the rank of a separate species, i. e. *H. simoizumii* (see Ramazzotti & Maucci 1983). Sudzuki's other (1964) tardigrade, "*Hypsibius* sp. 2" is most probably represented by *H. antarcticus* also. Its buccal apparatus is the same as that of the latter species (op. cit., pl. 7, Figs. 11–13). A remark by author that "macroplacoids three pairs, the first round..." is incorrect, since "the first

round...“ (macroplacoids) evidently represent apophyses. Thus, there are only two pairs of macroplacoids and not three. He also pointed out that "...the eye lacking..“, but eye spots are indicated in the illustration (op. cit., Fig. 13). On the other hand, his record of *H. antarcticus* may also represent this same species, as judged from the description of adults. According to him, macroplacoids are "situated at the middle of pharynx and never developed at the posterior (sic! remark of H. D.) half of the pharynx“. However, Sudzuki pointed out that "the egg shell is smooth“ (op. cit.).

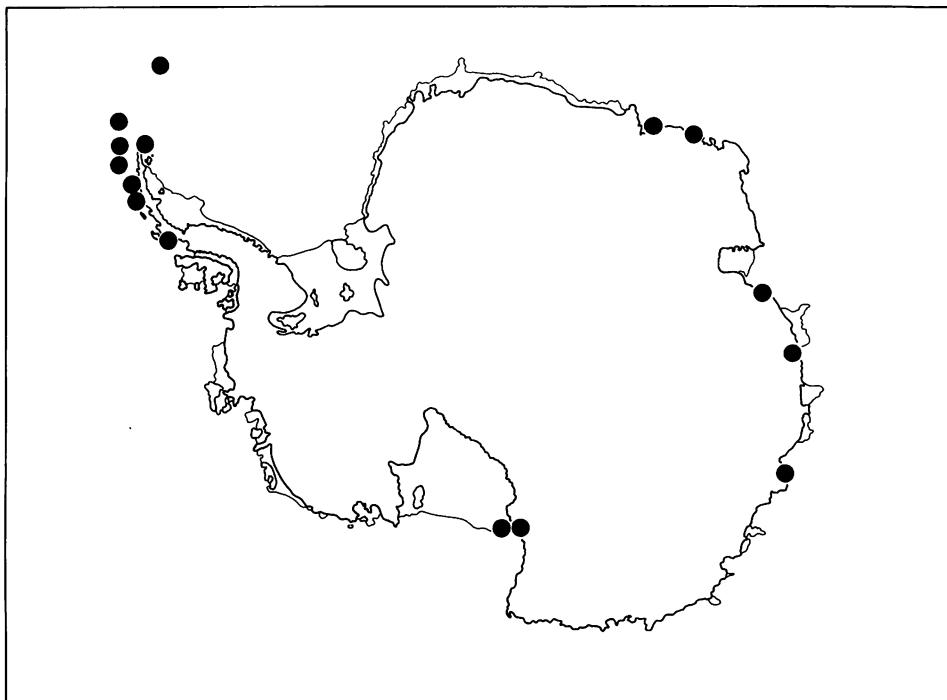


Fig. 41 – Localities of *Hypsibius antarcticus* (Richters) in Antarctica (the sites in South Sandwich Islands and South Georgia are not included).

A problem which remains is the real taxonomic status of *H. arcticus*. There are two solutions to the question: (1) if *H. arcticus* and *H. antarcticus* are conspecific then *H. arcticus* is a junior synonym of the latter species, or (2) these taxa belong to two similar but separate species. At present an acceptable answer is not possible due to insufficient morphological information about *H. arcticus*. The majority of data on the species originate from Antarctic material, thus they in fact concern *H. antarcticus*. The remaining scant information comprises merely an insufficient original description (Murray, 1907 a), a fragmentary report from Scotland (Murray, 1907 b), not much credited later (1910) by the same author himself, records from Canada, Australia, South Africa and New Zealand, as well as reports from Spitsbergen and Greenland (Richters, 1909), casual remarks by Marcus (1930) and a report by Rudescu (1964) which is very unreliable. All this data is inadequate to full species characterization in the light of modern taxonomic standards.

The analyse of available meagre material from the Northern Hemisphere, identified by various authors as *H. arcticus* or *H. cf. arcticus* does not contribute much to the above question either. The Thulin specimen ("H. arcticus?") differs

from the examined individuals of *H. antarcticus* in a slightly different shape of its decidedly shorter claws. Details of the mouth cavity are not visible due to the positioning of the specimens and the kind of mounting medium (glycerogelatine). The individuals of "*H. ? arcticus*" (Dastych, 1985) from West Spitsbergen cryoconites have distinctly longer legs, a slightly different shape of claws and no thickening in the antero-dorsal wall of the mouth tube, compared to *H. antarcticus*. Eggs were not found in the above two cases, so that no information about the chorion structure is available.

On the other hand, the variability of egg processes in Kristensen's material from West Spitsbergen, spans the range observed in *H. antarcticus*. However, the only available adult individual which originated from a sample other than the eggs, has in its mouth cavity no granules and no ring of roundish thickenings. The lateral aspect of the mouth tube also cannot be examined due to the dorso-ventral orientation of the mounted specimen. Some slight differences from *H. antarcticus* also occur in the sculpturing of the claws. Thus, a definite answer if these two taxa are conspecific or not will only be possible when more representative material from the Arctic is available.

It should be noted, that some characters of *H. antarcticus*, i. e. the shape and armature of the buccal cavity and mouth tube and particularly, freely layed eggs and the structure of chorion processes, distinguish the species from all reliably described taxa in the genus *Hypsibius*. This indicates that its present generic status needs further studies.

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Zusammenfassung

Es wurde ein in der Antarktis vorkommendes Bärtierchen *Hypsibius antarcticus* (Richters, 1904) auf Grund seines Typenmaterials nachbeschrieben. Taxonomische Verwirrung, die diese Art betrifft, wurde durch eine unvollständige Originalbeschreibung und spätere irreführende Ergänzungen hervorgerufen (Richters 1904 a, 1908 a). Alle Funde von *H. antarcticus* aus der nördlichen Hemisphäre wurden verifiziert und erwiesen sich als falsche Bestimmungen. Andererseits müssen alle Funde einer weiteren, ähnlichen, polaren Art, *H. arcticus* (Murray, 1907) aus der Antarktis *H. antarcticus* zugerechnet werden. Der taxonomische Status von *H. arcticus* und seine offensichtliche Synonymie mit *H. antarcticus* wurde diskutiert, aber das Problem bleibt weiterhin nicht ganz gelöst.

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