Acta Biologica Benrodis 18 (2016): 21-43

Redescription and taxonomic status of the Antarctic water-bear *Isohypsibius tetradactyloides* (Richters, 1907), as concluded from the rediscovered type material (Tardigrada)

Neubeschreibung und taxonomischer Status des antarktischen Bärtierchens *Isohypsibius tetradactyloides* (Richters, 1907) anhand des wiederentdeckten Typenmaterials (Tardigrada)

Hieronymus Dastych
Zoologisches Museum, Centrum für Naturkunde, Universität Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany: dastych@zoologie.uni-hamburg.de

Summary: The examination of recently rediscovered remains of the Tardigrada collection of Ferdinand Richters (1849-1914), the former curator of Crustacea at the Naturmuseum Senckenberg (Frankfurt am Main), brought to light type material of the taxonomically vague tardigrade species *Isohypsibius tetradactyloides* (Richters, 1907). This taxon, originally described from two sub-Antarctic islands, since then has been worldwide reported. A morphological comparison of the type material with the similar Antarctic tardigrade *Isohypsibius asper* (Murray, 1906) indicates a clear synonymy between these taxa. It results from the same type and appearance of cuticular sculpture, considered absent in the original description of *I. tetradactyloides,* as well as the same buccopharyngeal apparatus and claws in both taxa. Accordingly, *I. tetradactyloides* is a junior subjective synonym of *I. asper*.

Tardigrada, Isohypsibius tetradactyloides, Isohypsibius asper, synonymy, Antarctica

Zusammenfassung: In den vor kurzem wiederentdeckten Resten der Tardigradensammlung von Ferdinand Richters (1849-1914), ehemaliger Kurator für Crustacea am Naturmuseum Senckenberg (Frankfurt am Main), wurde Typenmaterial der taxonomisch diffusen Art *Isohypsibius tetradactyloides* (Richters, 1907) gefunden. Dieses Taxon, ursprünglich von zwei subantarktischen Inseln beschrieben, wurde seitdem weltweit gemeldet. Ein morphologischer Vergleich dieser Art mit dem sehr ähnlichen, ebenfalls antarktischen Bärtierchen *Isohypsibius asper* (Murray, 1906) belegt die Synonymie beider Taxa. Die ergibt sich aus dem gleichen Typus und Aussehen der kutikulären Skulptur, angegeben als abwesend in der ursprünglichen Beschreibung von *I. tetradactyloides*, sowie dem gleichen Buccalapparat und den gleichen Krallen. Dementsprechend ist *I. tetradactyloides* ein jüngeres subjektives Synonym von *I. asper*.

Tardigrada, Isohypsibius tetradactyloides, Isohypsibius asper, Synonymie, Antarctica

1. Introduction

Among invertebrates collected during an early German Antarctic expedition (Deutsche Südpolar-Expedition 1901-1903 under the leadership of Erich von Drygalski), those inhabiting bryophytes such as Protozoa, Nematoda, Rotatoria, Tardigrada, Acari, Crustacea, Insecta and Mollusca have been elaborated by Ferdinand Richters, one of the pioneers of tardigrade taxonomy. He reported for the first time the presence of tardigrades on the Antarctic continent describing the new species *Macrobiotus ant-*

arcticus (now *Acutuncus antarcticus*) from the extinct volcano Gaussberg Mt in the East Antarctic (RICHTERS 1907a). Moreover, the author named several other new tardigrades from some sub-Antarctic islands, including the taxonomically vague *Macrobiotus tetradactyloides* (now *Isohypsibius tetradactyloides*). The latter species was described from the Possession- and Heard Island (l.c.) and afterwards reported from many other locations worldwide.

Several years ago Dr. Jason DUNLOP (Museum für Naturkunde, Berlin) kindly offered me for examination a small collection of old microslides and ethanol samples with tardigrades under his care. Amazingly, a bulk of the microslide material turned out to represent a part of the tardigrade collection of F. RICHTERS considered missed in World War II (DASTYCH 1990, 1991). The collection is ca. 120 years old and embodies some of the oldest microslides with mounted Tardigrada. Several of these slides contain also type specimens of *I. tetradactyloides,* until now thought to be lost.

Recently I have compared the rediscovered type material of *I. tetradactyloides* with diagnoses and descriptions of this species available in the current literature. On the one hand, there are distinct differences in some important taxonomic characters between the examined specimens of RICHTERS and literature data concerning this species; on the other hand a striking resemblance of this species to another Antarctic tardigrade exists, i.e. *Isohypsibius asper* (Murray, 1906). In this article, I redescribe *I. tetradactyloides* based on its type specimens, analyse its similarity to *I. asper*, include some morphological notes on the latter species and discuss the taxonomic status of both taxa.

2. Material and Methods

The specimens of *I. tetradactyloides* from RICHTERS' collection are mounted on eight non-standard sized microslides (Fig. 1 A-H) supposedly preserved in formalin (see also DASTYCH 1990, 1991). Six of the recently rediscovered slides are deposited in the Museum für Naturkunde Berlin (Fig. 1 A-F), and two slides (Fig. 1 G, H), representing another part of the remnants of the collection (see DASTYCH 1990, 1991), are housed in the Senckenberg Forschungsinstitut (Frankfurt a. M.). Each slide is provided with two narrow cardboard labels glued with Canada balsam, the latter medium rings also the cover glasses. The inscriptions in black ink on five successive slide labels read: "Possession Island" or, abbreviated, "Possession Isl/Isld", on three slides: "Kerguelen/Entenbucht" or only "Kerguelen". Moreover, seven slides are labelled "*Macrobiotus 4-dactyloides*", "*Macrobiotus tetradactyloides*" or "*Macrobiotus* aff. (or else "affin": remark H.D.) *tetradactyloides*". Three slides are numbered with ink (A100, A108, A109). All eight slides are additionally provided with blue-pencilled numbers (35, 37, 38, 51, 64, 65 and 6(6?), respectively). Two slides also contain individuals of other tardigrade taxa and tardigrade eggs. One of them (Fig. 1 E) is additionally labelled "*Macrobiotus intermedius*", another slide (Fig. 1 D) only with "*Macrobiotus echinogenitus*" (for the egg) and "*Diphascon crozetense*". The latter microslide bears also four syntypes of *I. tetradactyloides,* however, without such an inscription.

The mounting medium on all slides is more than less penetrated by air and the specimens are partly deteriorated. Nevertheless, a thin film of the mountant still surrounds the majority of animals (e.g. Fig. 2) allowing some observations. The buccopharyngeal apparatuses are generally well visible. However, problematic are the visibility of claws and the surface of the body cuticle. These restraints either come from the light-breaking phenomenon at the border between an air bubble and the remnants of mounting medium surrounding

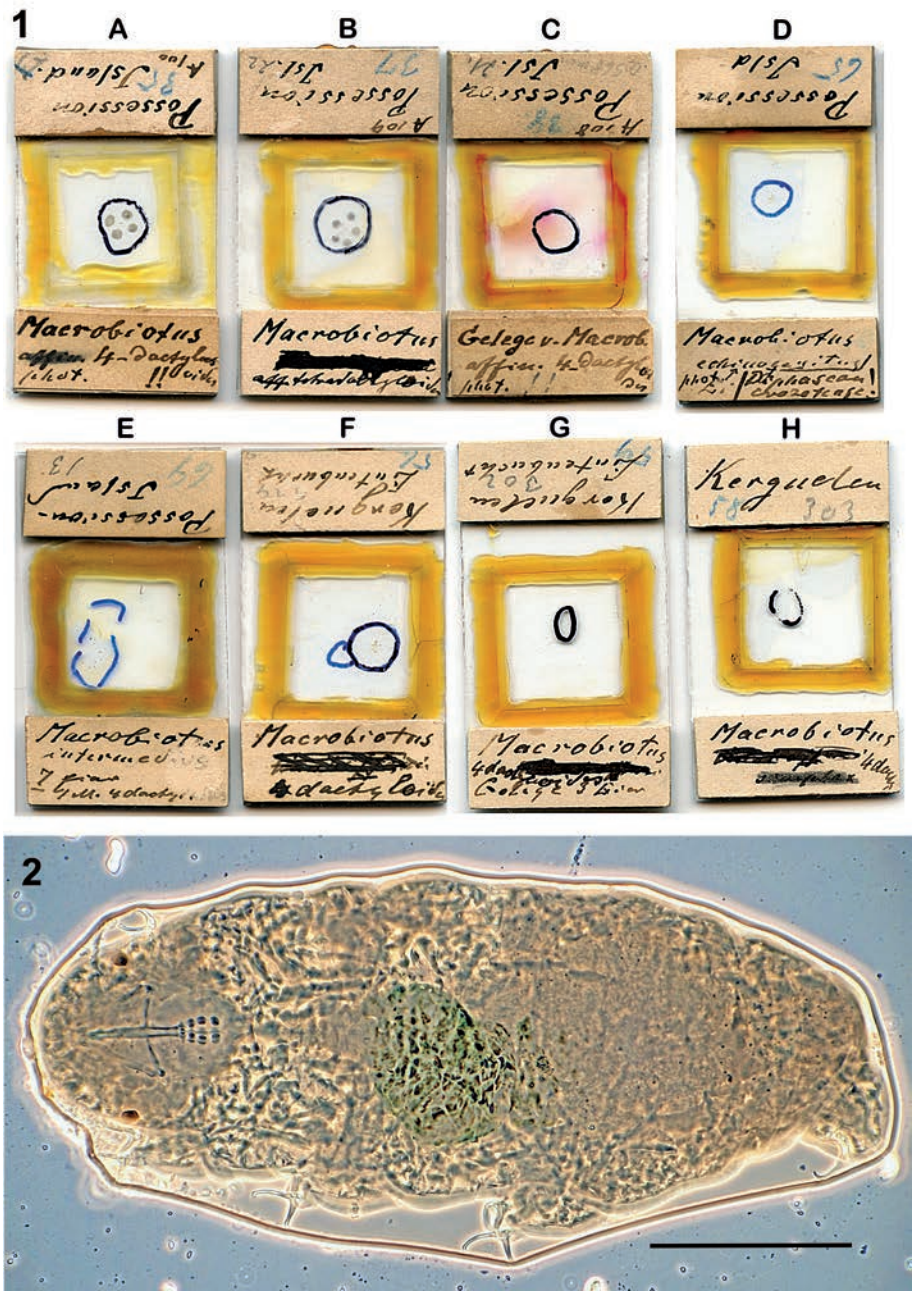


Fig. 1 and 2: *Isohypsibius tetradactyloides* (Richters, 1907), **1 A-H** Microslides with the taxon from Richters' collection; **2** Syntype in a remnant of the mounting medium (from the slide on Fig. 1 A). Scale bar in Fig. 2 = 100 µm.

Abb. 1 und 2: *Isohypsibius tetradactyloides* (Richters, 1907): **1 A-H** Mikroskopische Präparate aus der Tardigradensammlung von Richters; **2** Syntypus (siehe Präparat Fig. 1 A) mit Resten des Einbettungsmittels. Maßstab in Abb. 2 = 100 µm.

individual tardigrades under the cover glass or/and from the extreme clearing/deterioration of the body cuticular surface caused by the mountant. As a result, the cuticular sculpture ('granulation') which is present in this species is in most cases very difficult to discern. Moreover, only a few claws are sufficiently positioned for taking standard measurements.

Comparative material of *Isohypsibius asper* comes from maritime Antarctic (King George Is., Signy Is.), Crozet Archipelago (Possession Is.) and Kerguelen (altogether 49 specimens: for details see text below). The animals have been mounted on slides in Faure medium or polyvinyllactophenol (PVL) medium; the bulk of them is lodged at the Zoological Museum Hamburg, Centre of Natural History.

The tardigrades were examined and microphotographs were taken with the phase (PHC) - and differential interference contrast (DIC) microscopes ZEISS "Photomikroskop III" and "Axiomat", as well with scanning electron microscope (SEM) LEO 1512 and CamScan S4. For SEM examination tardigrades were prepared as described in DASTYCH et al. 2003**.** The measurements have been done only under phase contrast and using ocular micrometer. The morphometric indices and coefficients used in this paper are explained in DASTYCH et al. (2003) and DASTYCH (2004, 2006).

Abbreviations used: *cb* – claw base, *DIC* – differential interference contrast, *ec* – external claw, *hc* – hind claw, *lu* – lunula, *ic* – internal claw, *n* – sample size, *min-max* – minimum-maximum range, *mpl* – macroplacoid, *PHC* – phase contrast, *PT* – the whole buccal tube indices (comp. PILATO 1981; = *WTI* indices, see also DASTYCH 2006), *PVL* – polyvinyllactophenol, *r squared* (= r^2) – coefficient of determination, *SD* – standard deviation, *SEM* – scanning electron microscope, *ss* – stylet support, *V* – coefficient of variation, *pt ss* – stylet supports "anterior" index (= *WT SSA:* see also DASTYCH 2006), *0x̄* – (arithmetic) mean.

3. Results

3. 1. Redescription of *Isohypsibius tetradactyloides* (Richters, 1907)

(Figs 1-24)

Macrobiotus tetradactyloides sp. n.: RICHTERS 1907 (pp. 294-295; Plate XIX: Figs 32, 33, Plate XX : Figs 1, 2). Locus typicus: Île de la Possession (= Possession Island: Crozet Archipelago), Heard Island.

Macrobiotus tetradactylus GREEFF: RICHTERS 1904 (misidentification/lapsus linguae?)

Macrobiotus tetradactyloides: VANHÖFFEN 1906a, b: *nomen nudum*; MURRAY 1910, 1911; URBANOWICZOWNA 1924; URBANOWICZ 1925; RAHM 1928

Hypsibius tetradactyloides: THULIN 1911; RAHM 1925a, b; MARCUS 1928; RAHM 1932; CUÉNOT 1932; BARTOŠ 1933, 1934, 1937, 1939, 1941, 1942; IHAROS 1947, 1962, 1963, 1965, 1966, 1968, 1982; RAMAZZOTTI 1967, 1978; WEGLARSKA 1970; SLÁDEČEK 1977

Hypsibius (*Isohypsibius*) *tetradactyloides*: MARCUS 1929, 1930, 1933**,** 1936; RAMAZZOTTI 1956; MIHELČIČ 1960; RIGGIN 1962; WEGLARSKA 1962, 1965; SCHUSTER & GRIGARICK 1965; RUDESCU 1964; BARTOŠ 1967; BEASLEY 1968; BERTRAND 1975; MORGAN 1976, MORGAN & KING 1976: MAUCCI 1978; WRIGHT 1991

Hypsibius (*Isohypsibius*) *tetradactiloides* (sic !) : BERTOLANI 1946; MAUCCI 1951/1952; MIHELČIČ 1966

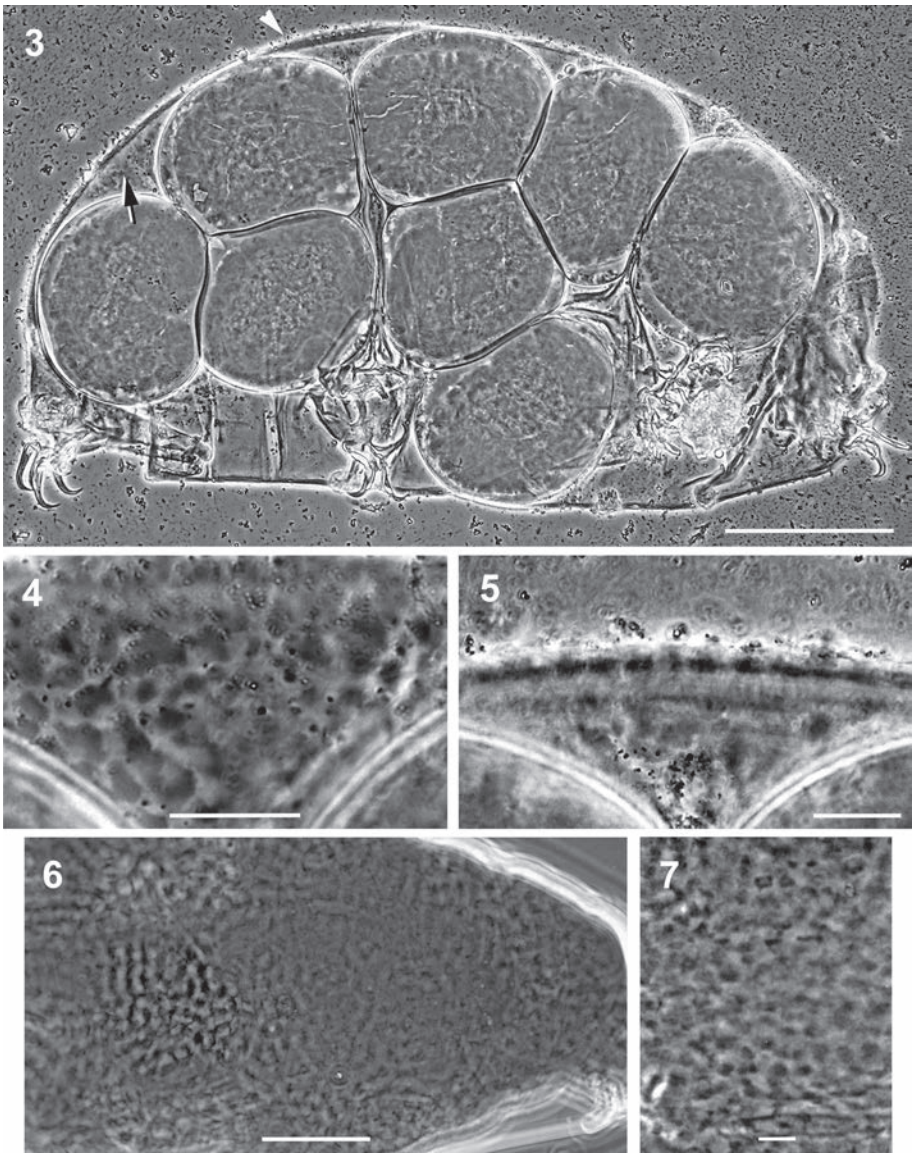
Hypsibius (*Isohypsibius*) *tetradasyloides* (sic !): SUDZUKI 1964

Isophisibius (sic!) *tetradactyloides:* WEGLARSKA & KUC 1980

Isohypsybius (sic!) *tetradactyloides*: SZYMANSKA 1994

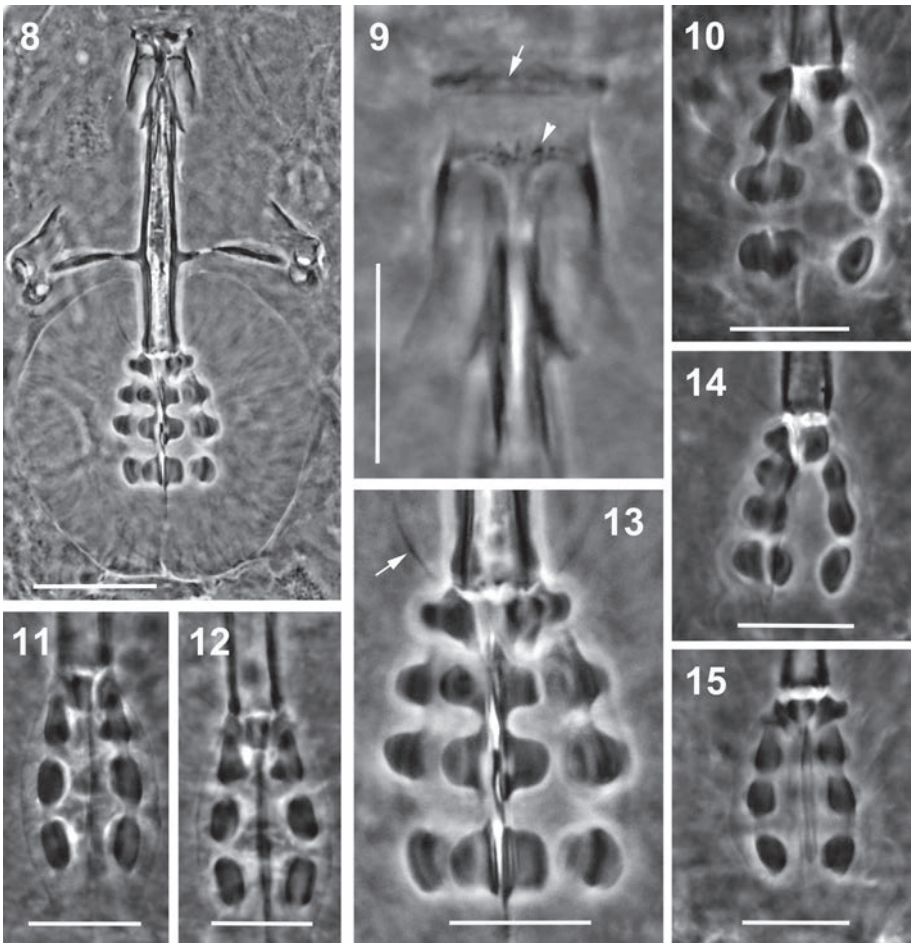
Isohysptybius (sic!) *tetradactyloides*: MOON & KIM 1988

Isohypsibius tetradactyloides: THULIN 1928; RAHM 1932; MATHEWS 1937; PILATO 1970, 1971, 1974; HECIAK 1976; BERTOLANI 1982; RAMAZZOTTI & MAUCCI 1983; IHAROS 1985; CLAPS & ROSSI 1984, 1988, 1997, ROSSI & Claps 1991, BISEROV 1986, MAUCCI 1986, DASTYCH 1987, 1988, 1997; KOVALCHUK 1987; BISEROV 1988, 1991, 1996; GARITANO-ZAVALA 1995; BISEROV et al. 2001; KINCHIN 1990; JORGENSEN & KRISTENSEN 1991; VAN ROMPU et al. 1991, 1992; MCINNES 1994; SÉMÉRIA 1994, 2003; BINDA et al. 1995; CHANG & RHO 1996; VAN ROMPU & DE SMET 1996; MEIER 1996; VARGHA 1996; DEGMA 1997; VARGHA



Figs 3-7: *Isohypsibius tetradactyloides* (Richters). **3** Exuvium with eggs, **4, 5** – exuvium's cuticular sculpture (details from Fig. 3, labeled with an arrow and an arrowhead, lateral view (4), view in profile (5). **6** Sculpture of the animal's body side. **7** Sculpture on the dorsum. PHC images. Scale bars in Figs 3, 5 = 50 μm, in Figs 4, 6, 7 = 10 μm).

Abb. 3-7: *Isohypsibius tetradactyloides* (Richters). **3** Exuvie mit Eiern. **4, 5** Skulpturierung der Exuvie (Details aus Fig. 3 mit einem Pfeil und einem Pfeilkopf markiert, lateral (4) und im Profil (5). **6** Skulpturierung der Körperseite. 7 Skulpturierung des Rückens. PHC-Aufnahmen. Maßstab für die Abb. 3, 5 = 50 μm, für die Abb. 4, 6, 7 = 10 μm.



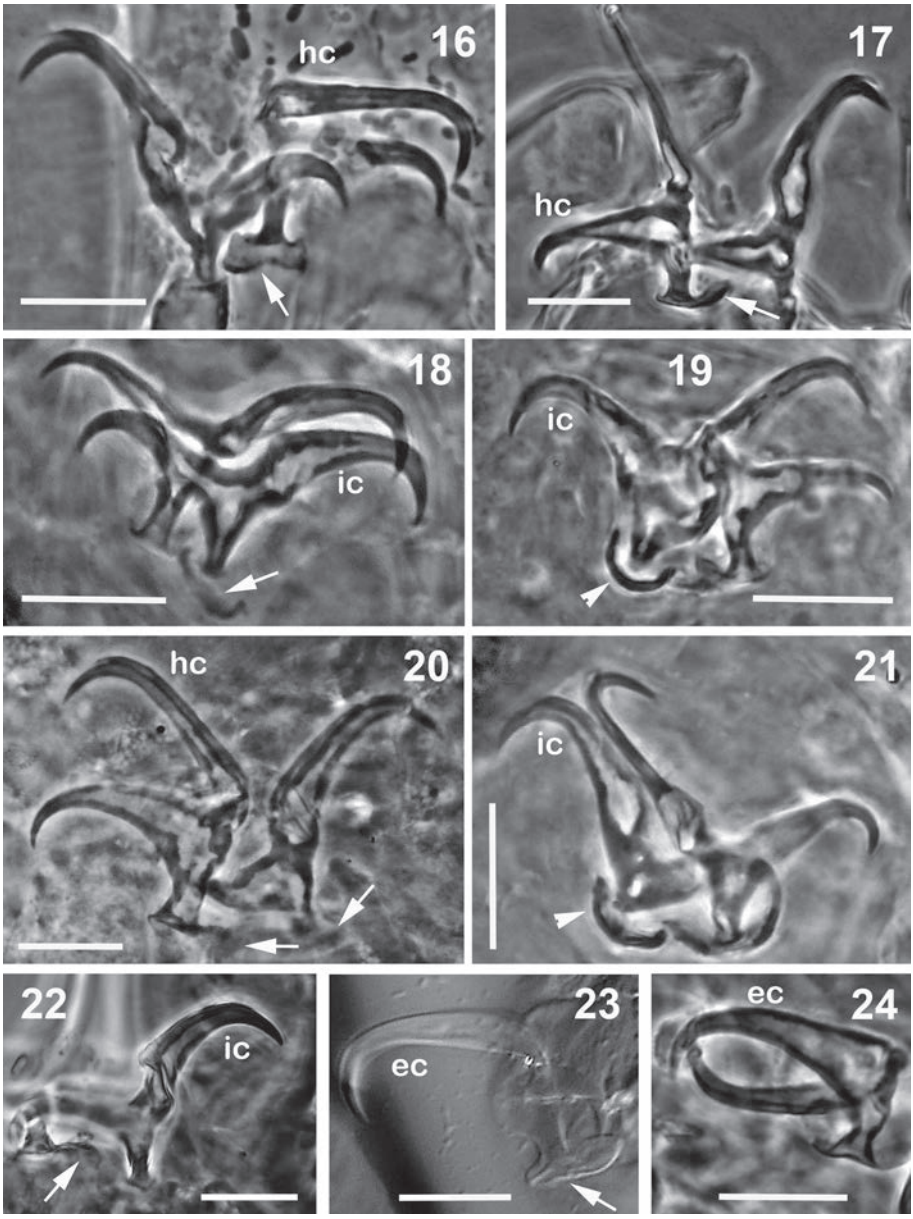
Figs 8-15: *Isohypsibius tetradactyloides* (Richters). **8** Buccopharyngeal apparatus (from Fig. 2). **9** Mouth cavity, dorsal view; structures at the mouth opening (arrows), mucrones (arrowhead). **10-15** Variability of placoids; note cuticular bar in 13 (arrow). PHC images. Scale bar in Fig. 8 = 20 μm, in Figs 9-15 = 10 μm.

Abb. 8-15: *Isohypsibius tetradactyloides* (Richters). **8** Buccalapparat (aus Abb. 2). **9** Mundhöhle, dorsal; Strukturen beim Mundoffnung (Pfeil), Körnchen (Pfeilkopf)**. 10-15** Variabilität der Plakoide; ein kutikulares Stäbchen in 13 (Pfeil). PHC-Aufnahmen. Maßstab für die Abb. 8 = 20 μm, für die Abb. 9-15 = 10 μm.

1998, YANG 1999, OPRAVILOVA & KUBICEK 1999; BATEMAN & COLLINS 2001; JORGENSEN 2001; KACZMAREK & BEASLEY 2002; LI & WANG 2005; GUIDETTI & BERTOLANI 2005, MILLER et al. 2005; BROECKNER et al. 2006; WANG & LIAN 2007; LI et al. 2007; GUIL 2008; GUIL et al. 2009, 2014; NELSON et al. 2010; FONTOURA et al. 2010; MEYER 2011, 2013.

3.1.1. Diagnosis and description

Material examined: 20 specimens and two exuviae mounted on eight microslides from Possession Island and Kerguelen (Fig. 1 A-H). Type material: Syntypes, eight animals and one exuvium with eight eggs on five micro-



Figs 16-24: *Isohypsibius tetradactyloides* (Richters), claws. **16**, **17**, **20** Leg IV. **19**, **21** Leg II. **18**, **23, 24** Leg II. **22** Leg I. Arrows point to the lunules, except Figs 18, 19, 21. PH-images except Fig. 23 (DIC). Scale bar = 10 μm.

Abb. 16-24: *Isohypsibius tetradactyloides* (Richters), Krallen: **16**, **17**, **20** Bein IV. **19**, **21** Bein III. **18**, **23**, **24** Bein II. **22** Bein I. Die Pfeile verweisen auf die Lunulen, außer Abb. 18, 19, 21. PHC-Aufnahmen außer Abb. 23 (DIC). Maßstab = 10 μm).

slides, i.e. 1+1+exuvium+4+2 tardigrades on each slide, respectively (Fig. 1 A-E) (all Possession Island).

Additional material: Twelve animals on two slides (eleven and one tardigrade: Fig. 1 F, H), one slide with exuvium containing three eggs (Fig. 1 G) (all Kerguelen).

Diagnosis (based on recovered type-material): Medium sized to large *Isohypsibius* with sculptured ('granulated') cuticle. Distinct eyes present. Pharynx with three macroplacoids, the first one very closely located to the pharyngeal apophyses. No microplacoids. Claws of *Isohypsibius* type, strongly developed, relatively large and with large lunules. The claw main branches on each claw distinctly longer than the secondary ones. Eggs smooth, laid in exuvium.

Description: Body 117.0-459.0 μm long, yellowish or light brownish in the mounted specimens. Some animals with greenish intestine contents. Eyedots blackish, relatively large (Fig. 2). The body cuticle, including legs, sculptured. The sculpture consists of irregularly sized knobs (tubercles, 'granules'), on average 3-5 μm, mostly arranged in a netlike, more than less irregular polygonal pattern (Figs 3-7, 25, 26).

Buccopharyngeal apparatus medium sized, mouth opening slightly ventroanterior and with a ring of distinct oval or roundish structures discernible in four animals (Fig. 9, arrow). The three largest animals with a row of several tiny granules (mucrones) in mouth cavity, just above and along the anterior edge of traverse crests (Fig. 9, arrowhead).

Buccal tube relatively wide, with distinct buccal crests (Figs 8, 9). No obvious terminal posterior apophyses on the tube could be discerned, but in their place the tube wall is slightly thickened (Figs 8, 13). Pharynx medium sized, spherical or slightly subspherical, with small roundish pharyngeal apophyses and three macroplacoids (Figs 8-15). The apophyses slightly smaller or of the same size as the first macroplacoid. Between pharyngeal apophyses and posterior edge of the buccal tube occur on both sides of the tube poorly discernible, very thin cuticular elongated bar (Fig. 13, arrow). The macroplacoids roundish or slightly elongated. No microplacoids. The first pair of macroplacoids located very closely to the pharyngeal apophyses or sometimes even partly covering them. Macroplacoids slightly increasing in size posteriorly, occasionally the first one of the same size as the second macroplacoid or, slightly larger. No lateral incisions in the caudal parts of macroplacoids. No microplacoids.

The claws moderately sized or large, well sclerotized (Figs 16-24). In the microslide preparations they are usually strongly distorted, particularly their branches (e.g. Fig. 24). The branches and the claws bases are distinctly sculptured inside, the main branches with definite but thin accessory spines. Claws with relatively large, thin and smooth structures, interpreted here as lunules (e.g. Figs 16, 23: arrow). The lunules are mostly strongly rolled up under the claw base and often disguised (covered) by artificial cuticular bulges. The bulges represent preparation artefacts (cuticular folds) at the claw base (e.g. Figs 19, 21: arrowhead). Thus, the lunules are largely very difficult to discern. No transversal barlike thickenings occur below bases of claws on legs I-III.

Eggs smooth, slightly oval, found in two exuviae, three (Kerguelen) and eight eggs (Possession Is.) in each exuvium.

3.1.2. Morphometric data

Measurements are in μm, all indices in %. Their values are presented in the following convention:

$0.\bar{x} \pm SD$ (*min-max*) [*n*] * *V* (for measurements);

$0.\bar{x} \pm SD$ (*min-max*) [*n*] * *V* / r^2 (for indices).

For the abbreviations and definitions see "Material and methods" and DASTYCH (2006).

A) Measurements (μm)

Body length	330.5 ± 88.5 (117.1-459.2) [21] * 26.7
Buccal apparatus length	73.3 ± 13.9 (40.5-90.0) [16] * 19.0
Pharynx length	38.7 ± 8.1(20.7-50.4) [14] * 21.2
Pharynx width	35.6 ± 8.2 (18.9-47.7) [14] * 23.1
Buccal tube length	40.2 ± 6.3 (23.4-47.7)[15] * 15.9
Stylet supports attachments	27.1 ± 4.6 (15.3-33.3) [15] * 16.9
Buccal tube width (external)	4.7 ± 2.0 (2.4-6.3) [17] * 25.5
Buccal tube width (internal)	3.0 ± 0.8 (1.4-4.1) [17] * 25.3
Macroplacoid row length	15.1 ± 3.1(7.2-18.5) [17] * 20.2
Macroplacoid 1 length	3.8 ± 1.0 (1.8-5.4) [17] * 26.6
Macroplacoid 2 length	3.8 ± 0.9 (1.8-4.8) [17] * 23.7
Macroplacoid 3 length	4.1 ± 1.0 (1.8-5.4) [17] * 24.0
Macroplacoid width	2.1 ± 0.6 (1.1-3.2) [14] * 27.9
External claw 1 length	(18.0, 22.5) [2]
External claw 1 base heigh	7.9 ± 1.1 (6.3-9.0) [6] * 14.4
External claw 1 main branch length	13.5 ± 2.5 (10.8-17.1) [6] * 18.9
External claw 1 secondary branch length	(9.0, 11.2) [2]
Internal claw 1 length	(13.5) [1]
Internal claw 1 base height	6.6 ± 0.9 (5.0-7.2) [5] * 13.9
Internal claw 1 main branch length	(9.0, 13.5) [2]
Hind claw length	(28.2, 37.8) [2]
Hind claw base height	(9.0, 13.5) [2]
Hind claw main branch length	(19.8, 22.5) [2]
Hind claw secondary branch length	(15.3, 20.7) [2]
Fore claw length	(14.9, 22.5, 27.0) [3]
Fore claw base height	(7.2, 9.0, 9.0) [3]
Fore claw main branch length	15.1 ± 4.9 (8.1-22.5) [4] * 32.5

B) Indices

PT stylet supports, *pt ss*	67.5 ± 2.1 (64.2-72.3) [15] * 3.2/0.965
PT buccal tube width (ext.)	11.8 ± 1.3 (9.2-13.5) [15] * 11.4/0.850
PT buccal tube width (int.)	7.7 ± 1.5 (6.0-13.5) [15] * 14.9/0.724
PT macroplacoid row length	37.5 ± 3.7 (30.8-42.9) [15] * 9.8/0.829
PT macroplacoid 1 length	9.7 ± 1.9 (5.7-11.9) [15] * 20.5/0.436
PT macroplacoid 2 length	9.6 ± 1.7 (6.4-12.7) [15] * 17.4/0.523
PT macroplacoid 3 length	10.9 ± 3.7 (7.5-22.8) [15] * 33.5/0.548

Eggs (n = 3 + 8, in two exuviae)
Size: 77-96 μm x 66-74 μm

Variability: The examined individuals of *I. tetradactyloides* are characterized by a high variability of the cuticular sculpturing on the body surface, including even its extreme clearing/vanishing. It resulted largely from the long-time deteriorating influence of the mounting medium on the structures (knobs, 'granules') and their soft texture (see also remarks in § 2

and 4.1). Moreover, distinct variability occurs in the length and shape of microplacoids. Remarkable is also relatively wide range of the *pt ss* index (= stylet support index) with its values equal 64.2-72.3 %. This limits the application of *pt ss* as a good identification character for *I. tetradactyloides*. The index is generally considered as having high diagnostic importance (PILATO 1981) and already standardized for eutardigrades. Therefore of interest here are low values of the coefficient of variation of the index *pt ss* ($V = 3.2$) and very high values of its coefficient of determination ($r^2 = 0.965$), confirming generally the stability of *pt ss* as a significant discrimination character.

3.1.3. Distribution

Isohypsibius tetradactyloides has been worldwide recorded, excepting the Continental Australia (for a summary of the majority of its records see MCINNES 1994, more recent data are presented above).

In the original description RICHTERS (1907a) cited barely "Possession-Eiland, Heard-Eiland", i.e. two localities representing loci typici for *I. tetradactyloides*. Strangely, RICHTERS then did not mention the occurrence of the species also on Kerguelen in the paper (l.c.), although he reported the taxon erroneously as *Macrobiotus tetradactylus* from that archipelago in his earlier publication (l.c. 1904). The microslides with *I. tetradactyloides* from Kerguelen are also present in the recently recovered material of RICHTERS (Fig. 1 F-H). However, the latter animals formally cannot represent type material, as being not found in the locus typicus, and they are listed here under "Additional material". No microslide with type specimen(s) of *I. tetradactyloides* from Heard Island, another type locality, is present in the rediscovered collection.

3.1.4. Nomenclatural note

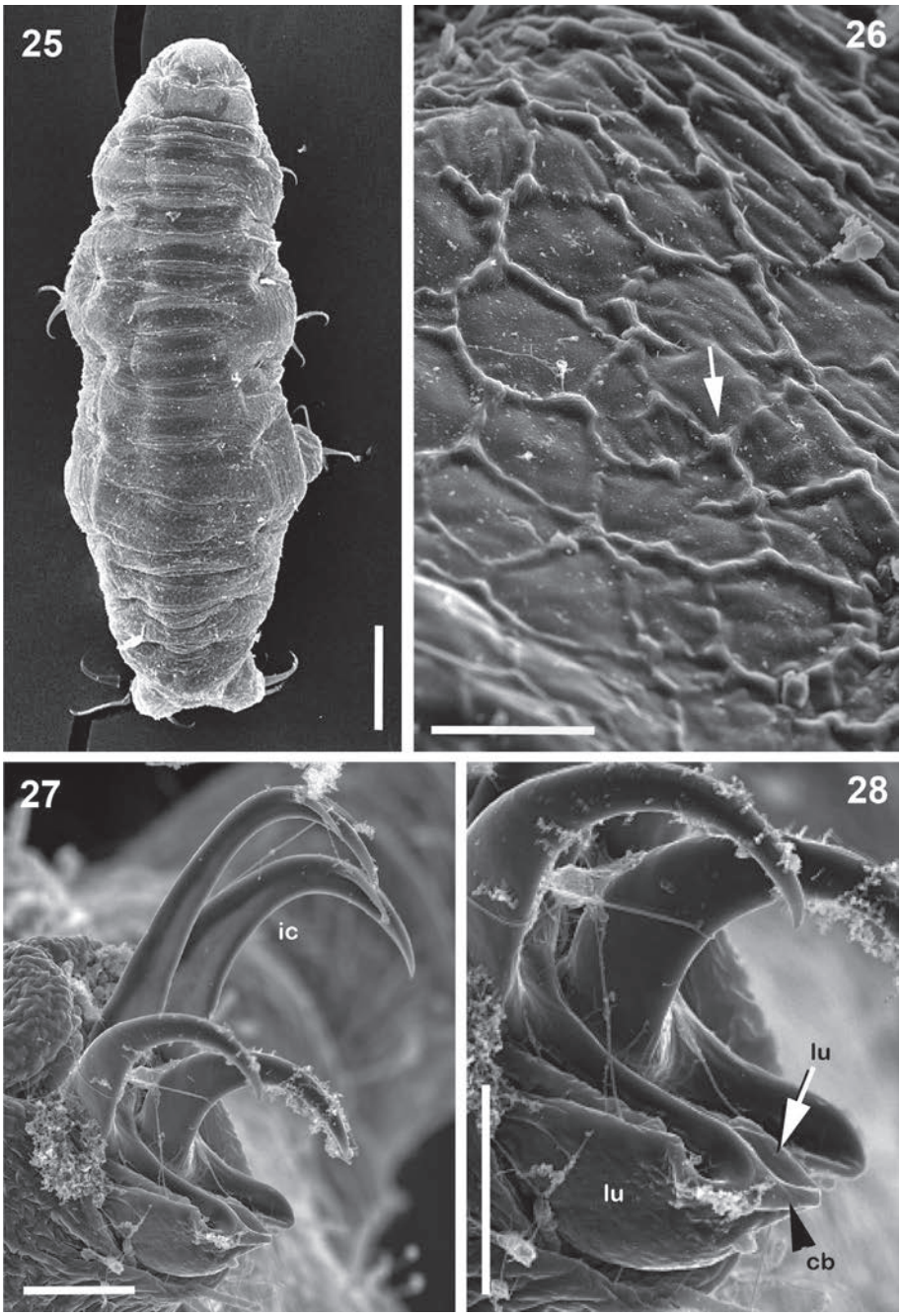
There is some confusion concerning the publication date of the original description of *I. tetradactyloides,* quoted in the literature as 1907 or 1908. The latter date is presented in the volume 9 of the series "Deutsche Südpolar-Expedition 1901-1903". However, according to the list of contents of this volume and within its (sub)volume "Zoology, Volume 1" (= "Inhalt des IX. Bandes", "Zoologie I. Band"), the paper by RICHTERS and three publications of other authors have been made public in the issue No. 4 of the volume, distributed already in March 1907 ("Heft 4, ausgegeben im März 1907").

Thus, considering the Article 21.3 of the ICZN, the correct citation of the date of the original description of *I. tetradactyloides* (and the respective publication) should be 1907 and not 1908. The above is valid (i.e. the date 1907) also for other new tardigrade species described in the same article by RICHTERS, namely *Macrobiotus* (now *Hypsibius*) *murrayi,* and *Diphascon crozetense*. For two other species described in the same paper also as "n. spec.", i.e. *Echiniscus kerguelensis* and *Macrobiotus* (now *Acutuncus*) *antarcticus*, the correct data is 1904, however. It is due to double description of these two taxa by RICHTERS, defined by him for the first time already in 1904 (see l.c., 1904).

MARCUS (1928, 1929, 1936) in his influential monographs cited RICHTERS' (l.c.) article and noted at the characteristics of *I. tetradactyloides* only as "1908 (07)". He provided no further comment, what contributed to the above ambiguity. Nevertheless, most authors after these monographs (and all of them before) cited the species' original description (and the date of the publication) as 1907.

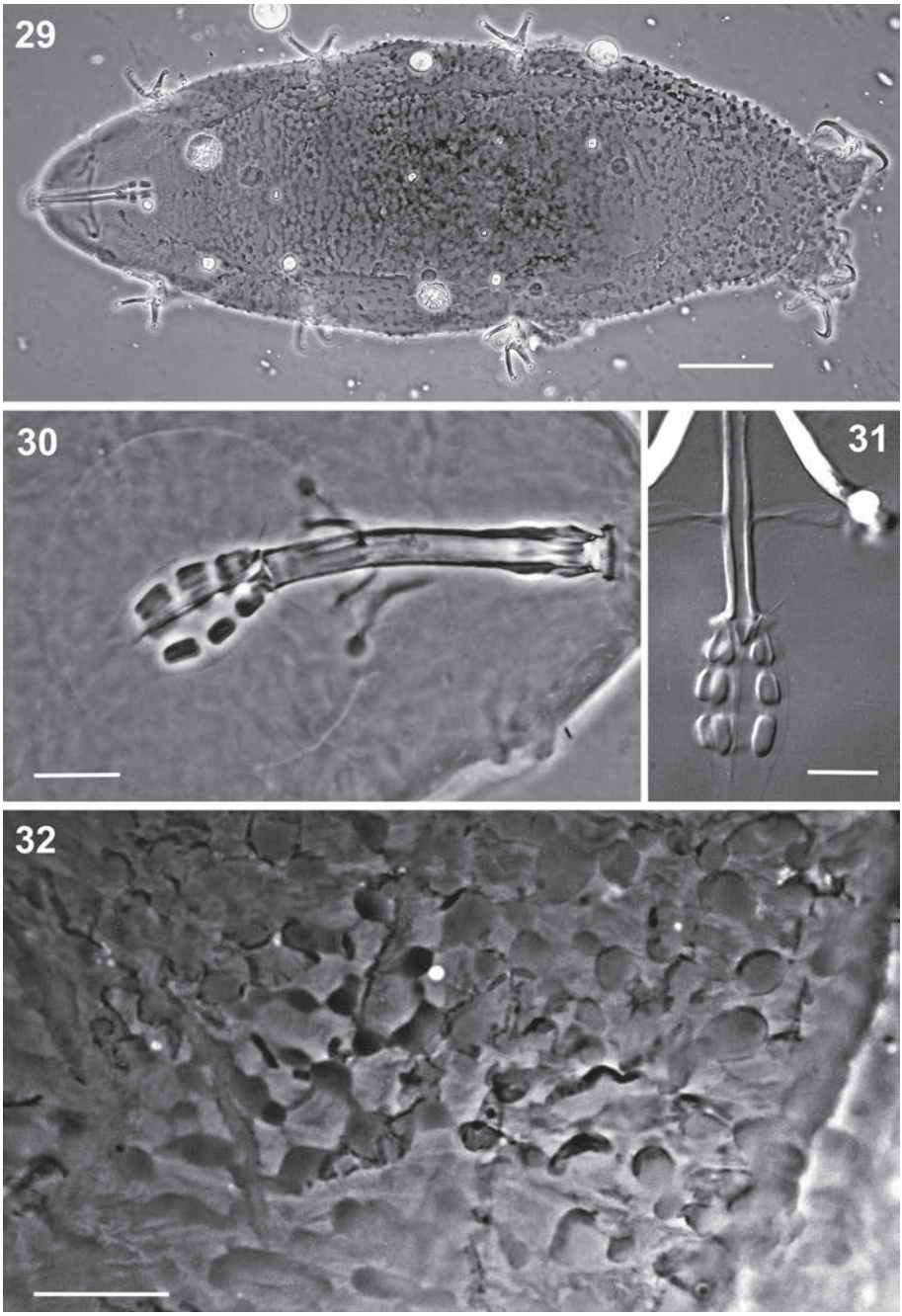
3.2. Supplementary notes on the morphology of *Isohypsibius asper* (MURRAY, 1906) (Figs 25-46)

Macrobiotus asperus n. sp.: MURRAY 1906. Locus typicus: South Orkneys
Isohypsibius tetradactyloides (Richters, 1907): **synonym nov.**



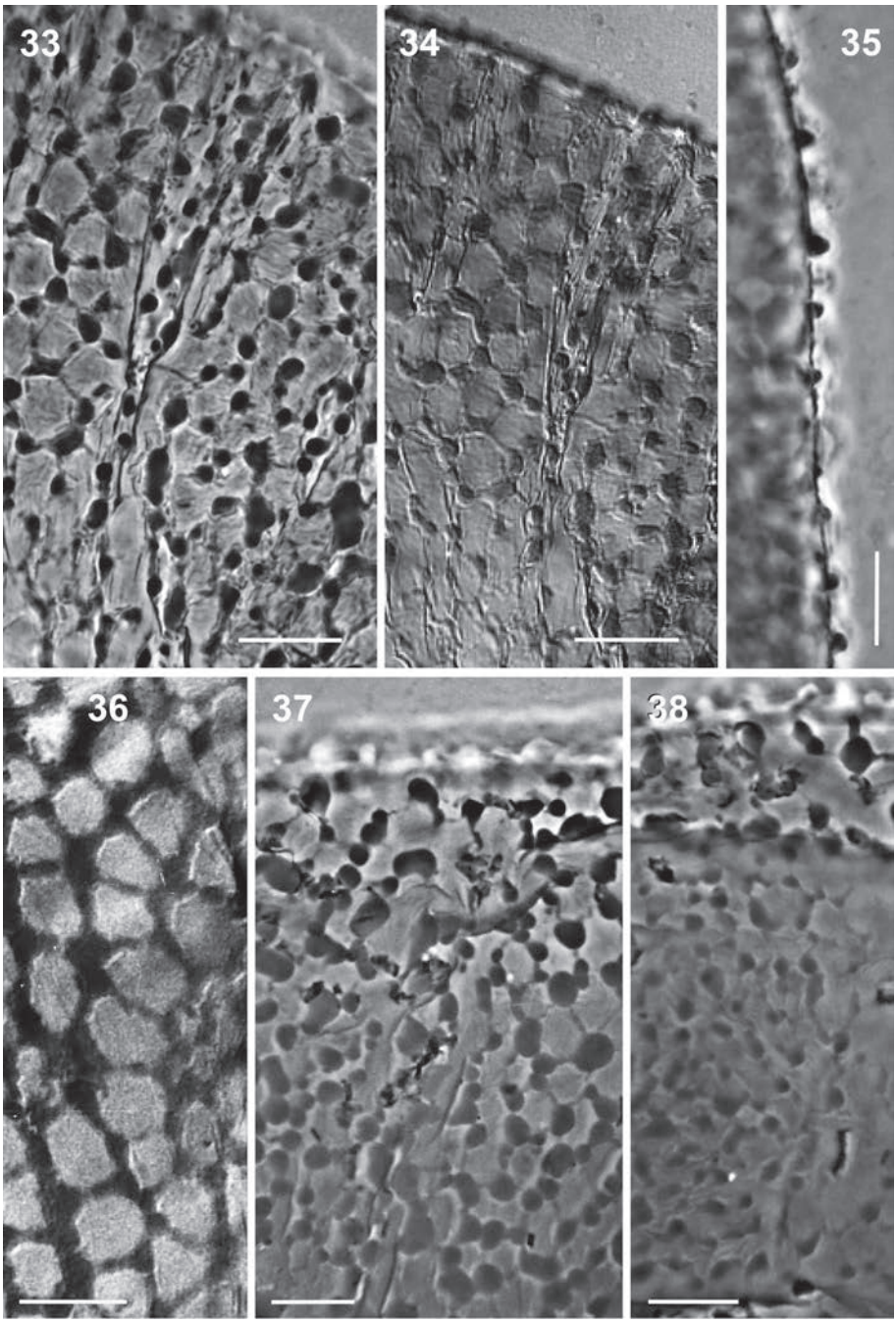
Figs 25-28: *Isohypsibius asper* (Murray). **25** Dorsal view. **26** Cuticular sculpture of the posterior part of the body, lateral view; knob (arrow). **27-28** Claws and their bases of leg III. SEM images. Scale bar in Fig. 25 = 50 μm, for Figs 26-28 = 5 μm.

Abb. 25-28: *Isohypsibius asper* (Murray): **25** Dorsalansicht. **26** Skulpturierung der Kutikula am Körperende, Seitenansicht.; Tuberkel (Pfeil). **27-2**: Krallen und deren Basis von Bein III. REM-Bilder. Maßstab in Abb. 25 = 50 μm, in Abb. 26-28 = 5 μm.

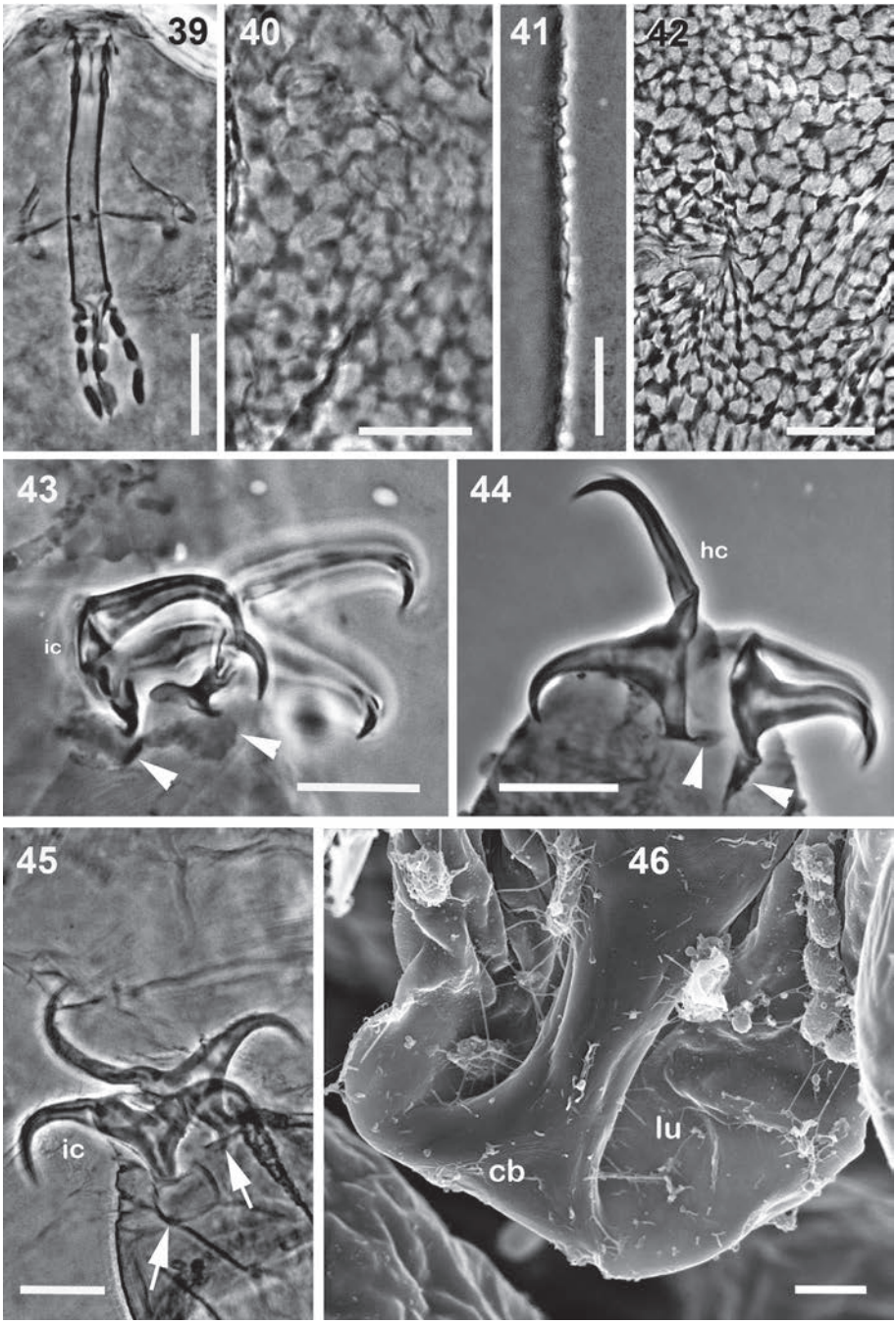


Figs 29-32: *Isohypsibius asper* (Murray, 1906). **29** Dorsal view. **30** Buccopharyngeal apparatus, lateral view. **31** Placoids, dorsally. **32** Cuticular sculpture of the hind of the body, dorsal view. PHC-images except Fig. 31 (DIC). Scale bar in Fig. 29 = 50 μm, in Figs 30-32 = 10 μm.

Abb. 29-32: *Isohypsibius asper* (Murray, 1906). **29** Dorsalansicht. **30** Buccalapparat, seitlich. **31** Plakoide, dorsal. **32** Skulpturierung des Kutikula am Körperende, dorsal. PHC-Aufnahmen außer Abb. (DIC). Maßstab in Abb. 29 = 50 μm, in Abb. 30-32 = 10 μm.



Figs 33-38: *Isohypsibius asper* (Murray, 1906), cuticular sculpture. **33-36** Body sides; view in profile (35); **37** Dorsum. **38** Hind of the body, ventral. PHC-images, except Figs 34, 36: DIC. Scale bar = 10 μm.
Abb. 33-38: *Isohypsibius asper* (Murray, 1906), Kutikulaskulpturierung. **33-36** Körper, lateral; im Profil (35). **37** Rücken. **38** Körperende, ventral. PHC-Aufnahmen außer Abb. 34, 36 (DIC). Der Maßstab = 10 μm.



Figs 39-46: *Isohypsibius asper* (Murray, 1906). **39** Buccopharyngeal apparatus. **40-42** Cuticular sculpture dorsally (40), laterally (41-42; 41 view in profile). **43-45** Claws on leg II, IV and III, respectively. Lunulae (arrows). **46** Claw base with lunula, leg II. PHC-images except Fig. 46 (SEM). Scale bar for Fig. 46 = 1 μm, for Figs 39-45 = 10 μm..

Macrobiotus asper: Richters 1907, 1908; Murray 1910, 1911; Rahm 1928
Hypsibius asper Thulin 1911; Marcus 1928
Hypsibius (*Isohypsibius*) *asper*: Marcus 1929, 1936, 1940; Weglarska 1959; Rudescu 1964; Jennings 1976a, b, 1979; Sudzuki 1964
Isohypsibius asper: Thulin 1928; Sudzuki & Shizmoizumi 1967; Ramazzotti & Maucci 1983; Dastych 1984, 1988, 1997; McInnes & Ellis-Evans 1987; Rossi & Claps 1991; Utsugi & Ohyama 1991, 1993; McInnes 1994, 1995; McInnes & Pugh 1999; Vargha 2000; Convey & McInnes 2005; Sands at al. 2008

3.2.1. Diagnosis and description

Material examined: South Orkney Islands (Signy Island): Heywood Lake, 19.1.1994, ded. S. McInnes - 3 specimens; South Shetland Islands (King George Island: 1) at Bellingshausen Station - 4 specimens, 2) Uchatka Point - 9 specimens; for details see Dastych 1984); Crozet Archipelago (Possession Island): goat path ("Chemin des chèvres"), 100 m a.s.l., ca 300 m from seashore, 14.1.1997, leg. Y. Frenot - 5 specimens; Kerguelen (Grande Terre: Lac Superior), submerged moss, 15.1.2002, leg. W. H. De Smet - 20 specimens, excluding 8 used for SEM.
Diagnosis: as for *Isohypsibius tetradactyloides* (Richters, 1907).
Description: Body 156-423 µm long, light-brownish or brown, with large, black eye-spots located anteriorly. The thick body cuticle, including legs, is sculptured ('granulated') and, to some extend, the sculpture occurs also on the body venter, mostly in its rear part (Fig. 38). The sculpture consists of small, irregularly sized knobs (tubercles, 'granules') on average 3-5 µm, more or less increasing in size towards the body rear (Figs 25, 29). The knobs are mostly connected by cuticular striae or thin bars, creating then distinct but variable net-like pattern on the body surface. The pattern is usually polygonal in shape (Figs 29, 32-38, 40-42). The knobs and the striae seem to be of soft texture and their shape and size can strongly vary, including their extreme clearing through the mounting medium. Thus, in some examined specimens the knobs and the net-like pattern were hardly visible in a light microscope, making then an impression of the presence of only a smooth cuticular surface.
Buccopharyngeal apparatus median sized, pharynx roundish, with three macroplacids mostly increasing in size posteriorly. The first macroplacoids located very close to the pharyngeal apophyses (Figs 30, 31, 39). Sometimes the first and the second macroplacoid of the same length or the first slightly longer than the second one. No microplacoids.
The claws medium sized or large (Figs 25, 27, 43-45), well sclerotized and distinctly sculptured inside (Figs 44, 45). Main branches with thin and well discernible accessory spines. Each claw with a large, thin, and smooth lunula, mostly rolled up under the claw base **(**Fig. 46) and then poorly or even not discernible. No transversal bar below the bases of claws on legs I-III.

3.2.2. Some morphometric data

A) Measurements (µm)

Abb. 39-46: *Isohypsibius asper* (Murray, 1906). **39** Buccalapparat. **40-42** Kutikulaskulpturierung dorsal (40), seitlich (41-42; 41 im Profil). **43-45** Krallen an Bein II, IV und III. **46** Krallenbasis mit Lunula, Bein II. PHC-Aufnahmen, außer Abb. 46 (SEM). Maßstab für Abb. 46 = 1 µm, für Abb. 39-45 = 10 µm.

Body length	286.5±78.9 (151.0-423.0) [15] * 27.5
Buccal tube length	19.4±2.5 (15.0-23.0) [15] * 13.0
Stylet support attachments	13.4±1.7 (10.0-16.0) [15] * 13.2

B) Indices

PT stylet supports, *pt ss* 69.0±1.8 (66.7-72.5) [15] * 2.7 / 0.965

Variability: The cuticular sculpture is very variable, ranging from distinct structures to hardly or even not discernible cuticular ornamenting. Variable is also the shape of macroplacoids, from short, corn-like structures to relatively elongated bars. The lengths of the first and second macroplacoid vary as well, the first one being more often slightly longer than the second one. The lunules on claws were mostly very difficult to discern, due to their rolled-up position at the claw base and, frequently, as well as an additional masking effect caused by cuticular folds occurring often at those bases. Noteworthy is wide range (66.7-72.5 %) of the stylet support index (*pt ss*) alongside with very high values of its coefficient of determination (*r* squared) and its low coefficient of variation (*V*). That wide range suggests, however, relatively low advantage of the index as identification character in this species. Until now the index *pt ss* has not been presented for *I. asper*.

3.2.4. Distribution

South Shetland Islands, South Orkney Islands, South Georgia, Kerguelen and Crozet Archipelago. *I. asper* has been also reported from the Northern Hemisphere (Polen, Romania, Ukraine and recently Hungary: WEGLARSKA 1959, RUDESCU 1964, VARGHA 2000), but these records represent erroneous identifications (comp. DASTYCH 1984).

3.2.5. Nomenclatural note

MURRAY (1906) originally named his new species *Macrobiotus asperus* and not *M. asper*, although the latter specific name is cited throughout the whole literature. It results from the first misspelling of the original specific name by RICHTERS (1907a), which after that has never been corrected. As the misspelled name "*asper*" is already well established in the literature, an application to the Nomenclatural Commission of the ICZN for its change to "*asperus*" should not be recommended, due to possible confusion.

4. Diskussion

4.1. Historical perspective and comments

Over the last century the short original description of *I. tetradactyloides* has been successively repeated, supplemented or compiled by various authors (see their list at the species redescription). RAHM (1925a) reported for the first time *I. tetradactyloides* from the Northern Hemisphere (Eifel, Germany) and MARCUS in his first tardigrade monograph (1928) recorded the taxon at Sager Meer bei Oldenburg (Germany) and later (l.c. 1930) from Zermatt (Switzerland). MARCUS (1928, 1929, 1936) most decidedly influenced the present understanding of this species. He initially illustrated the description of *I. tetradactyloides* with original figures by RICHTERS (1907a), including his own drawing based on RICHTERS microphotograph (MARCUS 1928: Fig. 236a). In his second monograph (MARCUS 1929), the author provided, apart from figures the mentioned above by RICHTERS, two unpublished drawings of the species (claw and buccopharyngeal apparatus) furnished him by THULIN (MARCUS

1929: Figs 332 C and E). Supposedly they are based on specimens from Sweden. The last monograph by Marcus (1936) has already no original illustrations of *I. tetradactyloides* by Richters (l.c.), but, apart from the figures mentioned by Thulin, two additional drawings of this species. The latter are, however, based on Marcus' material from Africa (Marcus 1933: Ivory Coast) and his unpublished material from the Harz Mts (Germany) (Marcus 1936: Figs 248 A and B; see also Marcus 1933: "Harz", "Broken"). Strangely, Marcus presented in figure 248 B (specimen from the Harz Mts) distinct microplacoids in the pharynx, a character never mentioned in any description(s) of *I. tetradactyloides*. The compilation by Marcus includes probably at least three different taxa in the characteristics of this species. This, with all presented illustrations (Marcus 1936) heavily predisposed the understanding and interpretation of *I. tetradactyloides* by successive tardigradologists, including the recent and influential monographs on Tardigrada by Ramazzotti (1972) and Ramazzotti & Maucci (1983). The latter authors uncritically repeated the description and all figures provided by Marcus (1936). In consequence and since then various similar *Isohypsibius* spp. with a smooth cuticle, three macroplacoids and without cuticular bars under claws of I-III pair of legs have often been erroneously reported as *I. tetradactyloides* and some of them originally illustrated (e.g. Bertolani 1982: Fig. 32, Dastych 1988: Plate 16a). All these ambiguities resulted from a vague, in part erroneous original description followed by different interpretations not based on type material. All these contributed to the incorrect recognition of this taxon as a worldwide distributed species.

Since the original description of *I. asper*, several authors provided illustrations and supplementing notes on its morphology, based on examination of their own materials from the sub-/and Antarctic region (Richters 1908; Marcus 1940; Jennings 1976a, b, 1979, Dastych 1984; Mcinnes 1995). The species is now relatively well characterized. The type of cuticular sculpture of the body surface plays a very important role as the discriminating feature in this taxon (and in tardigrades generally) and the marked variability of this ornamentation in *I. asper* has been discussed by various authors. Murray (1906: p. 330) mentioned in the original description alleged soft texture of the cuticular granulation and its bad state after preservation. Richters (1908: p. 10) confirmed Murray's observation when examining material of *I. asper* from Kerguelen (provided by the Swedish Antarctic Expedition); he wrote "... auch bei meinen Konservierungsversuchen verschwanden die Körner der Cuticula; die konservierten Tiere zeigten dieselbe polygonale Felderung wie Präparate von *M. sattleri*..." (= "...also during my preserving attempts the cuticle tubercles vanished; the preserved animals then exhibited the same polygonal network like preparations of *M. sattleri*..."; translation H.D.). Marcus (1940: Fig. 2d) was the first who supplied a good illustration of the specific cuticular sculpture in *I. asper*. The detailed characteristics of this sculpture by Marcus (1940) were later confirmed by other workers (Dastych 1984: Fig. 16 b, f, Phot. 26, 27; Mcinnes 1995: Fig. 9a, d; this paper: Figs 26, 32-38, 40-42).

4.2. Concluding remarks

Analysis and comparison of available taxonomic characters found in specimens of *Isohypsibius tetradactyloides* from Richters collection and between those of *Isohypsibius asper,* the latter originating from various sub-Antarctic islands (including the type locality of the former taxon: Possession Is.), leave no doubts that all these presently examined animals represent the same (morphological) species. The conclusion comes from the same type and appearance of specific

cuticular sculpture, buccopharyngeal apparatus and claws. Consequently, the taxon *I. tetradactyloides* (Richters, 1907) should be recognized as the junior subjective synonym of *I. asper* (Murray, 1906).

The past and long-lasting taxonomic ambiguities concernig *I. tetradactyloides* arouse chiefly from incorrect information in the original description about the alleged presence of a smooth cuticular body surface. RICHTERS (1907a: Plate XX, Fig. 2) photographed and published the exuvium of *I. tetradactyloides*, but overlooked the specifically sculptured cuticle in this species. However, as shown here in the same exuvium, this sculpturing is clearly seen (see Figs 3-5). The mistake is supposedly connected with the soft texture of the sculpture, which can often be reduced to a faint or even hardly visible ornamentation after preparation (see comments in § 2.1). Interestingly, RICHTERS (1908) examined also material of *I. asper* from Kerguelen and then noted such a vanishing of the cuticular sculpture. Nevertheless, he had not equated these specimens with the animals which he described earlier from Possession Is. as *I. tetradactyloides*.

From the worldwide recognized distribution of the now synonymised *I. tetradactyloides,* only these data, which involve reports of the taxon from the southern hemisphere, can be, after revision, attributed to *I. asper*. Most probably also (not revised) information about the second locus typicus of the former taxon provided by RICHTERS (1907a) belongs to them, i.e. Heard Island. Hitherto, *I. asper* has been reported from the maritime Antarctic and several sub-Antarctic islands (for details see § 3.2.3) but, to my knowledge, still not from the continental Antarctica.

Acknowledgements

I very much thank Dr. Jason DUNLOP (Museum für Naturkunde, Berlin), Mr. Andreas ALLSPACH (Senckenberg Forschungsinstitut, Frankfurt a. M.) for access to the specimens of *I. tetradactyloides* in the remains of the RICHTERS collection of Tardigrada and Dr. Yves FRENOT (Universitè de Rennes, Paimpont), Dr. Sandra J. MCINNES (British Antarctic Survey, Cambridge) as well Prof. Dr. Willem H. DE SMET (University of Antwerp) for making comparative material of *I. asper* available to me. I am very grateful to Ms. Renate WALTER for her assistance in obtaining SEM micrographs and Dr. Frank FRIEDRICH (both Universität Hamburg) for admittance to the SEM facility. I am thankful to Prof. Dr. Hartmut GREVEN (Universität Düsseldorf) for his valuable comments. All support for this project from the University Hamburg is gratefully acknowledged.

Literature

BARTOŠ, E., 1933: Tardigrada z okolic Oravy. – Priroda **26**, 149-151.

BARTOŠ, E., 1934: Prispevek k poznani Tardigrad Č.S.R. – Časopis Československé Společnosti Entomologické **31**, 50-58, 99-107.

BARTOŠ, E., 1939: Tardigraden aus Böhmen und der Slovakei. – Zoologischer Anzeiger **127** (3/4), 95-101.

BARTOŠ, E., 1941: Studien über die Tardigraden des Karpathengebietes. – Zoologische Jahrbücher (Systematik) **74**, 435-472.

BARTOŠ, E., 1942: Prispevek k faune ceskych Tardigrad. II a III. – Sbornik Prirodovedeckego klubu v Brne **24**, 1-5.

BARTOŠ, E., 1967: Želvusky-Tardigrada. – Fauna ČSSR **17**, 1-190.

BATEMAN, L., COLLINS, M., 2001: A preliminary account of the tardigrades of Newfoundland. – Zoologischer Anzeiger **240**, 223-232.

BEASLEY C.W., 1967: Tardigrades from Kansas. – Transactions of the Kansas Academy of Science **70**, 464-470.

BERTOLANI, M., 1946: Ulteriore contributo alla conoscenza dei tardigradi italiani. – Atti della Societa Toscana di Scienze Naturali **54** (5), 1-4.

BERTOLANI, R., 1982: Tardigradi. – In: Guide per il riconoscimento delle specie animali delle acque interne italiane, Consiglio Nazionale delle ricerche AQ/1/168 **15**, 1-103.

Bertrand M. 1975: Répartition des Tardigrades «terrestres» dans le Massif de L'Aigoual. – Vie et Milieu **25**, 283-298.

Binda, M.G., De Zio Grimaldi, S., Pilato, G. 1995: Tardigrada. – Checklist delle specie della fauna Italiana, Edizione Calderini, Bologna **107**, 1-10.

Biserov, V.I., 1986 : Terrestrial water bears from the North Caucasus. – Zoologicheskii Zhurnal **65**, 981-993.

Biserov, V.I., 1988: Limnetic tardigrades of some areas in the USSR. – Zoologicheskii Zhurnal **67**, 1799-1811.

Biserov, V.I., 1991: An annotated list of Tardigrada from European Russia. – Zoologische Jahrbücher (Systematik) **118,** 193-216.

Biserov, V.I., 1996: Tardigrades of the Taimyr peninsula with descriptions of two new species. – Zoological Journal of Linnean Society **116**, 215-237.

Biserov, V.I., Dudichev, A.L., Biserova, N.M., 2001: Preliminary data on tardigrades of Lake Biwa (Japan). – Arthropoda Selecta **10**, 307-310.

Boeckner, M., Collins, M., Finney-Crawley, J., Bateman, L., 2006: The Bryofauna of Remote Coastal Labrador: including a review of current Canadian records. – Zootaxa **1105**, 1-16.

Chang, C.Y., Rho, H.S., 1996: *Isohypsibius granditintinus*, a new psammobenthic tardigrade from an estuary of South Korea. – Korean Journal of Systematic Zoology **12**, 245-252.

Claps, M.C., Rossi, G.C., 1984: Contribucion al conocimiento de los tardigrados de Argentina. IV. – Acta Zoologica Lilloana **38**, 45-50.

Claps, M.C., Rossi, G.C., 1988: Tardigrados de Argentina VI. – Iheringia, Sér. Zool., Porto Alegre **67** (3-11), 3-11.

Claps, M.C., Rossi, G.C. ,1997: Tardigrados de Uruguay, con descripcion de dos nuevas especies (Echiniscidae, Macrobiotidae). – Iheringia, Sér. Zool., Porto Alegre **83**, 17-22.

Convey, P., McInnes, S.J. 2005: Exceptional tardigrade-dominated ecosystem in Ellsworth Land, Antarctica. – Ecology **86**: 519-527.

Cuénot, L., 1932. Tardigrades. – Faune de France **24**, 1-96.

Dastych, H. 1984: The Tardigrada from Antarctica with description of several new species. – Acta zoologica cracoviensia **27**, 377-436.

Dastych, H., 1987: Altitudinal distribution of Tardigrada in Poland, pp. 169-176. In: Biology of Tardigrades (Bertolani, R., ed.). Proc. 4th Int. Symp. Tardigrada, Modena, September 3-5, 1985. – Selected Symposia and Mongraphs U.Z.I., Mucchi, Modena.

Dastych, H., 1988: The Tardigrada of Poland. – Monografie Fauny Polski **16**, 1-255.

Dastych, H., 1990: *Isohypsibius sattleri* (Richters 1902), a valid species (Tardigrada). – Senckenbergiana biologica **71**, 181-189.

Dastych, H., 1991: Redescription of *Hypsibius antarcticus* (Richters, 1904), with some notes on *Hypsibius arcticus* (Murray, 1907) (Tardigrada). – Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut **88**, 141-159.

Dastych, H., 1997: Tardigrada-Niesporczaki. – Checklist of Animals of Poland, Krakow (Institute of Systematics and Evolution, Polish Academy of Sciences) **4**, 141-144.

Dastych, H., Kraus, H., Thaler, K. 2003: Redescription and notes on the biology of the glacier tardigrade *Hypsibius klebelsbergi* Mihelčič, 1959 (Tardigrada), based on material from the Ötztal Alps, Austria. – Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut **100**, 77-100.

Dastych, H., 2004: *Hypsibius thaleri* sp. nov., a new species of a glacier-dwelling tardigrade from the Himalayas, Nepal (Tardigrada). – Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut **101**, 169-183.

Dastych, H., 2006: A new tardigrade species of the genus *Ramazzottius* Binda & Pilato, 1986 (Tardigrada) from the nival zone of the Mont Blanc Massive (The Western Alps), with some morphometric remarks. – Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut **103**, 33-45.

Degma P., 1997: Synopsis of Tardigrada fauna of Slovakia. – Acta zoologica Universitatis Comenianae **41**, 3-23.

Garitano-Zavala, A., 1995: Primer reportede las especies de tardigrados muscicolas (Phylum Tardigrada) presentes en la vertiente occidental de la Cordillera Real de los Andes (La Paz – Bolivia). – Ecologia en Bolivia **24**, 1-39.

Fontoura, P., Pilato, G., Lisi, O., 2010: First record of Tardigrada from São Tomé (Gulf of Guinea, Western Equatorial Africa) and description of *Pseudechiniscus santomensis* sp. nov. (Heterotardigrada: Echiniscidae). – Zootaxa **2564**, 31-42.

Guidetti, R., Bertolani, R., 2005: Tardigrade taxonomy: an updated check list of the taxa

and a list of characters for their identification. – Zootaxa **845**, 1-46.

GUIL, N., 2008: New records and within-species variability of Iberian tardigrades (Tardigrada), with comments on the species from the *Echiniscus blumi-canadensis* series. – Zootaxa **1757**, 1-30.

GUIL, N., SANCHEZ-MORENO, S., MACHORDOM, A., 2009: Local biodiversity patterns in micrometazoans: Are tardigrades everywhere? – Systematics and Biodiversity **7**, 259-268.

GUIL, N., RODRIGO, E, MACHORDOM, A., 2015: Soil tardigrade biodiversity with the description of a new eutardigrade genus and its phylogenetic position. – Systematics and Biodiversity **13**, 234-256.

HECIAK, S., 1976: Niesporczaki (Tardigrada) Gór Swietokrzyskich. – Badania Fizjograficzne nad Polska Zachodnia, Seria C – Zoologia, **29**, 111-128.

IHAROS A., 1947a: The Tardigrada fauna of the Tihany Peninsula. – Archiva Biologica Hungarica **17**, 38-43.

IHAROS, A., 1947b: Relation between moos-association and Tardigrade-fauna on the northern shores of the Tihany Peninsula. – Borbásia **7** (1-6), 31-38.

IHAROS, G., 1962: A Tihanyi-Félsziget Tardigrada Faunája. – Különlenyomat Az Allattani Közlemények **49** (1-4), 55-61.

IHAROS, G., 1963: A Bakony - Hegység Tardigrada-Faunája, I. – Különlenyomat Az Allattani Közlemények **50** (1-4), 59-67.

IHAROS, G., 1965: Die Tardigrada-Fauna des Bakony-Gebirges, II. – Különlenyomat Az Allattani Közlemények **52** (1-4), 47-56.

IHAROS, G. 1966: Neue Tardigraden-Arten aus Ungarn (Neuere Beiträge zur Kenntnis der Tardigraden-Fauna Ungarns, VI). – Acta Zoologica Scientarum Hungaricae **12** (1-2), 111-122.

IHAROS, G., 1968: Neue Angaben zur Tardigraden-Fauna des Bakony Gebirges, IV. – Mitteilungen der Museen Komitates Veszprém **7**, 327-336.

IHAROS G., 1982: Tardigradologische Notizen, I. – Miscelanea Zoologica Hungarica **1**, 85-90.

IHAROS, G., 1985: A Barcsi borokas Tardigrada faunaja. – Dunántúli Dolgozatok Termwszettudomanyi Sorozat, Pecs **5**, 71-84.

JENNINGS, P.G., 1976a: Tardigrada from the Antarctic Peninsula and Scotia Ridge Region. – British Antarct Survey Bulletin **44**, 75-95.

JENNINGS, P.G., 1976b: The Tardigrada of Signy Island, South Orkney Islands, with a note on the Rotifera. – British Antarct Survey Bulletin **44**, 1-25.

JENNINGS, P.G., 1979: The Signy Island terrestrial reference sites: X. Population dynamics of Tardigrada and Rotifera. – British Antarct Survey Bulletin **47**, 89-105.

JORGENSEN, A., 2001: Graphical presentation of the African tardigrade fauna using GIS with the description of *Isohypsibius malawiensis* sp. n. (Eutardigrada: Hypsibiidae) from Lake Malawi. – Zoologischer Anzeiger **240**, 441-449.

JORGENSEN, M., KRISTENSEN, R.M., 1991. Tardigrada, pp. 61-80. In: Meiofauna investigations from Igloolik, N.W.T.Arctic Canada, Arctic Biology Course 1989 Igloolik N.W.T Canada – University of Copenhagen.

KACZMAREK, L., BEASLEY, C.W., 2002: Water bears (Tardigrada) of China, pp. 65-76. In: – Fauna of China (Zhang, Z.-Q., ed.), Magnolia Press, Auckland.

KINCHIN, I.M., 1990: Observations on the structure of *Ramazzottius* (with a checklist of British Eutardigrada). – Microscopy (London) **36**, 475-482.

KOVALCHUK N.E., 1987: On the fauna and ecology of tardigrades of the Dniestr River Basin reservoirs. – Zoologicheskii Zhurnal **66**, 298-301.

LI, X., WANG, D., 2005: *Isohypsibius taibaiensis* sp. nov. (Tardigrada, Hypsibiidae) from China. – Zootaxa **1036**, 55-60.

LI, X.-C., WANG, L.-Z., YU, D., 2007: The Tardigrada fauna of China with descriptions of three new species of Echiniscidae. – Zoological Studies **46**, 135-147.

MARCUS, E., 1928: Spinnentiere oder Arachnoidea IV: Bärtierchen (Tardigrada), pp. 1-230. In: – Die Tierwelt Deutschlands und der angrenzenden Meeresteile. 12. Teil (DAHL, F., ed.). – Gustav Fischer, Jena.

MARCUS, E., 1929. Tardigrada, pp. 1-608. In: Dr. H.G. Bronn's Klassen und Ordnungen des Tierreichs 5, IV, 3. – Akademische Verlagsgesellschaft, Leipzig.

MARCUS, E., 1930: Beiträge zur Tardigradensystematik. – Zoologische Jahrbücher (Systematik) **59**, 363-386.

MARCUS, E., 1933: III. Tardigrada (Voyage de Ch. ALLUAUD et P. A. CHAPPUIS en Afrique Occidentale Francaise). – Archiv für Hydrobiologie **26**, 91-100.

Marcus, E., 1936: Tardigrada, pp. 1-340. In: Das Tierreich 66. Lieferung (Hesse, R., ed.). – Walter de Gruyter & Co., Berlin und Leipzig.

Marcus, E. 1940: VIII. Tardigrades (Croisière du Bougainville aux Iles Australes Francaises). – Mémoires du Muséum National d'Histoire Naturelle **14**, 285-292.

Mathews, G.B., 1937: More tardigrades from the Far East. – China Journal **27**, 32-35.

Maucci, W., 1951/1952: Contributo alla conoscenza dei Tardigradi d'Italia. – Bollettino della Societa Adriatica di Scienze di Trieste **44**, 99-110.

Maucci, W., 1978: Tardigradi muscicoli della Turchia (terzo contributo). – Memorie del Museo Civico di Storia Naturale di Verona **5**, 111-140.

Maucci, W., 1986: Tardigrada. – Fauna d'Italia, Edizioni Calderini, Bologna **24**: 1-388.

McInnes, S.J., 1994: Zoogeographic distribution of terrestrial/freshwater tardigrades from current literature. – Journal of Natural History **28**, 257-352.

McInnes, S.J., 1995: Tardigrades from Signy Island, South Orkney Islands, with particular reference to freshwater species. – Journal of Natural History **29**, 1419-1445.

McInnes, S.J., Ellis-Evans, J.C., 1987: Tardigrades from maritime Antarctic freshwater lakes, pp. 111-123. In: Biology of Tardigrades (Bertolani, R., ed.). Proc. 4th Int. Symp. Tardigrada, Modena, September 3-5, 1985. – Selected Symposia and Mongraphs U.Z.I., Mucchi, Modena.

McInnes, S.J., Pugh, J.A., 1999: Zonation in Antarctic lake-dweling benthic meiofauna, with emphasis on the Tardigrada. – Zoologischer Anzeiger 238: 283-288.

Meier, T., 1996: Tardigrada, 89-91. In: Limnofauna Norvegica, Aagaard, K. & Dolmen, D., eds), Tapir Forlag, Trondheim.

Meyer, H.A., 2011: The terrestrial and freshwater Tardigrada of Northeastern North America, with new records from Maine. – Northeastern Naturalist **18**, 534-541.

Meyer, H.A., 2013: Terrestrial and freshwater Tardigrada of the Americas. – Zootaxa **3747**, 1-71.

Miheličič,F., 1960: Ein Beitrag zur Kenntnis der Süsswassertardigraden Europas (Frankreich). – Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien **100**, 88-95.

Miheličič, F., 1966: Tardigradi del Carso Triestino e Gorziano. – Bollettino della Societa Adriatica di Scienze di Trieste **54** (4), 5-13.

Miller, W.R., McInnes, S.J., Bergstrom, D.M., 2005: Tardigrades of the Australian Antarctic: *Hypsibius heardensis* (Eutardigrada: Hypsibiidae: *dujardini* group) a new species from sub-Antarctic Heard Island. – Zootaxa 1022, 57-64.

Moon, S.N., Kim, H.S., 1988: Eutardigrada (Tardigrada) from Korea. – Korean Journal of Systematic Zoology. Special Issue **2**, 87-96.

Morgan C.I., 1976: Studies on British tardigrade fauna, some zoogeographical and ecological notes. – Journal of Natural History **10**, 607-632.

Morgan C.I., King P.E., 1976: British tardigrades (Tardigrada). – Synopses of the British Fauna (new series), The Linnean Society of London, Academic Press London & New York **9**, 1-133.

Murray, J. 1906: Scottish National Antarctic Expedition: Tardigrada of the South Orkneys. – Transaction of the Royal Society Edinborough **45**, 323-334.

Murray, J., 1910: Tardigrada. – In: British Antarctic Expedition 1907-9, Reports on the Scientific Investigations, William Heinemann, London, **1** (5) (Biology), 1-185.

Murray, J., 1911: Water-bears, or Tardigrada (supplementary notes). – Journal of the Quekett Micrroscopical Club **11**, 181-198.

Nelson, D.R., Guidetti, R., Rebecchi, L., 2010: Chapter 14: Tardigrada, pp. 455-484. In: Ecology and classification of North American Freshwater Invertebrates. 3rd ed,, San Diego (Thorp, J.H & A.P. Covich, eds.). – Elsevier/Academic Press, Amsterdam, Boston.

Opravilova, V., Kubicek, F., 1999: Tardigrada. – Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Bruensis, Biologia **101**, 103-105.

Pilato, G., 1970: Osservazioni sui Tardigradi delle Alpi Apuane. – Lavori della Societa Italiana di Biogeografia **1**, 335-347.

Pilato, G., 1981: Analisi di nuovi caratteri nello studio degli Eutardigradi. – Animalia **8**, 51-57.

Pilato, G., 1971: Tardigradi delle acque dolci siciliane. Nota prima. – Bollettino delle Sedute dell 'Accademia Gioenia di Scienze Naturale in Catania **11**, 126-134.

Pilato, G., 1974: Struttura dell'armatura boccale di alcune specie di *Isohypsibius* (Eutardigrada). – Animalia **1**, 43-58.

Rahm, G., 1925a: Beitrag zur Kenntnis der Moostierwelt der preußischen Rheinlande.

2. Tardigrada. – Archiv für Naturgeschichte, Jahrgang **90** (7): 153-214.

RAHM, G., 1925b: Die Zystenbildung bei den wasserbewohnenden Tardigraden. – Verhandlungen der internationalen Vereinigung für Theoretische und Angewandte Limnologie, Leningrad-Moskau **3**, 364-371.

RAHM, G,. 1928: Bärtierchen, Tardigrada, pp. 1-21. – Tierwelt Mitteleuropas (P. BROHMER et al., eds), 3. Leipzig, Quelle & Mayer.

RAHM, G,. 1932: Tardigrada, Bärtierchen, pp. 454-459. – In: Fauna von Deutschland: ein Bestimmungsbuch unserer heimischen Tierwelt (P. BROHMER, ed.), 4. Leipzig, Quelle & Meyer.

RAMAZZOTTI, G., 1956: I Tardigradi delle Alpi. – Memorie dell'Istituto Italiano di Idrobiologia **9**, 273-290.

RAMAZZOTTI, G, 1967: Tardigrada, pp. 121-123. – In: Limnofauna Europaea (ILLIES, J., et al. eds), Gustav Fischer Verlag, Stuttgart, New York.

RAMAZZOTTI, G., 1978: Tardigrada, pp. 151-153.– In: Limnofauna Europaea (ILLIES J., et al., eds), Gustav Fischer Verlag, Stuttgart, New York.

RAMAZZOTTI, G., MAUCCI, W., 1983: Il philum Tardigrada (III edizione riveduta e aggiornata). – Memorie dell'Istituto Italiano di Idrobiologia **41**, 1-1012.

RICHTERS, F., 1904: Vorläufiger Bericht über die antarktische Moosfauna. – Verhandlungen der Deutschen Zoologischen Gesellschaft, 236-239.

RICHTERS, F., 1907a: Die Fauna der Moosrasen des Gaußbergs und einiger südlicher Inseln. – Deutsche Südpolar-Expedition 1901-1903, 9 (Zool., Band 1, Heft 4: 259-302, 1907), Berlin (1908).

RICHTERS, F., 1907b: Antarktische Tardigraden. – Zoologischer Anzeiger **31**, 915-916.

RICHTERS, F., 1908: Moosbewohner. – Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition, Stockholm **6** (2), 1-16.

RIGGIN, G.T., 1962: Tardigrada of South West Virginia: with the addition of and description of a new marine species from Florida. – Technical Bulletin, Virginia Agriculture Experimental Station **152**, 1-145.

ROSSI, G.C., CLAPS, M.C., 1991: Tardigrados dulceacuicolas de la Argentina. – Fauna de agua dulce de la Republica Argentina **19**, 1-70.

RUDESCU, L. 1964. Tardigrada: – Fauna Republici Populare Romine **4** (7), 1-400.

SANDS, C.J., MCINNES, S.J., MARLEY, N., GOODALL-COPESTAKE, W.P., CONVEY, P., LINSE, K., 2008: Phylum Tardigrada: an "individual" approach. – Cladistics **24**, 861-871.

SCHUSTER, R.O., GRIGARICK, A.A., 1965: Tardigrada from Western North America. –University of California Publications in Zoology 7**6**, 1-67.

SÉMÉRIA, Y., 1994: Liste réviséé des Tardigrades de France. – Bulletin Mensuel de la Societe Linneenne de Lyon **63**, 366-378.

SÉMÉRIA, Y., 2003: Tardigrades continentaux. – Faune de France **87**, 1-293.

SLÁDECEK, V., 1977: Indicator value of freshwater Tardigrada. – Acta hydrochimica et hydrobiologica **5**, 87-89.

SUDZUKI, M., 1964: On the microfauna of the Antarctic Region I. Moss-water community at Langhovde. – Japan Antarctic Research Expedition Scientific Reports, Ser. E **19**, 1-41.

SUDZUKI, M., SHIMOIZUMI, J., 1967: On the freshwater microfaune of the Antarctic region II. Stability of faunistic composition of Antarctic microorganisms. – Japan Antarctic Research Expedition Scientific Reports, Special Issue **1**, 216-235.

SZYMANSKA, B., 1994: The Tardigrada from the Axel Heiberg Island and the associate bryophyte species. – Folia Entomologica Hungarica **55**, 359-368.

THULIN, G., 1911: Beiträge zur Kenntnis der Tardigradenfauna Schwedens. – Arkiv för Zoologi **7** (16), 1-60.

THULIN, G., 1928: Über die Phylogenie und das System der Tardigraden. – Hereditas **11**, 207-266.

UTSUGI, K., OHYAMA, Y., 1991: Tardigrades in King George Island (Antarctica). – Zoological Science **81**, 1198.

UTSUGI, K., OHYAMA, Y., 1993: Antarctic Tardigrada III. Fildes Peninsula of King George Island. – Proceedings of the NIPR Symposium on Polar Biology **6**, 139-151.

URBANOWICZ, C., 1925: Sur la variabilité de «*Macrobiotus oberhaeuseri*». – Bulletin Biologique de la France et da la Belgique **59**, 124-142.

URBANOWICZOWNA, K., 1924: O zmiennosci *Macrobiotus oberhaeuseri* Doyère. – Prace Wydzialu Matematyczno-Przyrodniczego Towarzystwa Przyjaciol Nauk **2**: 1-17.

VAN ROMPU, E.A., DE SMET, W.H., BAFORT, J.M., 1991: Contributions to the Tardigrada of the Canadian High Arctic. 2. Freshwater tardigrades from Little Cornwallis Island, N.W.T.

Canada. – Biologisch Jaarboek Dodonaea **59**, 132-140.

van Rompu, E.A., de Smet, W.H., Beyens, L., 1992: Contribution to the tardigrada of the Canadian High-Arctic. 1. Freshwater tardigrades from Devon Island, Northwest Territories. – Canadian Field-Naturalist **106**, 303-310.

van Rompu, E.A., de Smet, W.H., 1996: Additions to the tardigrade fauna of Belgium. – Biologisch Jaarboek Dodonaea **63**, 76-91.

Vanhöffen, E., 1906a: Tiere und Pflanzen der Heard-Insel. – Deutsche Südpolar-Expedition 1901-1903. Geographie und Geologie **2**, 264-271.

Vanhöffen, E., 1906b: Die Tiere und Pflanzen von Possession-Eiland der Crozet-Gruppe. – Deutsche Südpolar-Expedition 1901-1903. Geographie und Geologie **2**, 334-343.

Vargha B., 1996: New data to the Hungarian tardigrade fauna with a revised list of species. – Folia Entomologica Hungarica **57**, 285-290.

Vargha, B., 1998: Adatok a Duna-Dráva Nemzeti Park medveállatka (Tardigrada) faunájához. – Dunántúli Dolgozatok Termwszettudomanyi Sorozat, Pecs **9**, 73-80.

Vargha, B., 2000: Adatok a Villányi-hegység medveállataka (Tardigrada) faunájához. – Dunántúli Dolgozatok Termwszettudomanyi Sorozat, Pecs **10**, 121-125.

Wang, L.Z., Lian, Z.M., 2007: Newly recorded species of the genus *Isohypsibius* (Tardigrada; Hypsibiidae) from China. – Journal of Forestry Research **18**, 322-324.

Weglarska, B., 1959: Die Tardigraden (Tardigrada) Polens I. Tardigraden der Woiwodschaft Krakow. – Acta zoologica cracoviensia **4**, 699-745.

Weglarska, B. 1962: Die Tardigraden Vietnams. – Vestnik Československe Společnosti Zoologicke **26**, 300-307.

Weglarska, B., 1970: *Hypsibius* (*Isohypsibius*) *smreczynskii* spec. nov., a new species of freshwater tardigrade. – In: The IInd Int. Symp. Tardigrada, Krakow, Poland, July 28-30, 1977; Zeszyty Naukowe Uniwersytetu Jagiellonskiego, Prace zoologiczne **16**, 107-117.

Weglarska, B., Kuc, M., 1980: Heterotardigrada from Axel Heiberg Island. – In: The IInd Int. Symp. Tardigrada, Krakow, Poland, July 28-30, 1977; Zeszyty Naukowe Uniwersytetu Jagiellonskiego, Prace zoologiczne **172** (26): 53-66.

Weglarska, B., 1965: Die Tardigraden (Tardigrada) Spitzbergens. – Acta zoologica cracoviensia **11** (2), 43-51.

Wright, J.C., 1991: The significance of four xeric parameters in the ecology of terrestrial Tardigrada. – Journal of Zoology, London **224**, 59-77.

Yang, T., 1999: Three new species and six new records of the class Eutardigrada (Tardigrada) from China (Parachela: Macrobiotidae: Hypsibiidae). – Acta Zootaxonomica Sinica **24**, 444-453.