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Redescription and Revalidation of the Sub-Antarctic Tardigrade *Hypsibius murrayi* (Richters, 1907) Based on the Rediscovered Type Material (Tardigrada, Panarthropoda)

Neubeschreibung und Revalidierung des subantarktischen Bärtierchens *Hypsibius murrayi* (Richters, 1907) anhand des wiederentdeckten Typenmaterials (Tardigrada, Panarthropoda)

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Summary: The recently rediscovered remains of the Tardigrada collection of Ferdinand Richters (1849-1914), one of the pioneers of tardigrade taxonomy, also contain one microslide with type specimens of the taxonomically vague species *Hypsibius murrayi* (Richters, 1907) described from the sub-Antarctic Possession Island. This species has been considered as a synonym of *Hypsibius dujardini* (Doyère, 1840) for more than 80 years. In the type material some characters could be recognized not reported in the original description such as wide, rugose cuticular bars at the bases of the internal claws on legs I-III and microplacoids, which speaks against a synonymy with *H. dujardini* (Doyère, 1840), providing *H. murrayi* a valid species status. The examination of the type material of *H. heardensis* Miller, McInnes & Bergstrom, 2005, a species described from sub-Antarctic Heard Island, which is morphologically very similar to *H. murrayi*, indicates that both taxa represent the same species. Therefore, *H. heardensis* is a junior subjective synonym of *H. murrayi*.

Key words: Tardigrada, *Hypsibius murrayi*, redescription, revalidation, synonymy, *Hypsibius heardensis*, Antarctica

Zusammenfassung: Die vor Kurzem wiederentdeckten Fragmente der Tardigradensammlung von Ferdinand Richters (1949-1914), eines der Pioniere der Tardigradentaxonomie, enthält auch einen Objektträger mit Typenmaterial der taxonomisch umstrittenen Art *Hypsibius murrayi* (Richters, 1907) von der subantarktischen Possession-Insel. Diese Art wird seit mehr als 80 Jahren als Synonym von *Hypsibius dujardini* (Doyère, 1840) angesehen. Im Typenmaterial konnten einige Merkmale identifiziert werden, die in der Originalbeschreibung von Richters nicht erwähnt werden, so z.B. breite, runzelige kutikulare Leisten an den Basen der inneren Krallen der Beinen I-III und das Vorhandensein von Mikroplakoiden. Dies spricht gegen eine Synonymie mit *H. dujardini* (Doyère, 1840) und verleiht *H. murrayi* einen gültigen Artstatus. Eine Untersuchung des Typusmaterials von *H. heardensis* Miller, McInnes & Bergstrom, 2005, eine Art, die von der subantarktischen Heard Island beschrieben wurde und *H. murrayi* morphologisch sehr ähnlich ist, zeigt, dass beide zur selben Art gehören. Daher ist *H. heardensis* als jüngeres subjektives Synonym von *H. murrayi* anzusehen.

Schlüsselwörter: Tardigrada, *Hypsibius murrayi*, Neubeschreibung, Aufwertung, Synonymie, *Hypsibius heardensis,* Antarctica

1. Introduction

One of the pioneers of tardigrade taxonomy, Ferdinand Richters (1949-1914), a former curator at the Naturmuseum Senckenberg (Frankfurt am Main), contributed importantly to our knowledge on water-bears from Antarctica. When working on bryophyte

fauna collected during the German Antarctic expedition (Deutsche Südpolar-Expedition 1901-1903, under the leadership of ERICH VON DRYGALSKI), RICHTERS (1907a) described several new Tardigrada species from that region, among them, rather enigmatically, *Macrobiotus murrayi* (now *Hypsibius murrayi*). A very small amount of RICHTERS' collection (microscopical slides) has been saved and is still available. Altogether 14 of these slides with preserved tardigrades (including eight from Antarctica) are currently deposited in the Forschungsinstitut Senckenberg, Frankfurt (a.M.). The bulk of the collection has been considered lost (DASTYCH 1990, 1991), including *Hypsibius murrayi*, a species that is treated as a synonym of *Hypsibius dujardini* (Doyère, 1840) until today.

Surprisingly, a further part from RICHTERS' collection has been recently rediscovered in the Naturkunde Museum in Berlin (DASTYCH 2016). This part encompasses the majority of taxa described by the author from Antarctica (RICHTERS 1907a) mounted on 44 microslides. This collection is more than 110 years old, probably being the oldest collection of mounted tardigrades. One slide contains type specimens of *H. murrayi*. In the present article, I redescribe *H. murrayi* based on RICHTERS' type specimens and additional material from South Georgia and Kerguelen, compare the species with other *Hypsibius* taxa, including type material of *H. heardensis* Miller et al. 2005, *H. conwentzii* Kaczmarek et al. 2018, and discuss its taxonomic status in the light of this new information.

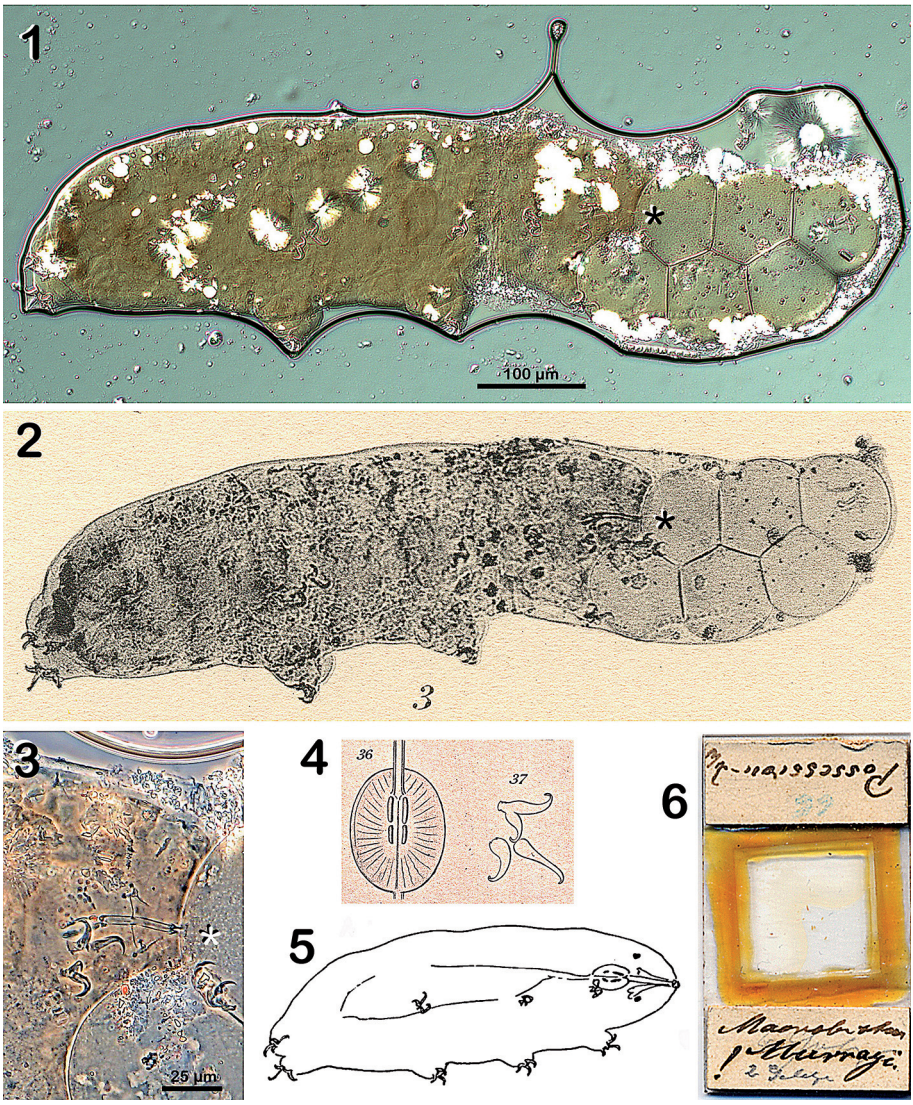
2. Material and Methods

The examined type specimens of *Hypsibius murrayi* are mounted on a non-standard microslide (Fig. 6) from RICHTERS' remaining collection at the Museum für Naturkunde, Berlin (for details on the microslides in this collection, their condition etc. see DASTYCH 2016). The mounting medium on the slide was strongly penetrated by air and the included specimens were more or less covered by whitish crystals (Fig. 1). The mounting medium probably consists of formalin or arsenic glycerine. The small inscription on the label made with pencil runs „2 Gelege" (= 2 exuviae; see Fig. 6), but in fact there are four exuviae on the slide.

Comparative material of *H. murrayi* comes from the Kerguelen and South Georgia in the southern Atlantic Ocean. Additionally, I examined some specimens of the *Hypsibius dujardini*-group from the Maritime Antarctic and some type specimens of *Hypsibius heardensis* Miller et al., 2005 and *Hypsibius conwentzii* (Kaczmarek et al. 2018). The numbers on slides loaned from the collection of W.R. MILLER are: holotype: MU-080-1, paratypes: MU-094-7 and MU 080-1, those from L. KACZMAREK: AT 49/3 and AT 49/4. Four specimens of *H. murrayi* from South Georgia were initially mounted in FAURE'S medium ca 30 years ago (see DASTYCH 1984); due to the advanced deterioration of the specimens on the slides they have been recently re-mounted into HOYER'S medium for clearing. Animals from Kerguelen were extracted from bryophytes ca 20 years ago with the method used in DASTYCH (1980) and mounted on slides in FAURE'S medium. Then, simultaneously several specimens from the same sample were mounted on a microslide in polyvinyllactophenol (PVL) for comparison. Also some of the slides from Kerguelen are deteriorated in part. The bulk of the herein examined specimens is deposited in the Zoological Museum Hamburg, Centre of Natural History.

Tardigrades were examined under the Photomikroskop III (Fa. Zeiss) and the

(1928) anhand des Originalfotos von RICHTERS (s. Abb. 2). Man beachte hier das Vorhandensein von Augen und die veränderte Form der Mundregion im Vergleich zum Originalfoto. **6** Objektträger mit Syntypen von *H. murrayi*. Abb. 1: DIC-Aufnahme; Abb. 3: PHC-Aufnahme; Mundregion (Stern).



Figs 1-6: *Hypsibius murrayi* (Richters, 1907). **1** Syntype, with the front part of the body inside the exuvia that contains the deposited eggs. Note numerous artificial crystals (white dots). The specimen is surrounded by remnants of the mounting medium. **2** Photogram of the same animal published by Richters (1907a; Fig. 2). **3** Enlarged head region of the same specimen. **4** Pharynx and claws from the original description. **5** The same animal drawn by E. Marcus in Marcus (1928) based on the original photo by Richters (see Fig. 2). Note the presence of eyes and the different shape of the mouth region compared to the photo. **6** Microslide with syntypes of *H. murrayi*. Fig. 1: DIC-image; Fig. 3: PHC-image; mouth region (asterisk).

Abb. 1-6: *Hypsibius murrayi* (Richters, 1907). **1** Syntyp; der Vorderkörper steckt in der Exuvie, in der sich die abgelegten Eier befinden. Man beachte die zahlreichen artifiziellen Kristalle (weiße Flecken). Das Tier ist von Resten des Einbettungsmittels umgeben. **2** Photogramm desselben Tieres, veröffentlicht in Richters (1907a; Fig. 2). **3** Vergrößerter Kopfbereich desselben Tieres. **4** Pharynx und Krallen aus der ursprünglichen Beschreibung. **5** Dasselbe Tier gezeichnet von E. Marcus in Marcus

Axioskop 2 (Zeiss), with which also the microphotographs were taken. Measurements were taken with eyepiece micrometer under phase contrast. The morphometric indices and coefficients used are explained in DASTYCH et al (2003) and DASTYCH (2004, 2006). Moreover, the following new indices are introduced here: HFCI (the percentage ratio between the length of the hind and the fore claw) and HFBrI (the percentage ratio between the length of the main branch of the hind claw and the main branch of the fore claw). The terms 'fore" and 'hind' claw denote anterior and posterior (i.e. internal and external) claw on IV legs.

Abbreviations used: cb – claw base; DIC – differential interference contrast; ICZN – International Code of Zoological Nomenclature; n – sample size; min-max – minimum-maximum range; PHC – phase contrast; PT – pt indices, see PILATO 1981 (= WTI indices, the whole buccal tube indices: see also DASTYCH 2006); PVL – polyvinyl-lactophenol; r squared (= r^2) – coefficient of determination; SD – standard deviation; SEM – scanning electron microscope; V – coefficient of variation; PT ss – stylet supports "anterior" index, $\bar{x}$ – (arithmetic) mean.

3. Results

3.1. Redescription of *Hypsibius murrayi* (Richters, 1907) (Figs 1-98)

Macrobiotus Murrayi n. spec.: RICHTERS (1907a); pp. 295; Plate XIX, Figs 36, 37, Plate XX, Fig. 3. Locus typicus: „Possession-Eiland" (= Île de la Possession, Possession Island: Crozet Archipelago), 20 animals.

Macrobiotus Murrayi: VANHÖFFEN (1906), nomen nudum
Macrobiotus murrayi: RICHTERS (1907b, 1908), MURRAY (1910, 1911a: "claws of *Diphascon*-type", 1911b), URBANOWICZOWNA (1924, URBANOWICZ (1925), RAHM (1928)
Macrobiotus Murrayi: RICHTERS (1911), THULIN (1911, transferred to the genus *Hypsibius*)
Macrobiotus Murrayi: THULIN (1928: listed under the genus *Hypsibius*)
Hypsibius murrayi: MARCUS (1928)
Hypsibius (s. str.) *murrayi*: MARCUS (1929)
"? Macrobiotus Murrayi": CUÈNOT (1932, listed under *Hypsibius dujardini*)
"1928 *Hypsibius dujardini* [part] + *murrayi,* E. MARCUS in..." and "1929 *Hypsibius* (*s. str.*) *dujardini* + *murrayi*, E. MARCUS in..."): MARCUS (1936)
"Hypsibius dujardini + *murrayi* E MARCUS (1928, 1929)": RAMAZZOTTI (1945)
murrayi: RAMAZZOTTI (1972, listed here only in the index and explained as: "*Hypsibius* Marcus, 1928: syn. di *H.* (*H.*) *dujardini"* and "*Macrobiotus* Richters, 1907: syn. di *H.* (*H.*) *dujardini"*, respectively)
Macrobiotus murrayi (as synonym of *Hypsibius dujardini*): RUDESCU (1964), BARTOŠ (1967), RAMAZZOTTI & MAUCCI (1983)
H. (H.) dujardini murrayi: BARTOŠ (1967: fig. 39 R)
Hypsibius heardensis Miller, McInnes & Bergstrom, 2005: **synonym nov.**

3.1.1 Diagnosis and description

Diagnosis (based on the recovered type specimens and other material: see section 3.3.1): Medium sized to large *Hypsibius* with smooth cuticle. Eye-dots present (but not discernible in the type material – pigment dissolved?). Pharynx with two macroplacoids and tiny microplacoids. The latter are connected with the second macroplacoids through very thin and elongated cuticular band. Claws of *Hypsibius* type, internal ones with poorly developed, small lunules. Legs I-III with cuticular bars at the bases of internal claws. The bars with rugose edges (i.e. irregularly curled or dentated) and variable in size. Between fore and hind claw (leg IV) occurs elongated bar (spur), protruding from the base of the hind claw. Eggs smooth, deposited in the exuvia.

3.1.2 Description of type material (Possession Island) (Figs 1-47)

Type material examined: Five syntypic specimens and four exuviae on microscope slide (Fig. 6). The exuviae with 22 eggs (5-6 per exuvia), 11 eggs with embryos. Possession Island (Crozet Archipelago).

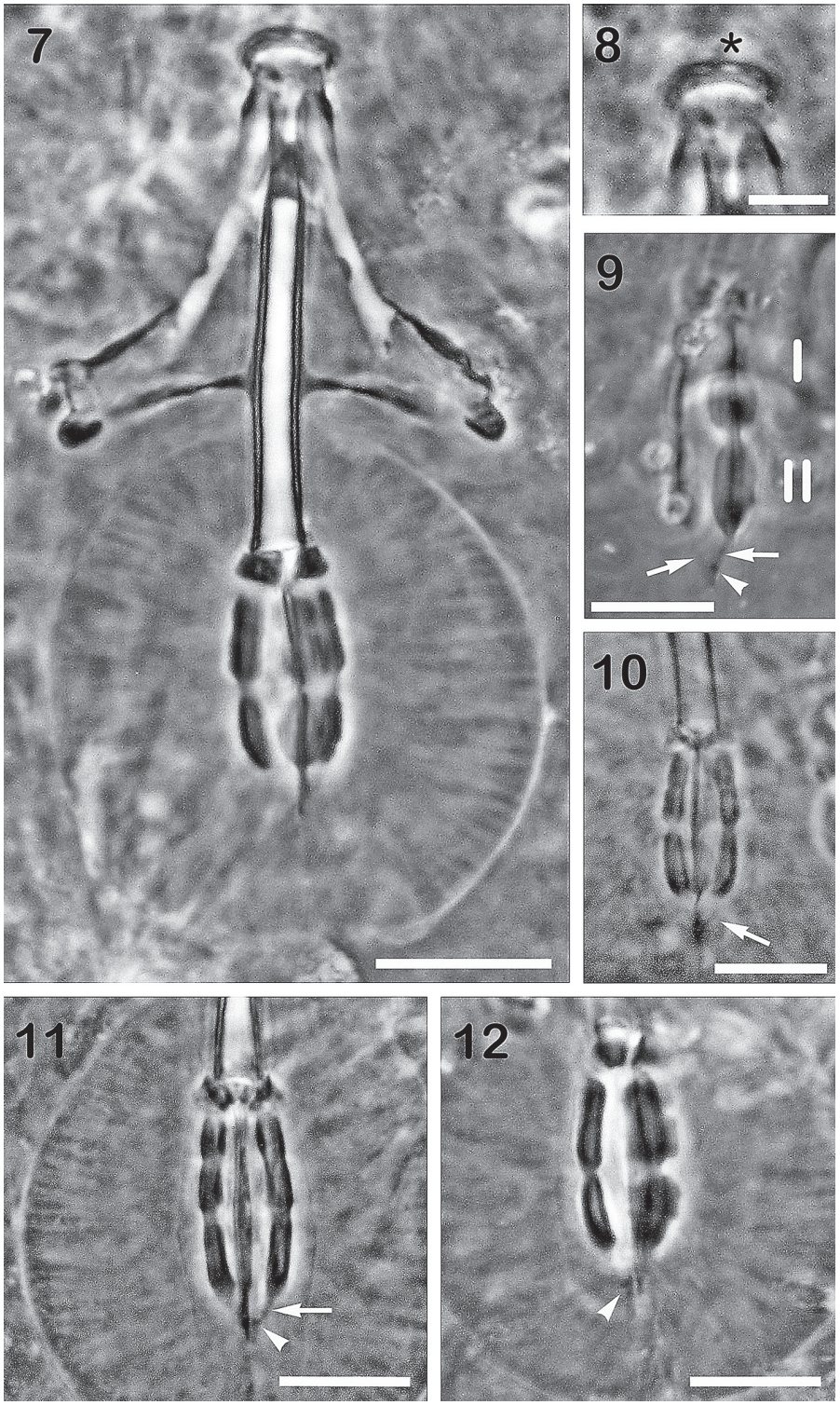
One of these five syntypes is designed here as lectotype (length 568 µm). Thus the remaining four syntypes represent paralectotypes. To the paralectotype series belong also 11 eggs with embryos. The designed lectotype represents the specimen of which a photogram was published in the original description (Richters 1907a: fig. 3) and is illustrated in the present article in Figs 1-5, 9, 13, 32, 34 and 45.

Body 338.0-603.0 µm long, light-brownish in the mounted animals. No eye-dots could be discerned. The cuticle is smooth.

Buccopharyngeal apparatus medium sized (ca. 10-15 % of the body length, n = 4). Mouth opening slightly ventro-anterior, with a ring of tiny, transversally oriented and poorly discernible oval structures (Figs 7, 8, asterisk). Mouth cavity without teeth or granules. Buccal tube relatively narrow, with tiny posterior apophyses (= terminal thickenings of the tube wall). No thin lateral cuticular rods between posterior edge of the buccal tube and pharyngeal apophyses. Pharynx medium sized, slightly sub-spherical or spherical, with distinct pharyngeal apophyses (up to 1.8 µm long) and two macroplacoids. Macroplacoids in adults elongated (Figs 7, 9-13), the second one relatively long, ca. 70-85 % (n = 5) of the first macroplacoid length. The first macroplacoid is constricted in the middle (e.g. Figs 11, 25), the second with a small lateral incision in its caudal part, well discernible in only two specimens. The caudal part of the second macroplacoid connected with a very thin, elongated cuticular band. In most cases this band terminates in a tiny, hardly discernible granula-like, ca. 0.5 µm long (Figs 9-12) or slightly elongated (Figs 12, 27) microstructure located at the very rear of the pharyngeal lumen. This structure is interpreted here as microplacoid. Cuticular band and microplacoid are almost identical to those recently described by Tumanov (2018: figs 4A, B) in *Hypsibius pachunguis* Maucci, 1996. The band is also very similar to thin and elongated cuticular thickenings between the last macroplacoid and the microplacoid in several species of the „*Macrobiotus richtersi*"-group (now *Paramacrobiotus richtersi*).

Claws moderately sized, well sclerotized, robust and distinctly sculptured inside (Figs 37, 45). The length of claws increases slightly towards the body end; the length of external claw on leg I is ca 84 % (n = 1) of the external claw on leg IV (ECI index). The basal parts of the main claw branches slightly expanded; the branches with thin and relatively long accessory spines. The main branch of internal claws relatively long; ca 77 % (n = 1) of the length of the main branch of external claws (MBrI index). The claw bases distinctly extended, particularly those of external claws (e.g. Figs 21, 34, 37).

The bases of internal claws with poorly discernible lunula-like structures (e.g. Figs 33, 34, 36, 39, 43). The structures might occur also at the bases of external claws (see Fig. 42, asterisk) but, if present, they are strongly rolled up under the claw base. Their presence and shape should be confirmed with SEM due to the possibility to mistake the bedplate of the claw base or preparation artefacts, i.e. artificial folds around the claw base, for a lunula (see also Dastych 2016). These lunula-like structures, hardly visible in mostly curved upwards bases of external claws, are similar to structures described and illustrated as lunulae in *Hypsibius valeskae* by Tumanov (2018: figs 2 d, f, g). A relatively thick, elongated cuticular thickening (= bar or spur; Figs 21-23, arrowhead) protrudes from one side of the hind claw base, on the opposite side of the secondary branch of the claw. The spur looks like a separate cuticular bar between the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hind and fore claw. However, this structure is continuous with the hind claw base. Below the bases of internal claws on legs I-III occur well sclerotized and relatively wide cuticular bars of variable shape and size. Usually the bars are laterally distinctly ragged (e.g. Figs 39, 41, 42, 44, arrowhead). The smallest bars are on legs I (2.7-6.3 long, 0.9-2.7 µm wide), the largest mostly on legs III (6.3-13.5 µm long, 2.7-3.6 µm wide). In one case a very short additional cuticular thickening (small bar) occurred on leg III between the external and internal claw (Fig. 45, arrow).

Eggs large (81.0-98.0 µm in diameter), smooth, more or less spherical and deposited in the exuviae. Some (11) eggs with embryos. Compared to the pharynx of adults the pharynges of the embryos were sub-spherical and the second microplacoids were shorter than the first one (Figs 14, 15, 17, 20, 29). Moreover, in embryos the thin band behind the caudal part of the second macroplacoids as well as microplacoids are absent. Claws similar to those in adults, but much less sclerotized (Figs 16, 46). One embryo with a very small cuticular bar at the internal claw of the first (?) pair of legs (Fig. 46). Some morphometrical data of embryos are presented in section 3.1.4 (italic type). To my knowledge, no such information for embryos has been hitherto presented.

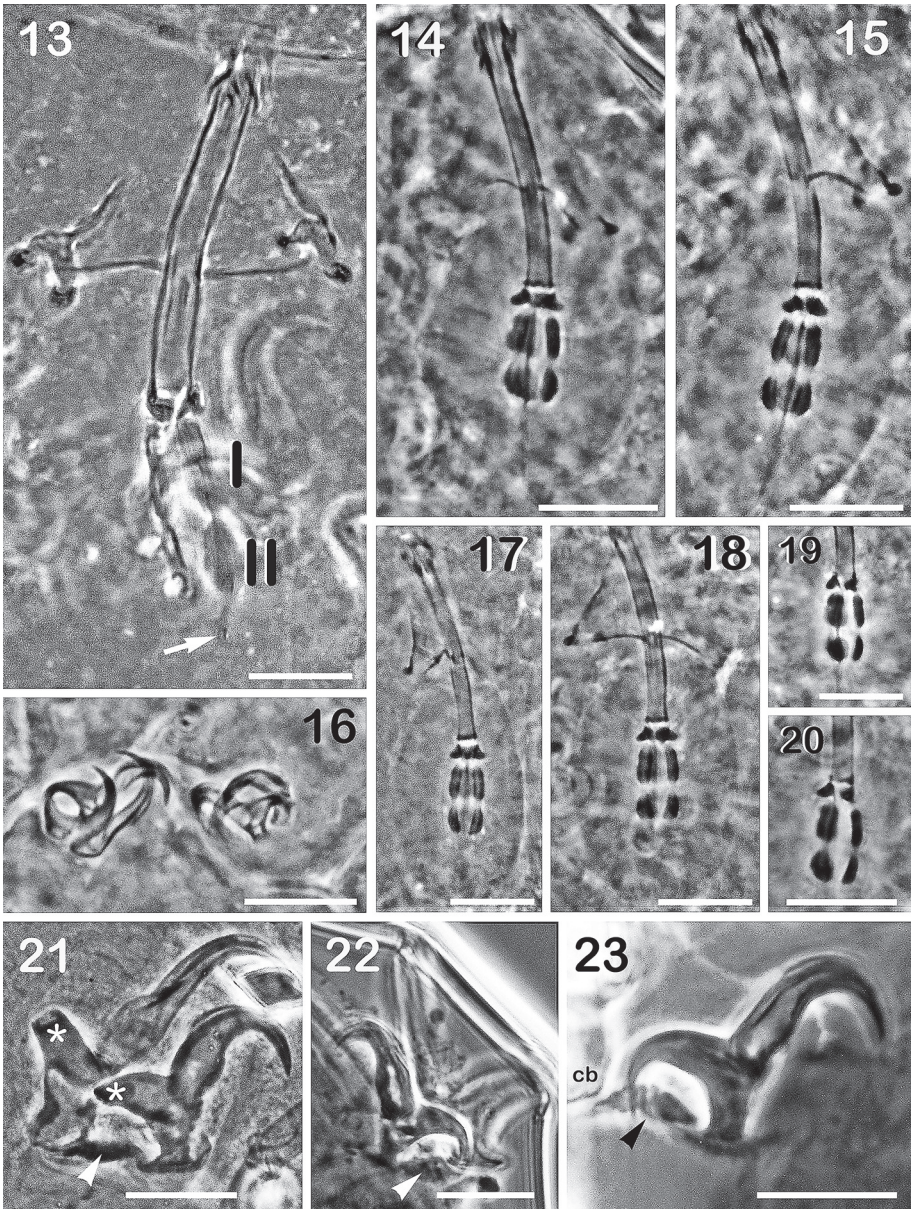
3.3.1 Description of other material examined (Kerguelen: 36, South Georgia: four specimens) (Figs 48-98)

Kerguelen Archipelago (all collected by J.L. Chapuis, number of animals in brackets):
Main Island: Roche Verte. Wetlands, moss from soil clump, 5 m a.s.l., 10 June 1996 (28).
Plaine Ampère. Wetlands, moss from soil, 1 m a.s.l., 10 July 1996 (4);
Guillou Island: Guillou. Closed *Acaena* sp. community, moss, 80 m. a.s.l., 3 June, 1996 (1);
Mayes Island: Grassland (*Festuca erecta*), moss, 30 m. a.s.l., , 30 August 1996 (4 + 2 exuviae with 5 and 6 eggs). Fell-field, moss with soil clumps, 40 m. a.s.l., same data (2);
Verte Island: Wetlands, 5 m. a.s.l., moss, 23 August 1996 (1 + exuvium with 8 eggs)
South Georgia: Grytviken. Moss from soil, 50 m a.s.l., 3 April 1977, leg. K. Zdzitowiecki, four specimens (see locality no. 22 in Dastych 1984, p. 327. These four of altogether 13 specimens reported in Dastych (1984). as *Hypsibius dujardini* (Doyère, 1840), represent in fact *H. murrayi* (Richters, 1907).
Body 197-551 µm long, light-brownish in mounted animals. Eye-dots distinct, present in Faure`s mounting medium, but absent in PVL mountant.

Buccopharyngeal apparatus ca 12-22 % of the body length (n = 16), proportionally larger in smaller (juvenile) animals. The pharynx in adults usually slightly sub-spherical, in juveniles more spherical. Pharyngeal structures very similar to or identical with those in type specimens. The ring of oval structures around the mouth opening usually more obvious as in the type specimens. Thin cuticular rods occurring laterally at pharyngeal apophyses hardly discernible and visible in only one (larger) animal. Other pharyngeal structures relatively variable (Figs 48-64). Macroplacoids are longer and narrower

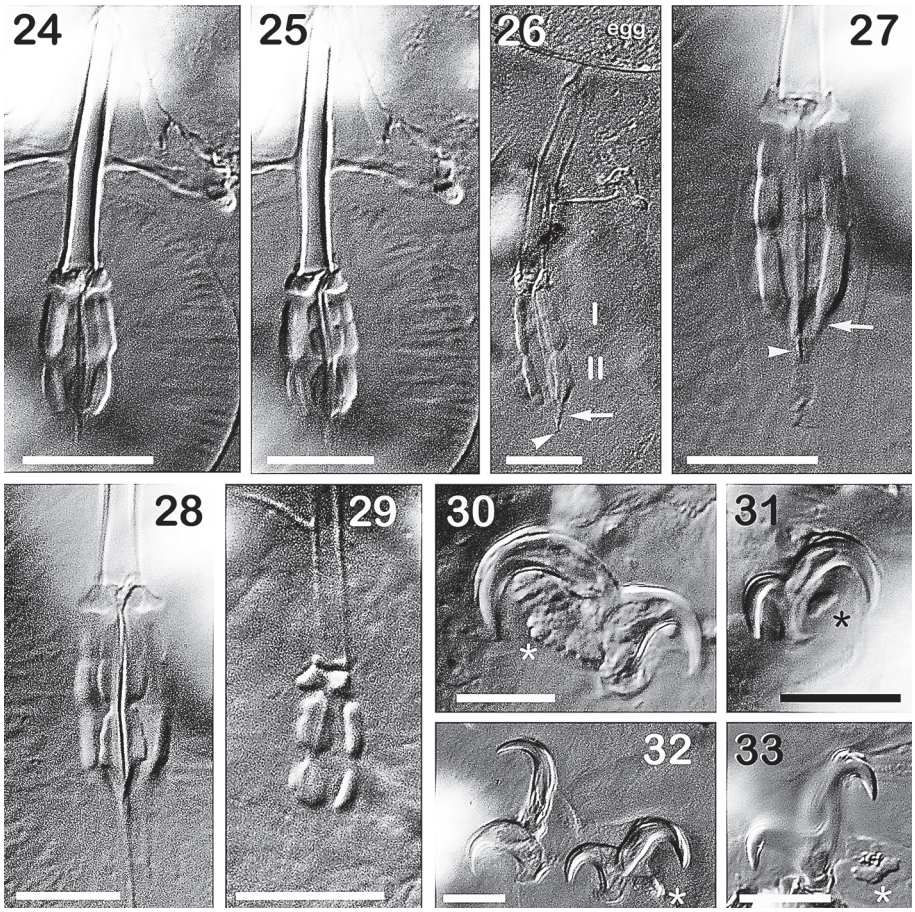
Figs 7-12: *Hypsibius murrayi* (Richters, 1907), syntypes. **7** Buccopharyngeal apparatus. **8** Mouth ring with oval structures (asterisk) and mouth cavity. **9-12** Placoids; thin cuticular band in the rear of pharynx lumen (arrow); microplacoid (arrowhead); the first and the second macroplacoid (I, II). PHC-images. Scale bar 10 µm, except Fig. 8 (5 µm).

Abb. 7-12: *Hypsibius murrayi* (Richters, 1907), Syntypen. **7** Buccalapparat. **8** Mundring mit ovalen Strukturen (Stern) und Mundhöhle. **9-12** Placoide; dünnes kutikuläres Band im posterioren Bereich des Schlundkopflumens (Pfeil); Mikroplacoid (Pfeilkopf), erstes und zweites Makroplakoid (I, II). PHC-Aufnahmen; Maßstab 10 µm, außer Fig. 8 (5 µm).



Figs 13-23: *Hypsibius murrayi* (Richters, 1907), syntypes. **13** Buccopharyngeal apparatus, adult. **14, 15, 17, 18**: Ditto, embryos. **19, 20** Pharyngeal structures, embryos. **16** Claws, leg II and I (?), embryo. **21-23** Claws on leg IV in adults with cuticular bar of the hind claw base (arrowhead). Fig. 13: Same animal as in Figs 1-3, 9; Fig. 21: ditto, the claws IV of the exuvia; broken claw branch (asterisk). PHC-images. Scale bar 10 µm.

Abb. 13-23: *Hypsibius murrayi* (Richters, 1907), Syntypen. **13** Buccalapparat, adult. **14, 15**, **17, 18**: Ditto, Embryonen. **19, 20** Strukturen im Schlundkopf, Embryonen. **16** Krallen, Bein II und I (?) im Embryo. **21-23** Krallen am Bein IV bei Adulten mit kutikulärer basaler Leiste an der hinteren Kralle (Pfeilkopf). Abb. 13: Dasselbe Tier wie in den Abb. 1-3, 9; Abb. 21: ditto, die Krallen IV der Exuvie; abgebrochener Krallenast (Stern). PHC-Aufnahmen, Maßstab 10 µm.

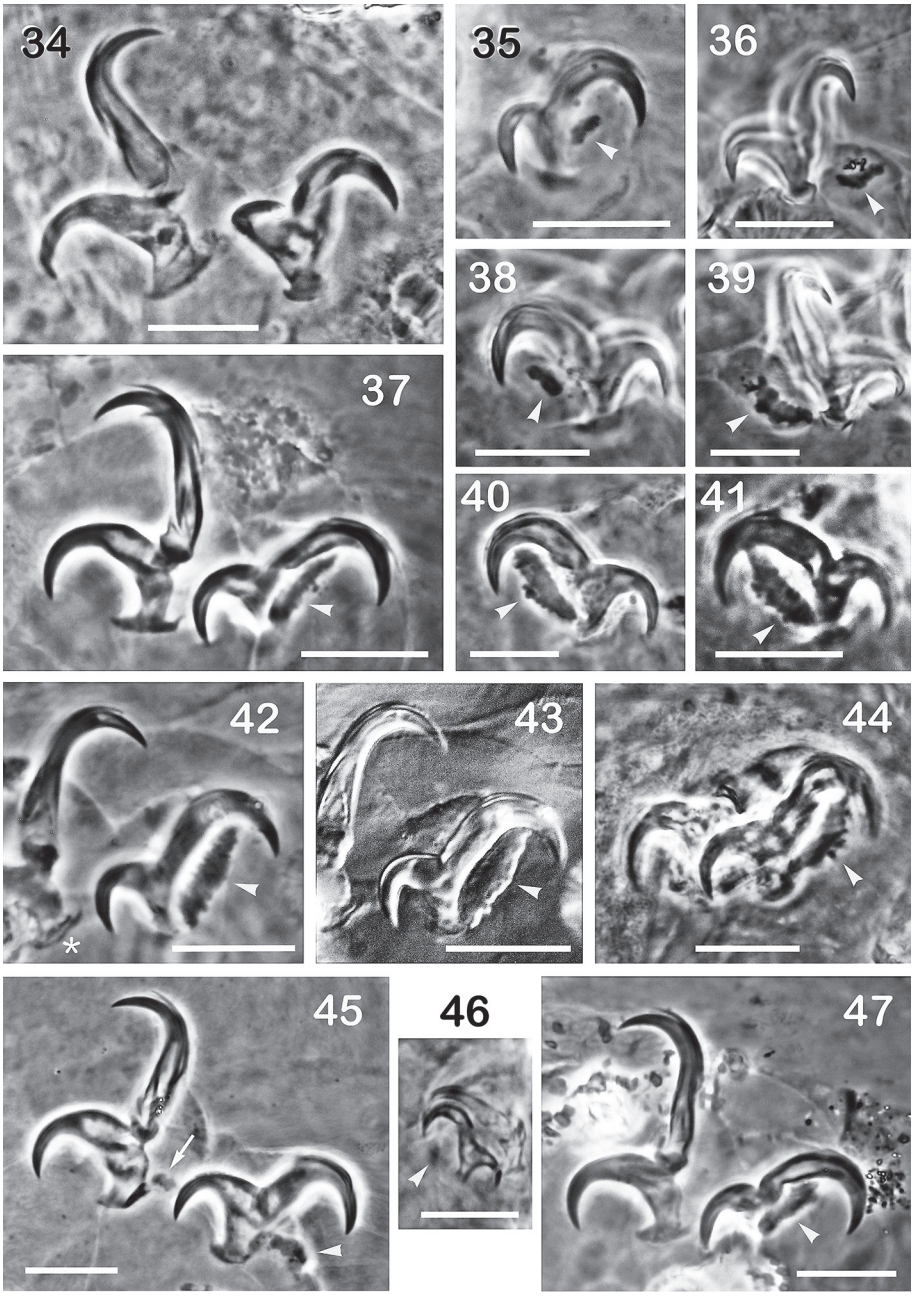


Figs 24-33: *Hypsibius murrayi* (Richters, 1907), syntypes. **24-26** Buccopharyngeal apparatuses. **27-29** Pharyngeal structures. **30-33** Claws and cuticular bars (asterisk) on leg I (Figs 31, 33) and leg III (Figs 30, 32). Fig. 26: Same animal as in Figs 1-3, 9. Thin cuticular band at the rear of the pharynx lumen (arrow); microplacoid (arrowhead); the first and the second macroplacoid (I, II). Fig. 29: Embryo. DIC-images. Scale bar 10 μm.

Abb. 24-33. *Hypsibius murrayi* (Richters, 1907), Syntypen. **24-26** Buccalapparate. **27-29** Pharyngeale Strukturen der Schlundköpfe. **30-33** Krallen und kutikuläre Leisten (Stern) an Bein I (Abb. 31, 33) und Bein III (Abb. 30, 32). Abb. 26: Dasselbe Tier wie in den Abb. 1-3, 9. Dünnes kutikuläres Band im posterioren Teil des des Schlundkopflumens (Pfeil); Mikroplacoid (Pfeilkopf); erstes und zweites Makroplakoid (I, II). Abb. 29: Embryo. DIC-Aufnahmen. Maßstab 10 μm.

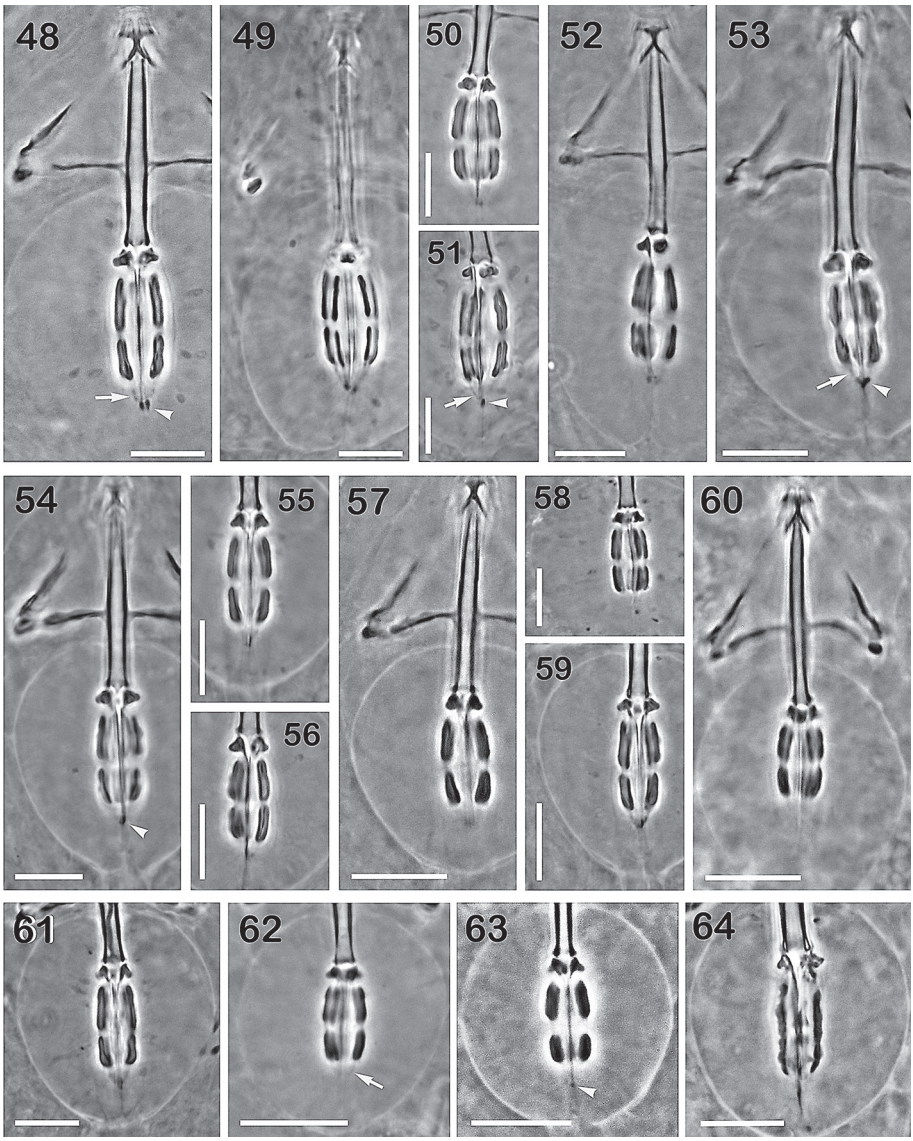
in larger animals; microplacoids and their associated thin cuticular bands mostly well formed and present. The shape, size and the presence of microplacoids vary and, although usually evident in adults (e.g. Figs 48, 49), they are poorer developed or even lacking in juvenile (smallest) animals (e.g. Figs 60, 62, 63). The same concerns the form and presence of the thin cuticular band associated with the second macroplacoid, the band is usually hardly discernible or absent in juveniles (e.g. Figs 60, 62).

Claws of the same form and similarly sized as those in the type material. In juveniles they are distinctly smaller, less sclerotized and bars of the internal claws I-III are



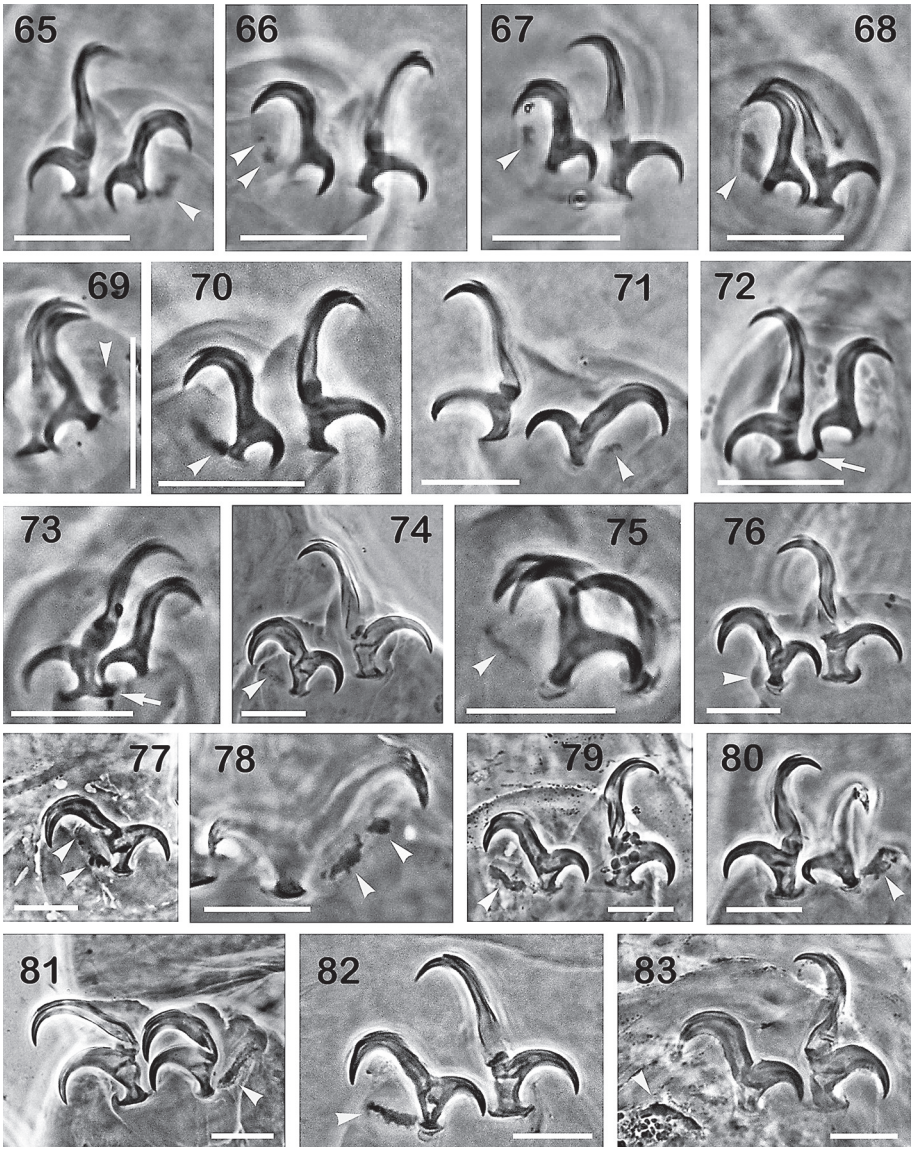
Figs 34-47: *Hypsibius murrayi* (Richters, 1907), syntypes. Variability of claws and cuticular bars (arrowheads). **34-36, 38** Claws on leg I; 37, **39** Ditto, leg II; **40-45, 47** Ditto, leg III. **46** Claws of embryo, leg I (?). Fig. 34: The same specimen as in Figs 1-3, 9; Fig. 44: Ditto, claws of the exuvium. Figs 42, 43: The same claw; lunula (?) (asterisk). Fig. 45: Bar-like structure (arrow). PHC-images, except Fig. 43 (DIC-image). Scale bar 10 μm.

Abb. 34-47: *Hypsibius murrayi* (Richter, 1907), Syntypen. Variabilität von Krallen und kutikulären Leisten (Pfeilkopf). **34-36, 38** Krallen am Bein I. **37, 39** Ditto, Bein II; **40-45, 47** Ditto, Bein III.



Figs 48-64: *Hypsibius murrayi* (Richters, 1907), additional material. Buccopharyngeal apparatuses, fragments of pharynges and variability of these structures. Figs 48-51: South Georgia, others: Kerguelen. Figs 60, 62, 63: Juveniles. Fig. 64: Aberrant placoids. Thin cuticular band in the posterior part of the pharynx lumen (arrow; microplacoid (arrowhead). PHC-images. Scale bar 10 µm.
Abb. 48-64: *Hypsibius murrayi* (Richters, 1907), zusätzliches Material. Buccalapparate, Fragmente von Schlundköpfen und Variabilität dieser Strukturen. Abb. 48-51: Südgeorgien, andere Abbildungen: Kerguelen. Abb. 60, 62, 63: Juvenile Tiere. Abb. 64: Aberrante Placoide. Dünnes kutikuläres Band an der Rückseite des Schlundkopflumens (Pfeil). Mikroplacoid (Pfeilkopf). PHC-Aufnahmen. Maßstab 10 µm.

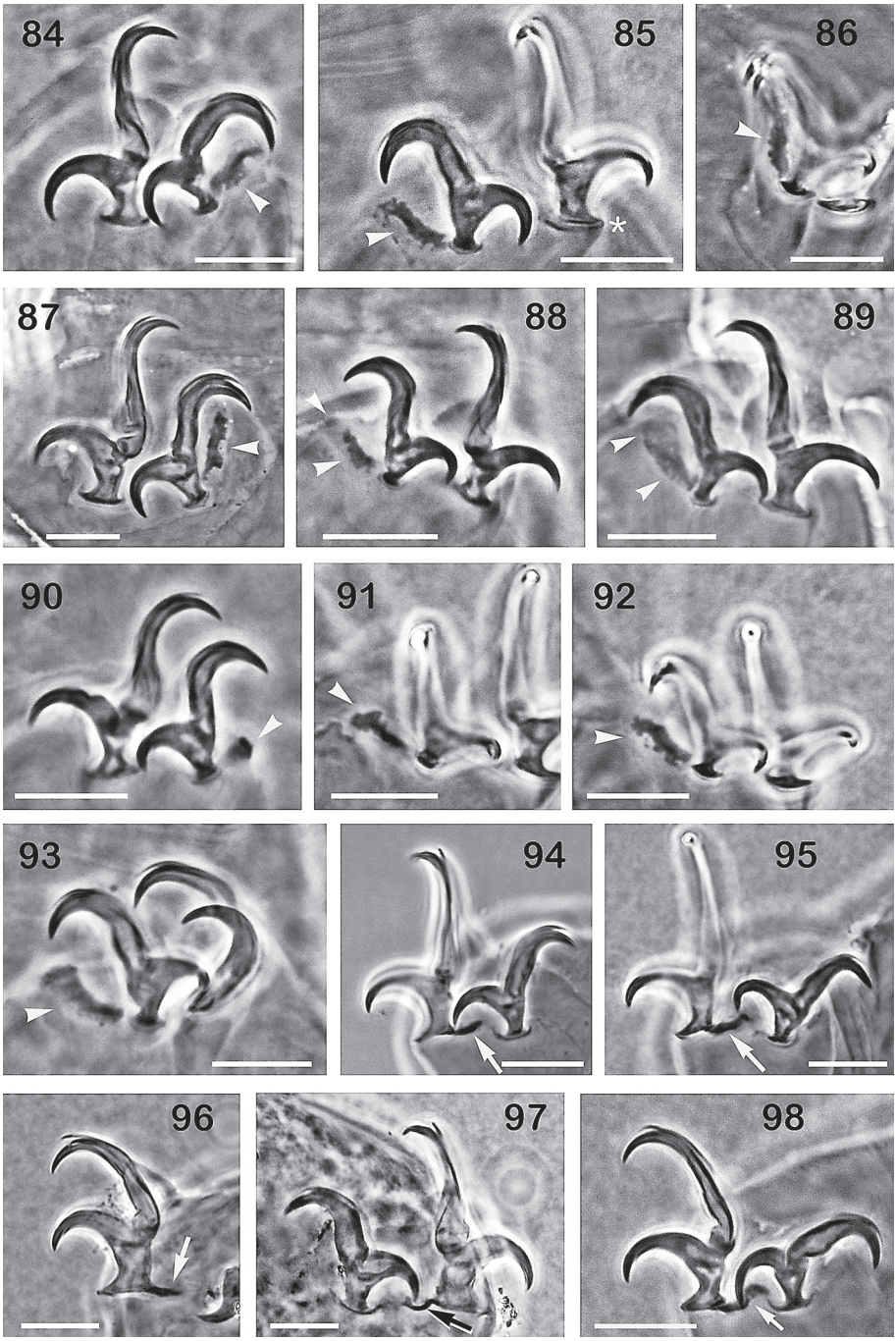
46 Krallen des Embryos, Bein I (?). Abb. 34: Dasselbe Tier wie in den Abb. 1-3, 9. Abb. 44: Ditto, Krallen der Exuvie. Abb. 42, 43: Dieselbe Kralle; Lunula (?) (Stern). Abb. 45: Leistenartige Struktur (Pfeil). PHC-Aufnahmen, Abb. 43: DIC. Maßstab 10 µm.



Figs 65-83: *Hypsibius murrayi* (Richters, 1907), additional material. Variability of claws and cuticular bars. **65-73** Juveniles, other images from adults. **65, 66, 74, 75, 76** Leg I. **67-69, 77-82** Leg II. **83** Leg III. **72, 73** Leg IV; cuticular bars on legs I-III (arrowhead); bar of the hind claw base (leg IV) (arrow). Figs 74, 81: South Georgia; other figures Kerguelen. PHC-images Scale bar 10 µm.

Abb. 65-83: *Hypsibius murrayi* (Richters, 1907), zusätzliches Material. Variabilität von Krallen und kutikulären Leisten. **65-73**: Juvenile Tiere. Die anderen Bilder von Erwachsenen. **65, 66, 74, 75, 76**: Bein I. **67-69, 77-82** Bein II. **83** Bein III. **72, 73** Bein IV. Kutikuläre Leisten an den Beinen I-III (Pfeilkopf); Fußleiste (Sporn) der hinterer Kralle (Bein IV) (Pfeil). Abb. 74, 81 Südgeorgien, die anderen Abbildungen Kerguelen. PHC-Aufnahmen. Maßstab 10 µm.

kutikulären Leisten. **84-93** Bein III, **94-98** Bein IV. Kutikuläre Leisten an den Beinen I-III (Pfeilkopf), Fußleiste (Sporn) der hinterer Kralle (Bein IV) (Pfeil). Abb. 85 Lunula(?) (Stern), Abb. 96, 97 Dasselbe Tier. Abb. 94: Südgeorgien, die anderen Abbildungen: Kerguelen. PHC-Bilder. Maßstab 10 µm.



Figs 84-98: *Hypsibius murrayi* (Richters, 1907), additional material. Variability of claws and cuticular bars**. 84-93** leg III; **94-98** Leg IV. Cuticular bars on legs I-III (arrowhead); bar (spur) of the hind claw base (leg IV) (arrow). Fig. 85 Lunula(?) (asterisk). Figs 96, 97: The same animal. Fig. 94: South Georgia, other figures: Kerguelen. PHC-images. Scale bar 10 µm.

Abb. 84-98: *Hypsibius murrayi* (Richters, 1907), zusätzliches Material. Variabilität von Krallen und

poor developed (Figs 65-71). Also the spur of the base of the hind claw is smaller (Figs 72, 73) than in adults. Main branches of internal claws in adults relatively long and wide (e.g. Figs 89, 90). Lunules on internal claws in juveniles hardly visible, but are better discernible in adults (Figs 75, 80, 82, 85, 89, 90). Lunula-like structures at the bases of external claws were detectable only on few claws (e.g. Figs 83, 89; 85, asterisk). The bases of external claws are distinctly expanded and very often curved more or less upwards at their ends (Figs 76, 81, 82).

3.1.4 Morphometric data

Bold type shows data of adult syntypes, italic type those of syntypic embryos and regular font those of specimens from Kerguelen and South Georgia. Measurements are in µm, all indices in %. Their values are presented in the following convention:
$\bar{x}$ ± SD (min-max) [n] * V (for measurements);
$\bar{x}$ ± SD (min-max) [n] * V / r^2 (for indices).
--- No data
// Measurements of the lectotype
For the abbreviations and definitions see "Material and methods".

A) Measurements (µm)

Body length
493.0 ± 106.2 (338.0-603.0) [5] * 21.5 // 568.0
358.0 ± 102.0 (197.0-551.0) [16] * 28.5
Buccopharyngeal apparatus length
59.2 ± 7.6 (53.1-70.2) [4] * 12.8 // ---
55.6 ± 10.2 (40.5-69.9) [16] * 18.3
Pharynx (length x width)
29.7-40.5 x 27.9-36.0 // ---
21.6-37.8 x 20.7-36.0
Buccal tube length
30.6 ± 3.0 (26.1-34.2) [5] * 9.9 // 31.5
26.8 ± 3.8 (20.7-32.4) [16] * 1.0
*22.3 ± 0.8 (21.5-23.4) [5] * 3.5*
Stylet supports (ss) attachement
19.7 ± 2.4 (16.7-22.5) [5] * 12.3 // 21.6
17.9 ± 2.5 (13.5-21.2) [16] * 0.6
*13.5 ± 0.0 (13.5) [5] * 0.0*
Buccal tube width (external)
3.2 ± 0.5 (2.7-3.6) [5] * 14.3 // 3.6
2.5 ± 0.6 (1.6-3.6) [16] * 22.9
*1.8 ± 0.1(1.6-1-8) [4] * 5.71*
Macroplacoid row length
13.0 ± 3.0 (10.4-17.1) [5] * 23.0 // 17.1
11.7 ± 2.8 (7.2-15.3) [16] * 24.5
6.5 ± 0.1 (6.4-6.7) [5] 2.08*
Macroplacoid 1 length
6.7 ± 1.7 (5.0-9.0) [5] * 24.9 // 9.0
5.8 ± 1.5 (3.6-8.1) [16] * 26.0
*4.0 ± 0.2 (3.6-4.1) [5] * 5.59*
Macroplacoid 2 length
5.3 ± 1.2 (4.1-7.2) [5] * 22.5 // 7.2
4.2 ± 1.2 (2.7-5.9) [16] * 27.8
*2.6 ± 0.2 (2.3-2.7) [5] * 6.8*
Pharyngeal cuticular band
2.9 ± 1.0 (1.8-4.1) [4] * 35.6 // 4.1
(1.8-4.5) [7]
Microplacoid length
(0.5, 0.5) [2] // 0.5
0.8 ± 0.3 (0.5-1.4) [14] * 33.5
External claw 1 length
(23.4, 26.1, 27.0) [3] //23.4
15.7 ± 5.1 (6.3-23.4) [13] * 33.0
External claw 1 base height
(6.3, 7.2) [2] // 7.2
5.7 ± 1.5 (3.6-8.1) [14] * 25.7
External claw 1 main branch length
(11.7, 15.3, 18.0) [3] // 15.3
11.4 ± 3.1 (6.3-16.2) [15] * 26.9
External claw 1 secondary branch length
(11.3) [1] // 11.3
7.4 ± 2.0 (4.5-11.7) [14] * 27.5
Internal claw 1 length
13.9 ± 2.6 (10.8-16.2) [4] * 19.5 // 14.4
10.6 ± 3.0 (15.3-16.2) [15] * 28.8
Internal claw 1 base height
(5.9, 5.9, 6.3) [3] // 5.9
5.5 ± 1.3 (3.2-7.7) [13] * 23.4
Internal claw 1 main branch length
8.3 ± 1.3 (6.3-9.0) [4] * 16.2 // 9.0
6.5 ± 1.5 (4.5-10.0) [15] * 23.0

Internal claw 1 secondary branch length
(5.4, 7.2) [2] // 7.2
5.6 ± 1.3 (3.6-7.7) [11] * 23.0
Hind claw (= ext. 4) length
26.1 ± 1.6 (24.3-27.9) [4] * 6.3 // 27.9
21.6 ± 6.1 (12.6-29.0) [12] * 28.2
Hind claw base height
(8.1, 9.0, 10.8) [3] // ---
7.0 ± 2.1 (3.6-9.0) [12] * 29.9
Hind claw main branch length
18.5 ± 0.9 (18.0-19.8) [4] * 4.9 // 19.8
14.5 ± 3.9 (9.0-21.6) [15] * 27.2
Hind claw secondary branch length
(10.8, 11.7) [2] // ---
*8.4 ± 2.3 (5.4-13.1) [14] * 28.0*
Fore claw (= int. 4) length
16.4 ± 2.1 (13.5-19.8) [6] * 12.9 // 17.1
13.5 ± 4.1(8.1-19.8) [14] * 30.4
Fore claw base height
8.1 ± 1.1 (6.3-9.0) [6] * 14.1 // 9.0
6.2 ± 1.9 (3.2-9.0) [14] * 30.1
Fore claw main branch length
9.6 ± 1.1 (9.0-11.6) [6] * 11.0 // 9.0
8.7 ± 2.3 (5.4-12.6) [15] * 26.2
Fore claw secondary branch length
7.1 ± 1.2 (6.3-9.0) [6] * 11.0 // ---
6.4 ± 2.1 (3.6-10.0) [14] * 34.3

B) Indices

1 -- *PT* = "*pt* indices": Pilato 1981 (= "*WTT*", the whole tube length indices: Dastych 2006)

PT stylet supports (*PT ss*)
65.3 ± 2.7 (61.4-68.6) [5] * 4.2 / 0.9080
64.2 ± 1.7 (61.7-66.7) [16] * 2.7 / 0.9702
*60.6 ± 2.1 (57.7-62.8) [5] * 3.5/---*
PT buccal tube width (ext.)
10.5 ± 1.3 (9.2-12.1) [5] * 12.0 / 0.2739
9.1 ± 1.2 (7.4-11.5) [16] *13.1 / 0.7385
*7.9 ± 0.4 (7.5-8.3) [4] * 4.4 / 0.3165*
PT macroplacoid row length
43.0 ±7.0 (36.9-54.3) [5] * 16.2 / 0.6132
44.0 ± 6.8 (33.3-58.3) [16] *15.4 / 0.8735
*29.0 ± 1.4 (27.4-31.0) [5] * 4.8 / 0.3306*
PT macroplacoid 1 length
22.0 ± 4.0 (18.4-28.6) [5] * 18.4 / 0.5591
21.4 ± 3.2 (16.0-27.6) [16] * 14.9 / 0.8621
*17,8 ± 0.8 (16.7-18.8) [5] * 4.5 / 0.3306*
PT macroplacoid 2 length
17.6 ± 3.2 (15.4-22.9) [5] * 18.0 / 0.3530
15.5 ± 2.6 (12.0-21.4) [16] * 16.6 / 0.8231
*11.7 ± 0.8 (10.5-12.5) [5] * 6.5 / 0.3306*
PT claw I (ext.) length
(73.4, 78.9, 100) [3]
61.4 ± 8.0 (46.3-74.3) [13] * 13.0 / 0.7401
PT claw I (ext.) base height
(17.5, 22.9) [2]
21.0 ± 2.7 (16.7-25.0) [14] * 12.8 / 0.9039
PT claw I (ext.) main branch length
(44.8, 48.6, 52.6) [3]
42.0 ± 6.4 (29.2-51.9) [15] * 15.1 / 0.8414
PT claw I (ext.) secondary branch length
35.9 [1]
27.9 ± 3.8 (20.8-37.1) [15] * 13.8 / 0.8404
PT claw I (int.) length
42.2 ± 5.2 (36.9-47.4) [4] * 12.3 / 0.7193
38.9 ± 6.4 (28.1-50.0) [15] * 16.3 / 0.7889
PT claw I (int.) base height
(17.3, 20.7, 21.5) [3]
19.8 ± 2.4 (15.5-24.4) [13] * 12.2 / 0.8383
PT claw I (int.) main branch length
27.4 ± 2.9 (21.1-30.7) [4] * 10.4 / 0.6586
24.2 ±2 .9 (18.8-30.9) [15] * 11.9 / 0.7173
PT claw I (int.) secondary branch length
(20.8, 21.1) [2]
20.5 ± 2.2 (17.4-24.3) [11] * 10.7 / 0.8683
PT hind claw (= ext. IV) length
82.9, 88.1) [2]
78.4 ± 12.3 (58.9-95.2) [12] * 15.7 / 0.8953
PT hind claw base height
(27.6) [1]
25.2 ± 5.2 (16.7-31.0) [12] * 20.7 / 0.7588
PT hind claw main branch length
(61.4, 62.9) [2]
53.9 ± 10.5 (41.1-78.0) [15] * 19.5 / 0.8643
PT hind claw secondary branch length
(36.9) [1]
31.3 ± 4.9 (25.0-41.6) [14] * 15.6 / 0.7963
PT fore claw (= int. IV) length
54.5 ± 2.6 (51.7-57.9) [4] * 4.7 / 0.9888
49.0 ± 8.6 (37.5-62.9) [14] * 17.5 / 0.9139
PT fore claw base height
25.9 ± 2.0 (24.1-28.6) [4] * 7.8 / 0.8797

23.6 ± 4.4 (14.8-34.0) [14] * 18.7 / 0.8498
PT fore claw main branch length
30.5 ± 2.5 (28.6-33.3) [4] * 8.0 / 0.5821
32.2 ± 4.6 (25.0-40.0) [15] * 14.4 / 0.7964
PT fore claw secondary branch length
(21.8, 26.3, 33.3) [3]
22.7 ± 5.5 (14.8-31.7) [15] * 23.9 / 0.8459

2 -- Other indices

Macroplacoid index (*MPLI*)
80.8 ± 5.8 (70.6-85.7) [5] * 7.2 / 0.8965
71.9 ±5.8 (59.2-81.9) [16] * 8.1 / 0.9103
*65.9 ± 1.9 (62.5-66.7) [5] * 2.9 / 1.000*
External claws index *(ECI*)
(83.9) [1]
80.7 ± 6.5 (70.3-90.3) [10] * 8.1 / 0.9250
Claw main branch index (*MBrI*)
(77.3) [1]
78.2 ± 7.3 (66.7-91.5) [14] * 9.4 / 0.9118
Hind claw base index (*HBaI*)
(45.0) [1]
46.7 ±6.5 (36.0-57.0) [12] * 13.9 / 0.8194
Hind/fore claw index length (*HFCI*)
(61.3, 65.0) [2]
63.9 ± 4.0 (57.1-71.4) [12] * 6.2 / 0.9542
Hind/fore main branch index (*HFBrI*)
45.5, 50.0) [2]
60.5 ± 6.1 (50.0-70.5) [15] * 10.0 / 0.8814

3 -- Eggs

Type material: four exuviae with eggs, two of them with embryos (5-6 eggs per exuvia, n = 22), eggs 81.0-98.0 μm in diameter.
Other material (Kerguelen): three exuviae with eggs, no embryos (5, 7, 8 eggs in exuvia, n = 20), eggs 56.0-72.0 x 74.0-92 μm in diameter.

4. Discussion

4.1. Taxonomical comments

CUÉNOT (1932) suggested a possible synonymy of *Hypsibius murrayi* (Richters, 1907) with *H. dujardini* (Doyère, 1840), a proposal adopted in influential monographs (see MARCUS 1936; RAMAZZOTTI 1972; RAMAZZOTTI & MAUCCI 1983) and other articles and being considered valid until now.
RICHTERS (1907a) very short original description of *H. murrayi* includes important diagnostic information about the length relation („4 : 3“) of both macroplacoids, but does not present the key taxonomic character of the taxon, i.e. the occurrence of the conspicuous, wide and rugose cuticular bars at the bases of the internal claws on legs I-III, tiny microplacoids and associated with them small cuticular bands, supposedly due to the poor optics available at that time. The presence or absence of eyes in *H. murrayi,* another diagnostic character of the species, is somewhat puzzling. RICHTERS (1907a, p. 295) wrote in the species description „Mit und ohne Augen“ (= with and without eyes). All five (from 20 animals originally mentioned by RICHTERS) rediscovered type specimens examined herein, including the specimen on the photogram in RICHTERS (1907a) designed here as lectotype, did not reveal even traces of the eye-pigment (comp. Figs 1, 3 with Fig. 2). However, MARCUS (1928) published a drawing of that specimen with very distinct eye-dots, strangely using the photogram as reference (comp. Fig. 5 and Fig. 2). It is known that various mounting media, e.g. PVL, HOYER and less severe FAURE's mountant, may completely dissolve eye-dots as well as some of the cuticular structures of tardigrades. RICHTERS probably used formol or arsenic glycerine as mounting that should preserve the pigments of the eye-dots. At least there are slides in RICHTERS collection, which include different tardigrade species with well preserved eye-pigment (e.g. in recently redescribed *Isohypsibius tetradactyloides* Richters, 1907 = *I. asper* Murray, 1906; see DASTYCH 2016).
The absence of eyes was reported as a specific character in the original description of *Hypsibius heardensis* Miller, McInnes & Bergstrom, 2005, based on specimens

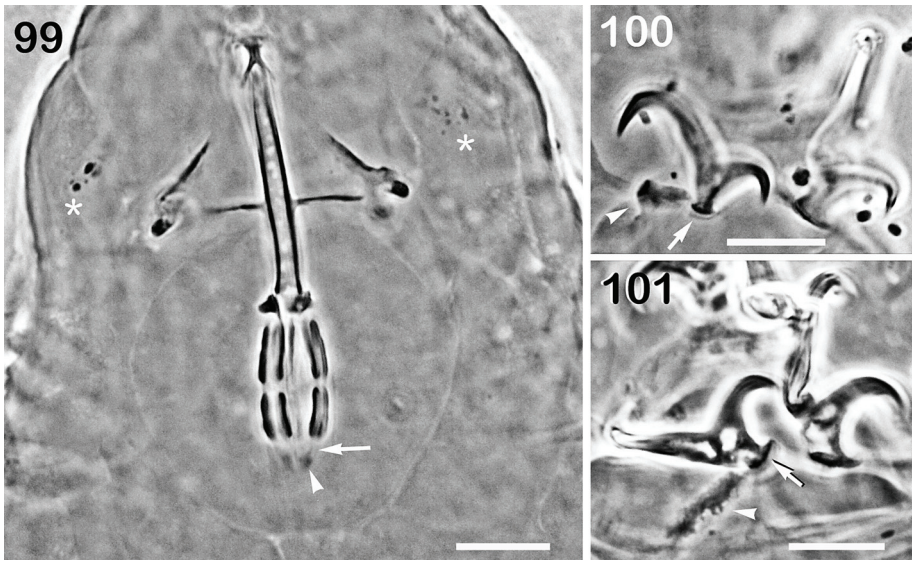
mounted in Hoyer's medium (Miller et al. 2005). However, in one of the three type specimens (paratype) of *H. heardensis* which I could examine, I found distinct traces of partly dissolved eye-dots (Fig. 99, asterisks). In the remaining (two) specimens, including the holotype, the eye-dots are totally absent, but there also pharynges are lacking, i.e. the latter dissolved through (too) strongly reacting/clearing mountant. Thus, it can not be excluded that the absence of the eye-dots might be attributed here to the mounting medium. Absence of eye-dots due to Hoyer's mountant were recently reported by Gasiorek et al. (2018) in *Hypsibius* spp. and by Stec et al. (2018) in some members of the genus of *Macrobiotus* and here in 80 % of the specimens. The specimens of *H. murrayi* from South Georgia and Kerguelen mounted in Faure's medium (a mountant with distinctly lesser clearing strength as Hoyer's medium) had distinct eye-dots (also those from South Georgia which have even been remounted recently into Hoyer mountant). However, some specimens from Kerguelen mounted polyvinyl-lactophenol (PVL) have lost their eye-dots, including most of the cuticular bars on legs I-III.

4.2. Differential diagnosis

According to the literature, the combination of characters such as smooth cuticle, the presence of cuticular bars at the bases of the internal claws on legs I-III and their absence between external and internal claws on these legs separate three species, *Hypsibius iskandarovi* Tumanov, 1997, *Hypsibius conwentzii* Kaczmarek, Parnikoza, Gawlak, Esefeld, Peter, Kozeretska & Roszkowska, 2018 and *Hypsibius heardensis* Miller, McInnes & Bergstrom, 2005, very well from other members of the genus *Hypsibius*. This group of three needs to be expanded by *Hypsibius murrayi*. However, *H. iskandarovi* differs from *H. murrayi* by the presence of a pseudoseptulum, lacking in the latter species and also by its second macroplacoid that is shorter than the first macroplacoid. In *H. murrayi* the second macroplacoid is relatively longer. Moreover, in *H. iskandarovi* the cuticular bars I-III are not rugose compared to those in *H. murrayi,* seen in the illustration provided by Tumanov (1997: Fig. 2). Both species differ also in the position of their pharyngeal microstructures, i.e. septulum vs. microplacoid (for their characteristics see Thulin 1928). In *H. iskandarovi* the septulum is located closer to the posterior edge of the second macroplacoid, whereas in *H. murrayi* the microplacoid is located further. Moreover, the thin cuticular band associated with the caudal part of the second macroplacoid was not reported in *H. iskandarovi*; but it occurs in *H. murrayi* and is here considered as an important taxonomic character.

The recently described *H. conwentzii* (see Kaczmarek et al. 2018) was reported earlier from Antarctica as *H. dujardini* or *H.* cf. *dujardini*. This species seems to have a wide distribution in the Maritime Antarctic (e.g. McInnes 1995, Miller et al. 2005). *H. conwentzii* differs from *H. murrayi* by the presence of a large septulum compared to the tiny microplacoid in the latter. Moreover, there are some differences in the position of these microstructures in both taxa. In *H. conwentzii* the septulum is placed closer to the posterior edge of the second macroplacoid. In *H. murrayi* the microplacoid is further away from the macroplacoid edge. Additionally, these species differ in the shape and size of their bars on legs I-III. In *H. murrayi* the bars are wider, larger and their edges are distinctly ragged, whereas in *H. conwentzii* the bars are smaller and thinner and have smoother edges.

H. heardensis is strikingly similar to *H. murrayi*. The analysis of their morphological characters reveals the identity of both taxa. They share the same type and organisation of the buccopharyngeal apparatus and its structures, the same type of claws and associated cuticular bars (comp. Figs 1-4, 7-98 with Figs 99-101 and fig. 3 in Miller et al. 2005). As a



Figs 99-101: *Hypsibius heardensis* Miller, McInnes & Bergstrom, 2005, type specimens. **99** Buccopharyngeal apparatus; thin cuticular band at the rear of the pharynx lumen (arrow); microplacoid(s) (arrowhead). Note remnants of pigment granules (asterisks) in the region of the eyes. **100, 101** Claws on leg III; lunula(?) (arrow), cuticular bar (arrowhead). Figs 99, 100: Paratype (MU-094-7). Fig. 101: Holotype (MU-080-1). PHC-images. Scale bar 10 μm.
Abb. 99-101: *Hypsibius heardensis* Miller, McInnes & Bergstrom, 2005, Typenmaterial. **99** Buccalapparat, dünnes kutikuläres Band an der Rückseite des Pharynxlumens (Pfeil), Mikroplakoid(e) (Pfeilkopf). Man beachte die Pigmentreste (Sterne) im Bereich der Augen. **100, 101** Krallen am Bein III; Lunula(?) (Pfeil); kutikuläre Leisten (Pfeilkopf). Abb. 99, 100: Paratypus (MU-094-7). Abb. 101: Holotypus (MU-080-1). PHC-Bilder. Maßstab 10 μm.

result, *H. heardensis* should be considered as junior synonym of *H. murrayi* (comp. ICZN, Article 61.3.1). At the time *H. heardensis* was described, the existence of type specimens of *H. murrayi* was not known. There are several discrepancies between the original description of *H. heardensis* and the data I obtained here from the three type specimens. This applies to some measurements of the holotype and some data on morphology. They are presented below including some further information. The originally published measurements of the holotype (μm) are given in brackets.

Body length: 406 (350), buccal tube 27.9 (24), stylet support 18(15): thus the pt ss index 64.5 % (62.5 %). External claw IV length 28 (16), internal claw IV length 13.5 (7). The external claw I in holotype is 19.8 μm long (data absent in the original description). The two paratypes examined here were 336 and 435 μm long. The MPLI and ECI indices for *H. heardensis*, not given in the original description and presented here (71.4-79.4 % and 73.3-83.6 %: n = 3 and n = 2, respectively), fit well the range of the particular such index calculated for *H. murrayi* (for details see section 2 and 3.1.4). In all type specimens a very narrow ring (ca 1 μm high) around the mouth opening was present, in two such rings tiny, hardly visible structures (some kind of a row composed of barely detectable points or circles) could be discerned. In my opinion they represent remnants of the mouth ring, usually composed of tiny oval structures that were probably dissolved at least in part in the HOYER's mountant. Remains of pigments

of the eye-dots have been found in one paratype (Fig. 99, see also remarks in section 4.1) and small lunules were visible on the bases of some internal claws (Figs 100, 101). Their presence was not mentioned in the original description. Not reported by Miller et al. (2005) was the occurrence of thin bands behind the posterior edge of the second macroplacoids. However, the bands were partly and oversimplified shown in the drawings but quite well recognizable on photograms (Miller at al. 2005: figs 2b, c, 3a, b). Thin, cuticular rods positioned laterally at pharyngeal apophyses on both posterior edges of the buccal tube were visible only in one paratype. In all type specimens examined here the cuticular spur at the base of hind claws was not separated from the claw base, as it was presented by Miller et al. (2005: fig. 2e).

4.3. Distribution

Hypsibius murrayi was described by Richters (1907a) from the sub-Antarctic Possession Island in the Crozet Archipelago. Later he reported the species also from some Arctic localities, i.e. Svalbard Archipelago (Spitsbergen: Advent Bay and Hope Island) and Novaya Zemlya (Richters 1911). Unfortunately then the author provided no morphological details on *H. murrayi* and his documentation (microslides) from the Arctic is probably lost. Since then, no further records of *H. murrayi* have been published.

According to accessible and here revised data, *H. murrayi* is characterized by a relatively wide distribution within the sub-Antarctic. The species is known from South Georgia, the Crozet- and the Kerguelen Archipelago as well as the Heard Island. Moreover, according to Miller et al. (2005), the species occurs also on Macquarie Island, reported earlier from there as *Hypsibius* sp. (Miller et al. 2001). Hitherto *H. murrayi* has not been reported from the Continental Antarctic. The records of this species from the Northern Hemisphere (Richters 1911) – preparations of these specimens are lost – are very doubtful and should be confirmed.

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