Organisms Diversity & Evolution (2025) 25:167–187
https://doi.org/10.1007/s13127-024-00668-5

ORIGINAL ARTICLE

Checklist of tardigrades in Germany as a contribution to biodiversity research

Rolf Schuster[1] · **Ralph O. Schill**[2]

Received: 24 September 2024 / Accepted: 2 December 2024 / Published online: 4 February 2025

Abstract

Over 250 years ago Johann August Ephraim Goeze, a Protestant pastor from Quedlinburg, Germany, discovered the first tardigrade. The German physiologist and anatomist Carl August Sigismund Schultze (1795–1877) later named the first species *Macrobiotus hufelandi* C.A.S. Schultze, 1834, a designation that remains valid today. By the first third of the twentieth century numerous new species had been discovered in Germany and were comprehensively compiled for the first time by the German zoologist Ernst Marcus in 1936. Since then additional faunistic studies have been conducted. This new checklist of tardigrades in Germany provides an overview of all known species found in the country to date. It includes 91 limnoterrestrial or limnic species and eight marine species, with 21 belonging to Heterotardigrada and 78 to Eutardigrada. Germany is the type locality (terra typica) for 24 tardigrade species. The number of identified tardigrade species varies significantly depending on the extent of studies conducted in different federal states. Baden-Württemberg has the highest number of species identified, with 80 species recorded across eleven studies. In this state the Black Forest, with its remarkable diversity of 72 identified tardigrade species is one of the most intensively studied regions worldwide. In Hesse 30 species have been recorded from five studies, while Berlin has documented 23 species from two studies. Fewer species have been reported from other federal states. The 99 tardigrade species identified in Germany represent about 7% of the total 1,488 described tardigrade species worldwide.

Keywords Tardigrada · Germany · Checklist · Taxonomy · Literature · Biodiversity · Microinvertebrates

Introduction

The animal group of tardigrades was discovered in Germany over 250 years ago. Johann August Ephraim Goeze (1731–1793) was a Protestant pastor in Quedlinburg, Germany (Saxony-Anhalt, ST). He began his career as a translator of various scientific and philosophical works and only in the last third of his life became a highly respected and productive zoologist, particularly as a helminthologist. He was the first to describe a tardigrade, probably a *Hypsibius* species. This description was published under the title “Von einigen merkwürdigen Wasserinsekten” (On some strange water insects) in an appendix of the German translation of Bonnet’s "Traité d’Insectologie." The appendix contains personal observations made by J.A.E. Goeze in the environment of his hometown Quedlinburg. He discovered water bears in duckweed (especially in winter) and wrote: “Seltsam ist dieses Thierchen, weil der ganze Bau seines Körpers ausserordentlich und seltsam ist, und weil es in seiner äusserlichen Gestalt, dem ersten Anblicke nach, die größte Aehnlichkeit mit einem Bäre im Kleinen hat. Das hat mich auch bewogen, ihm den Namen des kleinen Wasserbärs zu geben”. (Strange is this little creature, because the whole organisation of its body is extraordinary and strange and because of its external appearance. At the first glance, it has the closest similarity to a little bear. This also led me to give it the name little water bear.) (Goeze, 1773).

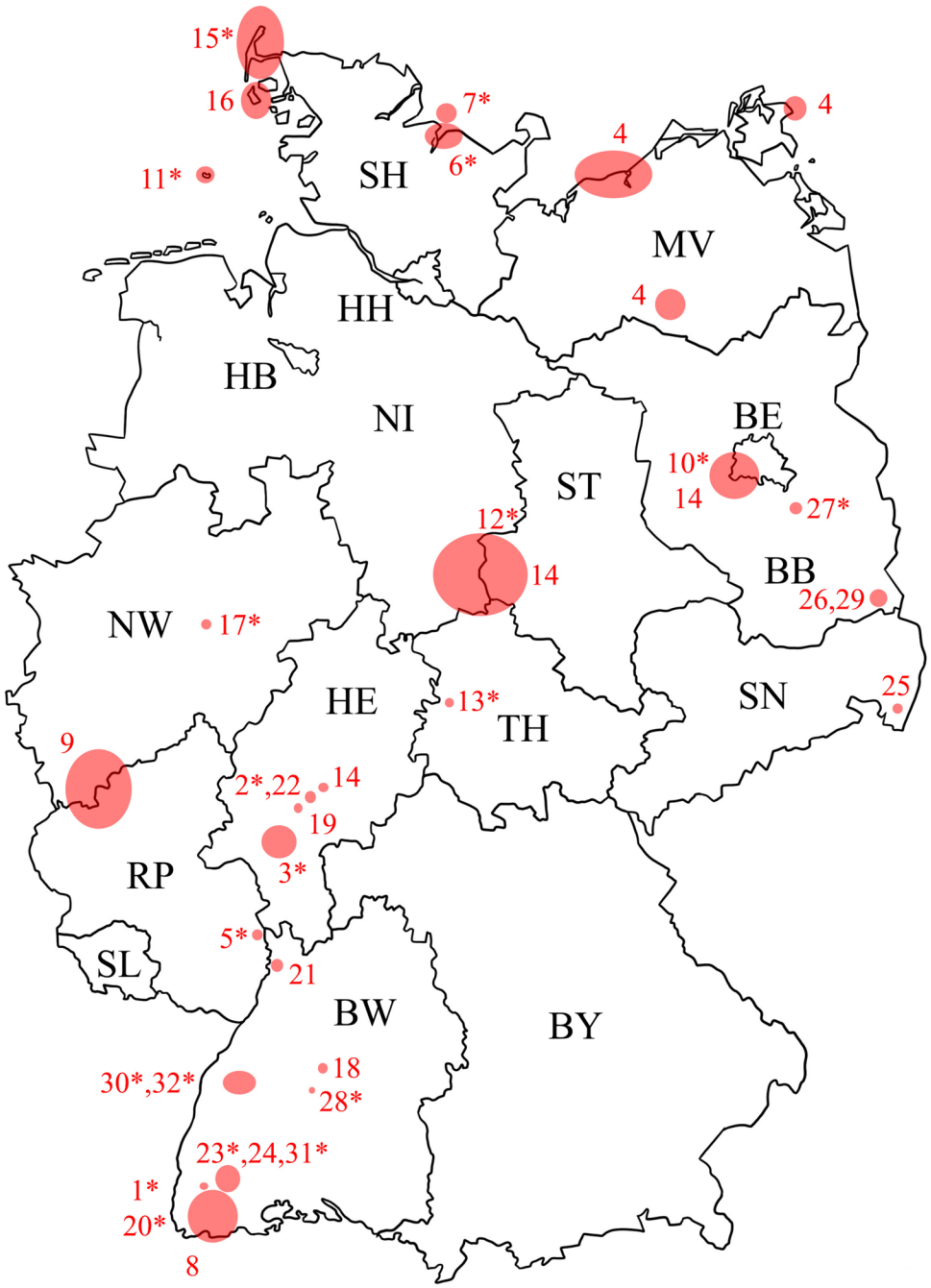
In 1834 Carl August Sigismund Schultze (1795–1877), a German physiologist and anatomist, named the first species *Macrobiotus hufelandi* C.A.S. Schultze, 1834a, 1834b, which is still valid today (Degma & Guidetti, 2024). Between 1927

✉ Ralph O. Schill
ralph.schill@bio.uni-stuttgart.de

Rolf Schuster
r.b.schuster@web.de

[1] Rolf Schuster, Mattenweg 9, 79856 Hinterzarten, Germany

[2] University of Stuttgart, Institute of Biomaterials and biomolecular Systems, Pfaffenwaldring 57, 70569 Stuttgart, Germany



and 1936 the German zoologist Ernst Marcus published four substantial and wide-ranging articles (Marcus, 1927, 1928, 1929, 1936). These included a synopsis of all tardigrade species previously described around the world in the series "Die Tierwelt Deutschlands" (Fauna of Germany). This first and as yet only overview of tardigrades in Germany (within the borders of 1918) was published nearly one hundred years ago (Marcus, 1928, 1936). However no other checklist of tardigrade species found in Germany has been compiled since. Marcus (1936) reported 44 species (valid according to Degma & Guidetti, 2024) from Germany. By this study, we aim to provide an overview of the tardigrade species found in Germany from the discovery and description of the first species to the present day.

◂**Fig. 1** Study areas on tardigrades in Germany. The areas where more than five species were identified are marked in red. Areas where a new species was described are marked with an asterisk (*). (1) Schultze (1834a, 1834b) near St. Ulrich, near Freiburg (BW); (2) Plate (1888) near Marburg (HE); (3) Richters (1900, 1902, 1903) in Frankfurt and surroundings (Taunus), (HE); (4) Richters (1904a) at Heiligendamm, Sassnitz, Markgrafenheide, Müritz (MV); (5) Richters (1907a) at Ludwigshafen (RP); (6) Richters (1908) at the Kiel Fjord (SH); (7) Richters (1909a) in the Eckernförde Bay (SH); (8) Heinis (1910) in the Southern Black Forest (BW); (9) Rahm (1925) at Rhineland Province (now parts of NW and RP), further surroundings of Bonn (NW); (10) Marcus (1928) at Schlachtensee (BE); (11) Schulz (1935) at Helgoland (SH); (12) Marcus (1936) in the Harz (SH); (13) Marcus (1936) near Wartburg, near Eisenach (TH); (14) Englisch (1936) near Berlin and surroundings, Harz (Brocken) (ST), Hesse-Nassau, near Marburg (HE); (15) Schulz (1951) at Sylt (SH); (16) Schulz (1953) at Amrum (SH); (17) Greven (1972) in the northern Sauerland near Volkringshausen (NW); (18) Adler (1987) at the University of Stuttgart-Hohenheim (BW); (19) Hofmann and Eichelberg (1986) in the Lahnauen near Gießen (HE); (20) Bertolani and Rebecchi (1993) near St. Ulrich, near Freiburg (BW); (21) Russel et al. (1994) in the Sandhausen Dunes near Heidelberg (BW); (22) Grabowski (1995) in the Lahnbergen near Marburg (HE); (23) Schuster (1999) near Hinterzarten, near Freiburg (BW); (24) Schuster (2003a, 2003b) in Hinterzarten and surroundings (BW); (25) Hohberg (2006) at Berzdorf, near Dresden (SN); (26) Hohberg et al. (2011) at Welzow, near Spremberg (BB); (27) Michalczyk et al. (2012) in Zeesen (BB); (28) Morek et al. (2019) in Bebenhausen, near Tübingen (BW); (29) Bingemer et al. (2020) at Welzow, near Spremberg (BB); (30) Guidetti et al. (2021) in the Black Forest National Park (BW); (31) Schuster (2021) in the Höllental (Black Forest), near Freiburg (BW); (32) Guidetti et al. (2022a) in the Black Forest National Park (BW). Abbreviations: BB = Brandenburg, BE = Berlin, BW = Baden-Württemberg, BY = Bavaria, HB = Bremen, HE = Hesse, HH = Hamburg, MV = Mecklenburg-Vorpommern, NI = Lower Saxony, NW = North Rhine-Westphalia, RP = Rhineland-Palatinate, SH = Schleswig–Holstein, SL = Saarland, SN = Saxony, ST = Saxony-Anhalt, TH = Thuringia

Materials and methods

The basis for this current checklist is the first summary of German tardigrades by Marcus (1928, 1936) and the data from Ramazzotti and Maucci (1983). The sources cited by Marcus primarily refer to the authors, and the listed tardigrade locations were assigned to the 16 federal states of Germany. Only those locations from Marcus that lie within the present-day territory of the Federal Republic of Germany were included. The term "Germany" refers to the borders of present-day Germany. The unspecific locality "Northern Germany" from Marcus (1936) encompasses the federal states Brandenburg (BB), Berlin (BE), Bremen (HB), Hamburg (HB), Mecklenburg-Vorpommern (MV), Lower Saxony (NI) and Schleswig–Holstein (SL); "Central Germany" North Rhine-Westphalia (NW), Saxony-Anhalt (ST), Saxony (SN) and Thuringia (TH); and "Southern Germany" refers to Baden-Württemberg (BW), Bavaria (BY), Rhineland-Palatinate (RP) and Saarland (SL). The term "German Central Uplands" includes the federal states of Central and Southern Germany. Rahm (1925) studied tardigrades in the Rhine Province, a former administrative unit, which is now part of NW and RP. The term "Harz" in Marcus (1936) refers to the federal states NI, ST and TH.

All faunistic and taxonomic studies on tardigrades conducted in Germany after Marcus's compilation (1936) have been incorporated into the current checklist of tardigrades in Germany. This includes recently discovered species from the last few years (Guidetti et al., 2021, 2022a; Morek et al., 2019; Schuster, 2021). Species used for physiological, molecular and biophysical studies which also originate from Germany are included in the current checklist of tardigrades of Germany but are not marked on the map of study areas (Fig. 1) (e.g., Baumann, 1961; Greven & Peters, 1986). Animal cultures of some species were established and subsequently used for various studies and publications over longer periods. Since these animals can be attributed to an original location and therefore do not represent a new site, these publications were only considered once. The species gathered from the literature were checked against the worldwide checklist with valid species names (Degma & Guidetti, 2024). Invalid and synonymized species were also listed (Tables 1, 2). Species for which Germany is the terra typica were highlighted separately (Table 3).

Also included in the list (Table 4) and on the map (Fig. 1) is the species *Milnesium tardigradum* Doyère, 1840. To account for the significantly expanded *Milnesium* taxonomy in recent years, a redescription was carried out by Michalczyk et al. (2012). The neotype of *M. tardigradum* s.s. and its 46 neoparatypes now originate from Zeesen, (BB), Germany.

Currently, there is no comprehensive study of tardigrades across all of Germany. Most research has been concentrated in specific regions: Richters examined the tardigrade fauna around Frankfurt (Richters, 1902) in Hesse and along the Mecklenburg coast (Richters, 1904a) in Mecklenburg-Vorpommern. Heinis conducted studies in the southern Black Forest (Heinis, 1910) in Baden-Württemberg, while Rahm (1925) focused on the Rhine Province, an area that now includes parts of North Rhine-Westphalia and Rhineland-Palatinate. The current checklist of tardigrades of Germany, summarizing all species found up until 1936, was compiled by Marcus (1936).

After Marcus emigrated to Brazil in 1936 (Greven, 2018) following his dismissal as Associate Professor from the Friedrich Wilhelm University of Berlin due to his Jewish faith, only a few studies on the distribution of tardigrades in Germany were conducted. Englisch (1936) investigated areas around Berlin, Hesse-Nassau and a region in the Harz Mountains, while Schultz (1935, 1951, 1953) focused on marine tardigrades from the North and Baltic Seas. Baumann (1961, 1964, 1966, 1970) reported on individual tardigrade species in Bremen and Lower Saxony.

Table 1 Species with uncertain taxonomic value reported from Germany

Species Name	Federal State	Reference	Status
Macrobiotus macronyx Dujardini, 1851, *Dactylobiotus macronyx* (Dujardin, 1851)	BW, HE, NW	Richters, 1909b; Heinis, 1910; Marcus, 1936	species dubia et inquirenda acccording to Dastych (1988), nomen dubium according to Dastych (2015) and Pogwizd and Stec (2020)
Diphascon alpinum (Murray, 1906a), *Hypsibius (Diphascon) alpinus* (Murray, 1906a)	BE, HE	Marcus, 1936; Englisch, 1936; Hofmann & Eichelberg, 1986; Adler, 1987; Hofmann, 1987	nomen dubium according to Dastych (2015) and Tumanov and Tsvetkova (2023)
Diphascon chilenense Plate, 1888, *Hypsibius (Diphascon) chilenensis* Plate, 1888	HE	Richters, 1904b; Marcus, 1936	nomen dubium according to Dastych (2015)
Echiniscus arctomys Ehrenberg, 1853	BW, NW, RP	Richters, 1902, 1904a; Heinis, 1910; Rahm, 1925; Marcus, 1936	nomen inquirendum according to Gąsiorek et al. (2019a)
Echiniscus muscicola Plate, 1888	BW, HE, NW, RP	Richters, 1902; Heinis, 1910; Rahm, 1925	species inquirenda according to Marcus (1936)
Echiniscus similis Plate, 1888	HE, NW, SN, ST, TH	Plate, 1888; Marcus, 1928	species dubia et inquirenda according to Marcus (1936)
Hypsibius wibbelti Rahm, 1925	NW, RP	Rahm, 1925	species dubia et inquirenda according to Marcus (1936)
Isohypsibius papillifer bulbosus (Marcus, 1928), *Hypsibius papillifer* f. *bulbosus* (Marcus, 1928), *Hypsibius (Isohypsibius) papillifer* forma *bulbosa* (Marcus, 1928)	BE	Marcus, 1936	suppressed by Gąsiorek et al. (2019b)
Isohypsibius schaudinni (Richters, 1909b), *Macrobiotus schaudinni* (Richters, 1909b), *Hypsibius (Isohypsibius) schaudinni* (Richters, 1909b)	BE, HE, NW, ST	Richters, 1909b; Marcus, 1936; Englisch, 1936; Hofmann & Eichelberg, 1986; Hofmann, 1987	nomen inquirendum according to Gąsiorek et al. (2019b)
Isohypsibius tuberculatus (Plate, 1888), *Macrobiotus tuberculatus* (Plate, 1888), *Hypsibius (Isohypsibius) tuberculatus* (Plate, 1888)	BE, BW, HE	Plate, 1888; Marcus, 1928, 1936; Hofmann & Eichelberg, 1986; Adler, 1987	nomen dubium according to Dastych (2015); nomen inquirendum according to Gąsiorek et al. (2019b)
Macrobiotus ferdinandi Reukauf, 1912a	HE, NW, SN, ST, TH	Reukauf, 1912a; Marcus, 1936	Ramazzotti and Maucci (1983) described the original identification process as nearly impossible
Oreella vilucensis Rahrm, 1931	NW	Rahm, 1931; Marcus, 1936; Ramazzotti & Maucci, 1983	species inquirenda according to Degma and Guidetti (2024)
Macrobiotus hibernicus (Murray, 1911), *Hypsibius hibernicus* (Murray, 1911)	BW	Schuster, 2003a, 2003b	nomen dubium according to Guidetti et al. (2022b)
Ramazzottius novemcinctus (Marcus, 1936), *Hypsibius (Hypsibius) novemcinctus* (Marcus, 1936)	NW, RP	Marcus, 1936	nomen dubium according to Stec et al. (2018)
Ursulinius nodosus (Murray, 1907d), *Macrobiotus nodosus* (Murray, 1907d), *Hypsibius (Isohypsibius) nodosus* (Murray, 1907d)	BE	Marcus, 1928, 1936	nomen dubium according to Dastych (2015)

Table 2 Species reported from Germany under synonymous species names

Valid Species Name	Federal State	Previous Species Name	Reference	Authority
Calohypsibius ornatus (Richters, 1900)	BW, BY, HE, NW, RP, SL, SN, ST, TH	*Hypsibius (Calohypsibius) ornatus* forma *spiniosissima* Richters, 1900	Marcus, 1936	synonymized with *Calohypsibius ornatus* according to Ramazzotti & Maucci, 1983
Echiniscus blumi Richters, 1903	HE	*Echiniscus bisetosus* Heinis, 1908	Hofmann & Eichelberg, 1986	synonymized with *Echiniscus blumi* according to Gąsiorek et al., 2019b
Echiniscus merokensis Richters, 1904a, 1904b	BB	*Echiniscus merokensis suecicus* Thulin, 1911	Marcus, 1936	synonymized with *Echiniscus merokensis* according to Gąsiorek & Vončina, 2023
Echiniscus quadrispinosus Richters, 1902	HE	*Echiniscus scrofa* Richters, 1902	Richters, 1902; Marcus, 1936	synonymized with *Echiniscus quadrispinosus* according to Ramazzotti & Maucci, 1983
Echiniscus testudo (Doyère, 1840)	HE, NW, RP	*Echiniscus filamentosus* Plate, 1888	Richters, 1902; Rahm, 1925; Marcus, 1936	synonymized with *Echiniscus testudo* according to Gąsiorek et al., 2017
Echiniscus testudo (Doyère, 1840)	HE	*Echiniscus inermis* Richters, 1902	Richters, 1902; Marcus, 1936	synonymized with *Echiniscus testudo* according to Marcus, 1936
Echiniscus testudo (Doyère, 1840)	NW, RP	*Echiniscus trifilis* Rahm, 1924	Rahm, 1925; Marcus, 1936	synonymized with *Echiniscus testudo* according to Marcus, 1936
Hypsibius convergens (Urbanowicz, 1925)	BW	*Macrobiotus tetradactylus* Greef, 1866	Heinis, 1910; Marcus, 1936	synonymized with *Hypsibius convergens* according to Marcus, 1936
Grevenius asper (Murray, 1906c)	NI, NW, RP, TH, ST	*Hypsibius tetradactyloides* (Richters, 1907b); *Hypsibius* (*Isohypsibius*) *tetradactyloides* (Richters, 1907b)	Rahm, 1925; Marcus, 1936	synonymized with *Grevenius asper* according to Dastych, 2016
Thulinius augusti (Murray, 1907c)	BW	*Macrobiotus lacustris* Dujardin, 1851; *Macrobiotus augusti* Murray, 1907a, 1907b, 1907c, 1907d; *Hysibius (Isohysibius) augusti* Murray, 1907a, 1907b, 1907c, 1907d	Richters, 1909b; Heinis, 1910; Wenck, 1914	synonymized with *Thulinius augusti* by Gąsiorek et al., 2019b
Hypsibius dujardini (Doyère, 1840)	Th	*Macrobiotus lacustris* Dujardin, 1851	Reukauf, 1912c	synonymized with *Hypsibius dujardini* according to Marcus, 1936
Orzeliscus belopus du Bois-Reymond Marcus, 1952	SH	*Orzeliscus septentrionalis* Schulz, 1953	Schulz, 1953	synonymized with *Orzeliscus belopus* according to Pollock, 1982

Table 3 Tardigrade species described from Germany and their terra typica. The numbers in the table refer to the overview map (Fig. 1)

Species	Terra typica	No
Actinarctus doryphorus doryphorus Schulz, 1935	Helgoland (SH)	11
Batillipes mirus Richters, 1909a	Eckernförder Bay (SH)	7
Bryocherus intermedius laevis (Marcus, 1936)	Wartburg near Eisenach (TH)	13
Calohypsibius ornatus (Richters, 1900)	Taunus (HE)	3
Cornechiniscus cornutus (Richters, 1907a)	near Ludwigshafen (RP)	5
Crenubiotus ruhesteini Guidetti et al., 2021	Black Forest (BW)	29
Diphascon birklehofi Rolf Schuster, 1999	Black Forest (BW)	23
Dianea sattleri (Richters, 1902)	Taunus (HE)	3
Diphascon pingue pingue (Marcus, 1936)	Wartburg (TH)	12
Doryphoribius evelinae (Marcus, 1928)	Schlachtensee Berlin (BE)	10
Echiniscus blumi Richters, 1903	Taunus (HE)	3
Echiniscus quadrispinosus Richters, 1902	Taunus (HE)	3
Fractonotus verrucosus (Richters, 1900)	Taunus (HE)	3
Halobiotus stenostomus (Richters, 1908)	Kieler Fjord (SH)	6
Macrobiotus echinogenitus Richters, 1903	Taunus (HE)	3
Macrobiotus hufelandi C.A.S. Schultze, 1834a, 1834b	St. Ulrich near Freiburg (BW)	1
Macrobiotus sandrae Bertolani & Rebecchi, 1993	St. Ulrich near Freiburg (BW)	20
Milnesium tardigradum Doyère, 1840	Zeesen (BB)	27
Milnesium inceptum Morek et al., 2019	Bebenhausen near Tübingen (BW)	28
Minibiotus bernhardi R. Schuster, 2021	Black Forest (BW)	30
Minibiotus intermedius (Plate, 1888)	Marburg (HE)	2
Pilatobius granifer (Greven, 1972)	Sauerland (NW)	17
Ramazzottius kretschmanni Guidetti et al., 2022a	Black Forest (BW)	31
Stygarctus bradypus Schulz, 1951	Sylt (SH)	15

From the 1970s onward smaller areas began to be studied for tardigrades. Greven (1972) explored tardigrades in the northern Sauerland region (NW), Adler (1987) conducted research at the University of Hohenheim in Stuttgart (BW) and Hofmann and Eichelberg (1986) studied the fauna near Gießen (HE). Russel et al. (1994) focused on tardigrades in sand dunes near Heidelberg (BW). In 1995 Grabowski examined tardigrades in mosses from the Lahnbergen Hills near Marburg (HE), and in 2003, Schuster investigated tardigrades in the southern Black Forest (BW). Soil-dwelling tardigrades were later studied by Hohberg (2006) near Berzdorf (SN), by Hohberg et al. (2011) and by Bingemer et al. (2020) near Welzow (BB). Michalczyk et al. (2012) studied tardigrades in Zeesen (BB). Since 2016, the tardigrade fauna of the Black Forest National Park in the Northern Black Forest (BW) has been studied as part of a large-scale biodiversity assessment and monitoring program (pers. communication R. Schill & R. Guidetti).

Results & Discussion

In 1936 Marcus reported 60 tardigrade species for the area of present-day Germany. The tardigrade species listed by Marcus from the former eastern territories of Germany (now Poland) are not included in this list. Of these 60 species Marcus classified three as species dubia et inquirenda (Table 1). Of the remaining 57 species, 44 are still listed in the current checklist (Degma & Guidetti, 2024). 15 species identified in Germany are now considered either nomen dubium (e.g. *Diphascon alpinum*), species dubia et inquirenda (e.g. *Echiniscus similis*), or have insufficient original descriptions (e.g. *Macrobiotus ferdinandi*) (Table 1). Twelve species have been synonymized with previously identified species (e.g. *Echiniscus scrofa* is synonymous with *Echiniscus quadrispinosus*; Table 2).

According to the current checklist with valid scientific names (Degma & Guidetti, 2024) a total of 99 tardigrade species have been recorded in Germany, including 91 limno-terrestrial or limnic species and eight marine species (Table 4). Of these 99 species, 21 belong to Heterotardigrada and 78 to the class Eutardigrada (Table 4). The 99 species represent about 7% of the total described tardigrade species of 1,488 worldwide (Degma & Guidetti, 2024). In similarly sized European countries, the number of tardigrade species is comparable: Norway (excluding Svalbard) has 102 species (Meier, 2017), Sweden and Poland each have 101 species (Guidetti et al., 2015), while Finland has fewer species 68 (Vuori et al., 2020) and Ireland has 51 (DeMilio et al., 2016). However, Italy has a

Table 4 Overview of Tardigrada species recorded in Germany. N—nonmarine species (limno-terrestrial or limnic ones), M—marine species

		Genus	Species	Authority	Federal State	Marine	Reference
HETEROTARDIGRADA Marcus, 1927							
ARTHROTARDGRADA Marcus, 1927							
Batillipedidae Ramazzotti, 1962							
	1	*Batillipes*	*mirus*	Richters, 1909a	SH	M	Richters, 1909a; Remane, 1924; Marcus, 1927; Marcus, 1936; Schmidt, 1971a
	2	*Batillipes*	*phreaticus*	Renaud Debyser, 1959	NI, SH	M	Pollock, 1971
	3	*Batillipes*	*tubernatis*	Pollock, 1971	NI, SH	M	Pollock, 1971; Ramazzotti & Maucci, 1983
Halechiniscidae Thulin, 1928 **Orzeliscinae Schulz, 1963**							
	4	*Orzeliscus*	*belopus*	du Bois-Reymond Marcus, 1952 (*O. septentrionalis* Schulz, 1953)	SH	M	Schulz, 1953; Ramazzotti & Maucci, 1983
Stygarctidae Schulz, 1951, **Stygarctinae** Schulz, 1951							
	5	*Stygarctus*	*bradypus*	Schulz, 1951	SH	M	Schulz, 1951; Schmidt, 1971a
Tanarctidae Renaud-Mornant, 1980							
	6	*Actinarctus*	*doryphorus doryphorus*	Schulz, 1935	SH	M	Schultz, 1935; Grell, 1936; Marcus, 1936
ECHINISCOIDEA Richters, 1926							
Echiniscoididae Kristensen & Hallas, 1980							
	7	*Echiniscoides*	*sigismundi*	(M.Schultze, 1865)	SH	M	Schultze, 1865; Richters, 1908; Marcus, 1927, 1936; Greven & Grohé, 1975; Greven & Kristensen, 2001
Echiniscidae Thulin, 1928							
	8	*Bryocherus*	*intermedius laevis*	(Marcus, 1936)	TH	N	Marcus, 1936; Ramazzotti & Maucci, 1995
	9	*Bryodelphax*	*parvulus*	Thulin, 1928	BY	N	Marcus, 1936
	10	*Bryodelphax*	*tatrensis*	(Węglarska, 1959)	BY	N	Węglarska, 1959; Ramazzotti & Maucci, 1995
	11	*Claxtonia*	*wendti*	(Richters, 1903)	BW	N	Heinis, 1910; Rahm, 1925; Marcus, 1936

Table 4 (continued)

		Genus	Species	Authority	Federal State	Marine	Reference
	12	*Cornechiniscus*	*cornutus*	(Richters, 1907a)	BW, RP	N	Richters, 1907a; Heinis, 1910; Marcus, 1936
	13	*Echiniscus*	*blumi*	Richters, 1903	BB, BE, BW, BY, HE, MV, NI, NW, RP	N	Richters, 1903; Heinis, 1910; Rahm, 1925; Marcus, 1928, 1936; Englisch, 1936; Baumann, 1970; Adler, 1987; Hofmann & Eichelberg, 1986; Hofmann, 1987; Schuster, 2003a, 2003b
	14	*Echiniscus*	*granulatus*	(Doyère, 1840)	BB, BE, BW, HE, NW	N	Richters, 1903; Marcus, 1928; Englisch, 1936; Greven, 1972; Schuster, 2003a, 2003b; Schill & Steinbrück, 2007
	15	*Echiniscus*	*merokensis*	Richters, 1904b	BB, BW	N	Marcus, 1936; Schuster, 2003a, 2003b
	16	*Echiniscus*	*quadrispinosus*	Richters, 1902	BW, HE, MV	N	Richters, 1902, 1904a; Heinis, 1910; Marcus, 1928; Schuster, 2003a, 2003b; Kaczmarek et al., 2022a
	17	*Echiniscus*	*spinulosus*	(Doyère, 1840)	BW	N	Schuster (unpublished)
	18	*Echiniscus*	*testudo*	(Doyère, 1840)	BB, BW, BY, HB, HE, MV, NI, NW, RP	N	Heinis, 1910; Marcus, 1928, 1936; Englisch, 1936; Baumann, 1964; Schmidt, 1971a; Greven, 1972; Greven & Peters, 1986; Adler, 1987; Hofmann & Eichelberg, 1986; Hofmann, 1987; Grabowski, 1995; Schuster, 2003a, 2003b; Schill & Steinbrück, 2007
	19	*Echiniscus*	*trisetosus*	Cuénot, 1932	HE	N	Marcus, 1936
	20	*Pseudechiniscus*	*suillus*	(Ehrenberg, 1853)	BB, BE, BW, BY, HB, HE, HH, MV, NI, NW, RP, SL, SN, ST, SH, TH	N	Heinis, 1910; Marcus, 1936; Greven, 1972; Schuster, 2003a, 2003b
	21	*Testechiniscus*	*spitsbergensis spitsbergensis*	(Scourfield, 1897)	BW, BY, HE, NI, NW, RP, SL, SN, ST, TH	N	Marcus, 1936; Ramazzotti & Maucci, 1983
EUTARDIGRADA Richters, 1926							
APOCHELA Schuster et al., 1980							
Milnesiidae Ramazzotti, 1962							

Table 4 (continued)

		Genus	Species	Authority	Federal State	Marine	Reference
	22	*Milnesium*	*inceptum*	Morek, Suzuki, Schill, Georgiev, Yankova, Marley & Michalczyk, 2019	BW	N	Morek et al., 2019
	23	*Milnesium*	*tardigradum tardigradum*	Doyère, 1840	BB, BE, BW, HB, HE, MV, NI, NW, RP, ST, SH, TH	N	Richters, 1904a; Heinis, 1910; Rahm, 1925; Marcus, 1928, 1936; Englisch, 1936; Baumann, 1964, 1966, 1970; Schmidt, 1971a, 1971b; Greven & Blom, 1977; Greven & Peters, 1986; Hofmann & Eichelberg, 1986; Hofmann, 1987; Russel et al., 1994; Grabowski, 1995; Schuster, 2003a, 2003b; Greven, 2007; Schill & Steinbrück, 2007; Schuster & Greven, 2007; Michalczyk et al., 2012
PARACHELA Schuster et al., 1980							
Eohypsibioidea Bertolani & Kristensen, 1987							
Eohypsibiidae Bertolani & Kristensen, 1987							
	24	*Bertolanius*	*weglarskae*	(Dastych, 1972)	BW	N	Schuster, 2003a, 2003b
Hypsibioidea Pilato, 1969b							
Caloyhypsibiidae Pilato, 1969b							
	25	*Calohypsibius*	*ornatus*	(Richters, 1900)	BW, BY, HE, NW, RP, SL, SN, ST, TH	N	Richters, 1900; Heinis, 1910; Marcus, 1936; Englisch, 1936; Schuster, 2003a, 2003b
Hysibiidae Pilato, 1969b							
Diphasconinae Dastych, 1992							
	26	*Diphascon*	*birklehofi*	Rolf Schuster, 1999	BW	N	Schuster, 1999, 2003a, 2003b
	27	*Diphascon*	*higginsi*	Binda, 1971	BB, BW, SN	N	Schuster, 2003a, 2003b; Hohberg, 2006; Schuster & Greven, 2007; Hohberg et al., 2011; Bingemer & Hohberg, 2017; Bingemer et al., 2020
	28	*Diphascon*	*humicus*	Bertolani, Guidetti & Rebecchi, 1994	BW	N	Schuster, 2003a, 2003b

Table 4 (continued)

		Genus	Species	Authority	Federal State	Marine	Reference
	29	*Diphascon*	*nobilei*	(Binda, 1969)	BB, BW, HE, SN	N	Russel et al., 1994; Grabowski, 1995; Schuster, 2003a, 2003b; Schuster & Greven, 2007; Bingemer & Hohberg, 2017; Bingemer et al., 2020
	30	*Diphascon*	*pingue pingue*	(Marcus, 1936)	BW, HE, NI, SN, ST, Th	N	Marcus, 1936; Russel et al., 1994; Grabowski, 1995; Schuster, 2003a, 2003b; Schuster & Greven, 2007, 2013; Bingemer & Hohberg, 2017
Hypsibiinae Pilato, 1969b							
	31	*Hypsibius*	*convergens*	(Urbanowicz, 1925)	BB, BE, BW, BY, HE, HB, MV, NI, NW, RP, SH, ST, TH	N	Marcus, 1928, 1936; Englisch, 1936; Baumann, 1961; Adler, 1987; Hofmann & Eichelberg, 1986; Hofmann, 1987; Russel et al., 1994; Grabowski, 1995; Ramazzotti & Maucci, 1983; Schuster, 2003a, 2003b; Schuster & Greven, 2007; Bingemer & Hohberg, 2017
	32	*Hypsibius*	*dujardini*	(Doyère, 1840)	BE, BW, HE, NI, NW, SN, TH	N	Heinis, 1910; Marcus, 1936; Englisch, 1936; Ammermann, 1962, 1967; Schmidt, 1971a, 1971c; Greven, 1972; Hofmann & Eichelberg, 1986; Hofmann, 1987; Grabowski, 1995; Schuster, 2003a, 2003b; Hohberg, 2006; Schuster & Greven, 2007; Bingemer & Hohberg, 2017
	33	*Hypsibius*	*microps*	Thulin, 1928	BW	N	Schuster, 2003a, 2003b
	34	*Hypsibius*	*pallidus*	Thulin, 1911	BW, HE, SN	N	Adler, 1987; Russel et al., 1994; Grabowski, 1995; Schuster, 2003a, 2003b; Hohberg, 2006; Schuster & Greven, 2007; Bingemer & Hohberg, 2017
	35	*Hypsibius*	*pradellii*	Bertolani & Rebecchi, 1996	BW	N	Schuster, 2003a, 2003b
	36	*Hypsibius*	*scabropygus*	Cuénot, 1929	BW, BY, He, NW, TH, ST, SN	N	Marcus, 1936; Schuster, 2003a, 2003b; Schuster & Greven, 2007; Guidetti et al., 2022a

Table 4 (continued)

		Genus	Species	Authority	Federal State	Marine	Reference
Itaquasconidae Rudescu, 1964							
	37	*Adropion*	*belgicae*	(Richters, 1911)	BE, BW	N	Marcus, 1928, 1936; Schuster, 2003a, 2003b
	38	*Adropion*	*scoticum*	(Murray, 1905b)	BE, BW, HE, NW	N	Heinis, 1910; Marcus, 1936; Englisch, 1936; Riemann, 1966; Hofmann & Eichelberg, 1986; Hofmann, 1987; Grabowski, 1995; Schuster, 2003a, 2003b; Schuster & Greven, 2007
	39	*Astatumen*	*trinacriae*	(Arcidiacono, 1962)	BW, He, NW, SN	N	Greven, 1972; Grabowski, 1995; Schuster, 2003a, 2003b; Hohberg, 2006; Bingemer & Hohberg, 2017
	40	*Guidettion*	*modestum*	(Binda et al., 1984)	BW	N	Schuster, 2003a, 2003b; Schuster & Greven, 2007
	41	*Guidettion*	*prorsirostre*	(Thulin, 1928)	BW, HB, HE, HH, MV, NI, SH	N	Thulin, 1928; Marcus, 1936; Grabowski, 1995; Ramazzotti & Maucci, 1983; Schuster, 2003a, 2003b
	42	*Itaquascon*	*placophorum*	Maucci, 1973	BW	N	pers. com. Schill & Guidetti, 2020
	43	*Mesocrista*	*spitzbergensis*	(Richters, 1903)	BB, BW, HE, NI, ST, TH	N	Richters, 1903; Marcus, 1936; Englisch, 1936; Grabowski, 1995; Schuster, 2003a, 2003b; Schuster & Greven, 2007
	44	*Platicrista*	*angustata*	(Murray, 1905a)	BW	N	Schuster, 2003a, 2003b
	45	*Raribius*	*pawlowskii*	Węglarska, 1973	BW	N	Schuster, 2003a, 2003b
Microhypsibiidae Pilato, 1998							
	46	*Microhypsibius*	*bertolanii*	Kristensen, 1982	BW	N	Schuster, 2003a, 2003b
	47	*Microhypsibius*	*truncatus*	Thulin, 1928	BW	N	Schuster, 2003a, 2003b
Pilatobiidae Bertolani et al., 2014							
	48	*Degmion*	*oculatum*	(Murray, 1906b)	ST, BW	N	Marcus, 1936; Englisch, 1936; Schuster, 2003a, 2003b; Schuster & Greven, 2007
	49	*Fontourion*	*recamieri*	(Richters, 1911)	BW	N	Schuster, 2003a, 2003b

Table 4 (continued)

		Genus	Species	Authority	Federal State	Marine	Reference
	50	*Pilatobius*	*bullatus*	(Murray, 1905b)	BE, BW, SN	N	Marcus, 1936; Schuster, 2003a, 2003b; Schuster & Greven, 2007; Bingemer & Hohberg, 2017
	51	*Pilatobius*	*granifer*	(Greven, 1972)	NW	N	Greven, 1972
	52	*Pilatobius*	*rugosus*	(Bartoš, 1935)	BW, SN	N	Schuster, 2003a, 2003b; Schuster & Greven, 2007; Bingemer & Hohberg, 2017
Ramazzottiidae Sands et al., 2008							
	53	*Hebesuncus*	*conjungens*	(Thulin, 1911)	BW	N	Schuster, 2003a, 2003b
	54	*Ramazzottius*	*kretschmanni*	Guidetti, Cesari, Giovannini, Ebel, Förschler, Rebecchi & Schill, 2022	BW	N	Guidetti et al., 2022a, 2022b
	55	*Ramazzottius*	*oberhaeuseri*	(Doyère, 1840)	BB, BE, BW, BY, HE, NI, NW, MV, RP, SH, ST	N	Richters, 1904a; Heinis, 1910; Rahm, 1925; Marcus, 1928, 1936; Englisch, 1936; Baumann, 1966, 1970; Adler, 1987; Hofmann & Eichelberg, 1986; Hofmann, 1987; Grabowski, 1995; Schuster, 2003a, 2003b; Bingemer & Hohberg, 2017
Isohypsibioidea Sands et al., 2008							
Doryphoribiidae Gąsiorek et al., 2019a, 2019b							
	56	*Apodibius*	*confusus*	Dastych, 1983	BB, BW, SN	N	Hohberg et al,. 2011; Dabert et al., 2014; Bingemer & Hohberg, 2017; Bingemer et al., 2020; Schuster (unpublished)
	57	*Doryphoribius*	*evelinae*	(Marcus, 1928)	BE	N	Marcus, 1928, 1936
	58	*Grevenius*	*asper*	(Murray, 1906c)	NI, NW, RP, ST, TH	N	Marcus, 1936
	59	*Grevenius*	*granulifer*	(Thulin, 1928)	BW, NW, ST	N	Englisch, 1936; Greven & Blom, 1977; Schuster, 2003a, 2003b
	60	*Pseudobiotus*	*megalonyx*	(Thulin, 1928)	BB, BE, BW, NW, RP, TH	N	Marcus, 1936
	61	*Thulinius*	*augusti*	(Murray, 1907c)	BB, BE, BW, NW, RP, TH	N	Richters, 1909b; Wenck, 1914; Marcus, 1936; Greven, 1972, 1976
	62	*Thulinius*	*ruffoi*	(Bertolani, 1981)	BW	N	Schuster, 2003a, 2003b

Table 4 (continued)

		Genus	Species	Authority	Federal State	Marine	Reference
Halobiotidae Gąsiorek et al., 2019a, 2019b							
	63	*Halobiotus*	*stenostomus*	(Richters, 1908)	SH	M	Richters, 1908; Marcus, 1936; Ramazzotti & Maucci, 1983
Hexapodibiidae Cesari et al., 2016							
	64	*Hexapodibius*	*micronyx*	Pilato, 1969a	BB	N	Bingemer et al., 2020
Isohypsibiidae Sands et al., 2008							
	65	*Dianea*	*papillifera*	(Murray, 1905a)	BE	N	Marcus, 1936; Ramazzotti & Maucci, 1983
	66	*Dianea*	*sattleri*	(Richters, 1902)	BE, BW, HE, NW, ST, SN	N	Richters, 1902; Marcus, 1936; Greven, 1972; Hofmann & Eichelberg, 1986; Hofmann, 1987; Russel et al., 1994; Grabowski, 1995; Schuster, 2003a, 2003b
	67	*Eremobiotus*	*alicatai*	(Binda, 1969)	BB, BW, BY, SN	N	Russel et al., 1994; Hohberg, 2006; Hohberg et al., 2011; Bingemer & Hohberg, 2017; Bingemer et al., 2020; Schuster (unpublished)
	68	*Fractonotus*	*verrucosus*	(Richters, 1900)	BE, BW, HE	N	Richters, 1900; Heinis, 1910; Marcus, 1936; Ramazzotti & Maucci, 1983; Schuster, 2003a, 2003b
	69	*Isohypsibius*	*dastychi*	Pilato et al., 1982	BB, HE	N	Grabowski, 1995; Bingemer & Hohberg, 2017; Bingemer et al., 2020
	70	*Isohypsibius*	*prosostomus*	Thulin, 1928	BE, BB, BW, HE	N	Marcus, 1936; Englisch, 1936; Adler, 1987; Russel et al., 1994; Grabowski, 1995; Schuster, 2003a, 2003b; Schuster & Greven, 2007; Guidetti et al., 2022a
	71	*Ursulinius*	*elegans*	(Binda & Pilato, 1971)	BW	N	Schuster (unpublished)
	72	*Ursulinus*	*lunulatus*	(Iharos, 1966)	HE	N	Grabowski, 1995
	73	*Ursulinus*	*pappi*	(Iharos, 1966)	BW	N	Schuster, 2003a, 2003b; Schuster & Greven, 2007
	74	*Ursulinus*	*ronsisvallei*	(Binda & Pilato, 1969a, 1969b)	BW	N	Russel et al., 1994

Table 4 (continued)

		Genus	Species	Authority	Federal State	Marine	Reference
Macrobiotoidea Thulin, 1928							
Adorybiotidae Stec, Vecchi & Michalczyk, 2020							
	75	*Crenubiotus*	*ruhesteini*	Guidetti, Schill, Giovanni, Massa, Goldoni, Ebel, Förschler, Rebecchi & Cesari, 2021	BW	N	Guidetti et al., 2021
Macrobiotidae Thulin, 1928							
	76	*Macrobiotus*	*echinogenitus*	Richters, 1903	BE, BW, HE, NW, RP	N	Richters, 1903; Heinis, 1910; Rahm, 1925; Marcus, 1928, 1936
	77	*Macrobiotus*	*hufelandi*	C.A.S. Schultze, 1834a, 1834b	BB, BE, BW, BY, HB, HE, HH, MV, NI, NW, RP, SL, SN, ST, SH, TH	N	Richters, 1904a; Heinis, 1910; Rahm, 1925; Marcus, 1928, 1936; Englisch, 1936; Baumann, 1970; Greven, 1972; Greven & Kuhlmann, 1972; Walz, 1979; Greven & Peters, 1986; Adler, 1987; Hofmann & Eichelberg, 1986; Hofmann, 1987; Bertolani & Rebecchi, 1993; Russel et al., 1994; Grabowski, 1995; Schuster, 2003a, 2003b; Schuster & Greven, 2007, 2013
	78	*Macrobiotus*	*macrocalix*	Bertolani & Rebecchi, 1993	BW	N	Schuster (unpublished)
	79	*Macrobiotus*	*persimilis*	Binda & Pilato, 1972	BW	N	Adler, 1987
	80	*Macrobiotus*	*sandrae*	Bertolani & Rebecchi, 1993	BW	N	Bertolani & Rebecchi, 1993
	81	*Macrobiotus*	*scoticus*	Stec, Morek, Gąsiorek, Blagden & Michalczyk, 2017	BW	N	Schuster (unpublished)
	82	*Macrobiotus*	*vladimiri*	Bertolani et al., 2011	BW	N	Bertolani et al., 2011
	83	*Mesobiotus*	*furciger*	(Murray, 1907a)	BE	N	Marcus, 1928, 1936
	84	*Mesobiotus*	*harmsworthi*	(Murray, 1907b)	BB, BE, BW, HE, NI, NW, RP, SN, ST, TH	N	Marcus, 1928, 1936; Englisch, 1936; Adler, 1987; Hofmann & Eichelberg, 1986; Hofmann, 1987; Russel et al., 1994; Grabowski, 1995; Schuster, 2003a, 2003b
	85	*Mesobiotus*	*patiens*	(Pilato et al., 2000)	BW	N	Schuster & Greven, 2007
	86	*Minibiotus*	*bernhardi*	R.Schuster, 2021	BW	N	Schuster, 2021

Table 4 (continued)

		Genus	Species	Authority	Federal State	Marine	Reference
	87	*Minibiotus*	*furcatus*	(Ehrenberg, 1859)	BW	N	Schuster, 2003a, 2003b
	88	*Minibiotus*	*intermedius*	(Plate, 1888)	BW, HE, MV, NW, RP, TH, SN, ST	N	Plate, 1888; Richters, 1904a; Heinis, 1910; Marcus, 1936; Englisch, 1936; Grabowski, 1995; Schuster, 2003a, 2003b; Schuster & Greven, 2007; Kaczmarek et al., 2022b
	89	*Paramacrobiotus*	*areolatus*	(Murray, 1907c)	BW, NW, RP	N	Rahm, 1925; Marcus, 1936; Schill & Steinbrück, 2007
	90	*Paramacrobiotus*	*richtersi*	(Murray, 1911)	BB, BE, BW, BY, HE, SN	N	Marcus, 1928, 1936; Adler, 1987; Hofmann & Eichelberg, 1986; Hofmann, 1987; Russel et al., 1994; Grabowski, 1995; Schuster, 2003a, 2003b; Hohberg & Traunspurger, 2005; Hohberg, 2006; Schill & Steinbrück, 2007; Schuster & Greven, 2007, 2013; Bingemer & Hohberg, 2017
	91	*Sisubiotus*	*spectabilis*	(Thulin, 1928)	BW	N	Schuster, 2003a, 2003b
	92	*Tenuibiotus*	*willardi*	(Pilato, 1977)	BW	N	Schuster (unpublished)
	93	*Xerobiotus*	*xerophilus*	(Dastych, 1978)	BW	N	Russel et al., 1994
Murrayidae Guidetti et al., 2000							
	94	*Dactylobiotus*	*dispar*	(Murray, 1907a)	BB, BE, BW, SN, TH	N	Reukauf, 1912b; Marcus, 1928, 1936; Schuster, 2003a, 2003b
	95	*Murrayon*	*hastatus*	(Murray, 1907c)	BW	N	Heinis, 1910; Marcus, 1928, 1936
	96	*Murrayon*	*pullari*	(Murray, 1907c)	BE, BW, NI, ST, TH	N	Marcus, 1936; Englisch, 1936; Schuster, 2003a, 2003b
	97	*Paramurrayon*	*meieri*	Guidetti, Giovannini, Del Papa, Ekrem, Nelson, Rebecchi & Cesari, 2022b	BW	N	Schuster (unpublished)
	98	*Paramurrayon*	*stellatus*	(Guidetti, 1998)	BW	N	Schuster (unpublished)
Richtersiusidae Guidetti et al., 2021							
	99	*Richtersius*	*coronifer*	(Richters, 1903)	NW, RP	N	Rahm, 1925; Marcus, 1936

significantly higher number of species, with 246 species reported (Guidetti et al., 2015).

The map (Fig. 1) provides an overview of the regions where tardigrade studies have been conducted from the time of the description of the first tardigrade species *Macrobiotus hufelandi* to the present. In these regions, either new species have been discovered and described, or more than five different tardigrade species have been found. Some regions mentioned in the literature could be localized precisely, while vague geographical references, such as "Northern Germany" or "Central Uplands," do not feature on the overview map (Fig. 1). However, as previously mentioned, these areas have been assigned to specific federal states, ensuring that these species are also included in the current checklist.

The number of identified tardigrade species varies greatly depending on the extent of studies conducted in different federal states. Baden-Württemberg (BW) has the highest number of species identified (78 species from eleven studies), followed by Hesse (HE) (30 species from five studies) and Berlin (BE) (23 species from two studies). The high number of studies in Schleswig–Holstein (SH) (ten studies) with relatively few identified species is due to the marine tardigrade research, where often only one species was identified (Schulz, 1935, 1951, 1953). The relatively high number of species identified in BE with only two studies is due to Marcus's intensive research in his local area. The high number of species in BW is attributed to Schuster's work (2003), which identified 54 species in his local area in the southern Black Forest, in conjunction with Heinis's work (1910). It is likely that the number of tardigrade species in many federal states is higher, especially in areas with similar geographical and climatic conditions to BW. All species from these 28 studies are listed in Fig. 1 and Table 4.

As in other countries, marine tardigrades have been inadequately studied. To date only eight marine tardigrade species have been identified along the coast of the North and Baltic Seas. Given the diverse ecological conditions in these seas, it is likely that additional species remain to be discovered. Similarly marine tardigrade species are underrepresented in the checklists of neighboring countries of the North and Baltic Seas, with the exception of the Faroe Islands, where Hansen et al. (2001) conducted a detailed study of interstitial meiofauna and identified 35 marine tardigrade species.

Macrobiotus hufelandi is the first described tardigrade species (Schultze, 1834a, 1834b) from near Freiburg (BW) and its name is still valid today. Marcus (1936) reported its distribution across northern, central and southern Germany, covering the entire country. A revision of the *Macrobiotus hufelandi* group by Bertolani and Rebecchi (1993) in the type locality of *Macrobiotus hufelandi* (St. Ulrich, near Freiburg im Breisgau, BW) revealed the presence of at least one additional species (*Macrobiotus sandrae*) very similar to *Macrobiotus hufelandi*. Bertolani et al. (2011) found a third species in this area, *Macrobiotus vladimiri*. Most of the studies mentioned above identified *Macrobiotus hufelandi*. It is likely that not all studies actually identified *Macrobiotus hufelandi* sensu stricto, particularly since many similar species were described later by Bertolani and Rebecchi (1993) and subsequently. It is expected that with an integrative taxonomic approach (i.e. combining morphological traits and molecular analysis for species identification), additional species in the *Macrobiotus hufelandi* group, previously identified as such, may be discovered in future research.

The taxonomy of tardigrades has changed significantly over the past two decades. Most of the listed studies date back 20 years or more, and tardigrade identification up until Bertolani et al. (2011) was based solely on morphological characteristics. With the advent of integrated descriptions of tardigrades, species identification has become increasingly differentiated and precise. Many species identifications from the past two centuries are incomplete by the standards of modern species descriptions. As a result, numerous identifications must be regarded as doubtful in the context of contemporary taxonomy. This is particularly true for species such as *Macrobiotus hufelandi*, *Pseudechiniscus suillus*, *Milnesium tardigradum*, *Ramazzottius oberhäuseri*, *Mesobiotus harmsworthi*, *Hypsibius convergens*, *Testechiniscus spitsbergensis spitsbergensis*, *Diphascon scoticum*, and others (see Kaczmarek et al., 2014). These identifications should be reassessed in light of modern taxonomic standards.

The type locality for 24 tardigrade species occurs in Germany (Fig. 1, Table 3). Most of these species were described in the first four decades of the past century, primarily by Richters (1900, 1902, 1903, 1907a, 1908, 1909a), Marcus (1928, 1936) and Schulz (1935). New species from Germany have been increasingly described in recent years: *Milnesium inceptum* in 2019, *Crenubiotus ruhesteini* in 2021, *Minibiotus bernhardi* and *Ramazzottius kretschmanni* in 2022 (Table 3). Kaczmarek et al., (2022a, b) redescribed *Minibiotus intermedius* and *Echiniscus quadrispinosus* using an integrative approach, and Michalczyk et al. (2012) made a redescription of *Milnesium* Doyère, 1840 taxa (Tardigrada: Eutardigrada: Milnesiidae), including the nominal species for the genus.

Schuster (2003a, b) reported 54 species in the Black Forest, including five species identified by Heinis (1910) that were not found by Schuster. Additionally Schuster identified *Hypsibius* cf. *convergens*, *Isohypsibius* cf. *annulatus*, and *Ramazzottius* cf. *cataphractus*. Since then, the following changes have occurred: *Minibiotus* cf. *poricinctus* has been described *as Minibiotus bernhardi* and *Minibiotus* cf. *scopulus* has been identified as *Macrobiotus scoticus*. *Macrobiotus hibernicus* is now considered nomen dubium (Degma & Guidetti, 2024). The species previously identified as *Macrobiotus hibernicus* are now split into *Paramurrayon*

meieri and *Paramurrayon stellatus*. The species previously identified as *Macrobiotus crenulatus* is now *Crenubiotus ruhesteini*. Thanks to the work of Heinis (1910), Bertolani and Rebecchi (1993), Bertolani et al. (2011), and Guidetti et al., (2021, 2022a), all conducted in the Black Forest, this region is now the most extensively studied in Germany with 70 identified tardigrade species and it ranks among the most intensively studied regions for tardigrades worldwide.

Acknowledgements We would like to express our deepest gratitude to Hartmut Greven from the University of Düsseldorf and to Franz Brümmer from the University of Stuttgart, both of whom actively supported and guided the authors' work over a long period. Many colleagues assisted us in research and in the compilation of this current checklist of tardigrades in Germany, and we extend our thanks to them as well. Moreover, we want to thank the anonymous reviewer, whose feedback greatly improved the quality of this manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL.

Declarations

Competing Interests The authors declare no competing interests.

References

Adler, M. (1987). Moosbewohnende Tardigraden von Stuttgart-Hohenheim. *Jahreshefte der Gesellschaft Für Naturkunde in Württemberg, 142*, 197–200.

Ammermann, D. (1962). Parthenogenese bei dem Tardigraden *Hypsibius dujardini* (Doy.). *Naturwissenschaften, 5*, 1–2.

Ammermann, D. (1967). Die Cytologie der Parthenogenese bei dem Tardigraden *Hypsibius dujardini*. *Chromosoma, 23*, 203–213.

Arcidiacono, R. (1962). Contributo alla conoscenza dei Tardigradi dei Monti Nebrodi e descrizione di una nuova specie di *Itaquascon*. *Bollettino Delle Sedute Dell'accademia Gioenia di Scienze Naturali in Catania, Serie IV, 7*(3), 123–134.

Bartoš, E. (1935). Vier neue Tardigradenarten aus der Tschechoslowakei. *Zoologischer Anzeiger, 110*, 257–260.

Baumann, H. (1961). Der Lebensablauf von *Hypsibius* (H.) *convergens* Urbanowicz (Tardigrada). *Zoologischer Anzeiger, 167*(9–12), 362–381.

Baumann, H. (1964). Über den Lebensablauf und die Lebensweise von *Milnesium tardigradum* Doyère (Tardigrada). *Veröffentlichungen Aus Dem Überseemuseum Bremen, A, 3*(3), 161–171.

Baumann, H. (1966). Lebenslauf und Lebensweise von *Hypsibius* (H.) *oberhaeuseri* Doyère (Tardigrada). *Veröffentlichungen aus dem Überseemuseum Bremen, A, 3*(5), 245–258.

Baumann, H. (1970). Lebenslauf und Lebensweise von *Macrobiotus hufelandii* Schultze (Tardigrada). *Veröffentlichungen Aus Dem Überseemuseum Bremen, A, 4*(6), 29–43.

Bertolani, R. (1981). A new genus and five new species of Italian freshwater Tardigrades. *Bollettino Del Museo Civico De Storia Naturale di Verona, 8*, 249–254.

Bertolani, R., & Rebecchi, L. (1993). A revision of the *Macrobiotus hufelandi* group (Tardigrada, Macrobiotidae), with some observations on the taxonomic characters of eutardigrades. *Zoologica Scripta, 22*(2), 127–152.

Bertolani, R., & Rebecchi, L. (1996). The tardigrades of Emilia (Italy). II. Monte Rondinaio. *A multihabitat study on a high altitude valley of the northern Apennines*. *Zoological Journal of the Linnean Society, 116*, 3–12.

Bertolani, R., Guidetti, R., & Rebecchi, L. (1994). Ulteriore contributo alla conoscenza dei Tardigradi delle Marche e dell'Umbria. *Atti della Società Toscana di Scienze naturali Ser. B, CI*, 21–34.

Bertolani, R., Biserov, V., Rebecchi, L., & Cesari, M. (2011). Taxonomy and biogeography of tardigrades using an integrated approach: New results on species of the *Macrobiotus hufelandi* group. *Invertebrate Zoology, 8*, 23–36.

Bertolani, R., Guidetti, R., Marchioro, T., Altiero, T., Rebecchi, L., & Cesari, M. (2014). Phylogeny of Eutardigrada: New molecular data and their morphological support lead to the identification of new evolutionary lineages. *Molecular Phylogenetics and Evolution, 76*, 110–126.

Bertolani, R., & Kristensen, R.M. (1987). New records of *Eohypsibius nadjae* Kristensen, 1982, and revision of the taxonomic position of two new genera of Eutardigrada. *In: R. Bertolani (ed.), Biology of Tardigrades. Selected Symposia and Monographs U.Z.I.,1, Modena, Mucchi Editore*, 359–372.

Binda, M. G., Pilato, G., & Dastych, H. (1984). *Diphascon modestum*, nuova specie di Eutardigrado dei monti Tatra. *Animalia, 11*(1–3), 45–48.

Binda, M.G. & Pilato, G. (1969). Ulteriore contributo alla conoscenza dei Tardigradi di Sicilia con descrizione di due nuove specie. *Bollettino delle seduté dell'Accademia Gioenia di Scienze naturali in Catania. Ser. IV, Vol. X, 2*, 205–214.

Binda, M.G. & Pilato, G. (1971). Nuovo contributo alla conoscenza dei Tardigradi di Sicilia. *Bollettino delle seduté dell'Accademia Gioenia di Scienze naturali in Catania. Ser. IV, Vol. X, 10*, 896–909.

Binda, M.G. & Pilato, G. (1972). Tardigradi muscicoli di Sicilia. *Ricerche sulla fauna e sulla zoogeografia della Sicilia, LVIII*, 47–60.

Binda, M.G. (1969). Nuovi dati su Tardigradi di Sicilia con descrizione di due nuove specie. *Bollettino delle seduté dell'Accademia Gioenia di Scienze naturali in Catania. Ser. IV, Vol. IX, 9*, 623–633.

Binda, M.G. (1971). Su alcuni Tardigradi muscicoli del Nord-Africa. *Bollettino delle seduté dell'Accademia Gioenia di Scienze naturali in Catania. Ser. IV, Vol. X, 9*, 758–765.

Bingemer, J., & Hohberg, K. (2017). An illustrated identification key to the eutardigrade species (Tardigrada, Eutardigrada) presently known from European soils. *Soil Organisms, 89*(3), 127–149.

Bingemer, J., Pfeiffer, M., & Hohberg, K. (2020). First 12 years of tardigrade succession in the young soils of a quickly evolving ecosystem. *Zoological Journal of the Linnean Society, 188*, 887–899.

Cesari, M., Vecchi, M., Palmer, A., Bertolani, R., Pilato, G., Rebecchi, L., & Guidetti, R. (2016). What if the claws are reduced? Morphological and molecular phylogenetic relationships of the

genus *Haplomacrobiotus* May, 1948 (Eutardigrada, Parachela). *Zoological Journal of the Linnean Society, 178*, 819–827.
Cuénot, L. (1929). Description d'un tardigrade nouveau de la faune française. *Archives D'anatomie Microscopique, 25*, 121–125.
Cuénot, L. (1932). Tardigrades. *Faune de France, 24, Paris*, 1–96.
Dabert, M., Dastych, H., Hohberg, K., & Dabert, J. (2014). Phylogenetic position of the enigmatic clawless eutardigrade genus *Apodibius* Dastych, 1983 (Tardigrada), based on 18S and 28SrRNA sequence data from its type species *A. confusus*. *Molecular Phylogenetics and Evolution, 70*, 70–75.
Dastych, H. (1983). *Apodibus confusus* New Water-Bear from Poland (Tardigrada). *Bulletin of the Polish Academy of Sciences Biological Sciences, 31*(1–12), 41–46.
Dastych, H. (1988). The Tardigrada of Poland. *Monografie Fauny Polski, 16*, 1–255.
Dastych, H. (1992). *Paradiphascon manningi* gen. n. sp. n., a New Water-Bear from South-Africa, with the erecting of a new subfamily Diphasconinae (Tardigrada). *Mitteilungen Aus Dem Hamburgischen Zoologischen Museum, Bd, 89*, 125–139.
Dastych, H. (2015). Tardigrada. *Biosystematics and Ecology Series, 31. Checklisten der Fauna Österreichs, 8*, 1–25.
Dastych, H. (2016). Redescription and taxonomic status of the Antarctic water-bear *Isohypsibius tetradactyloides* (Richters, 1907), as concluded from the rediscovered type material (Tardigrada). *Acta Biologica Benrodis, 18*, 21–43.
Dastych, H. (1972). *Isohypsibius weglarskae* sp. n. a New Species of Tardigrada from Poland. *Bulletin de l'Académie Polonaise des Scienzes, Cl. II, Vol. XX, 11*, 761–762.
Dastych, H. (1978). *Parhexapodibius xerophilus* sp. nov., a New Species of Tardigrada from Poland. *Bulletin de l'Académie Polonaise des Scienzes, Cl. II, Vol. XXVI, 7*, 479–481.
Degma, P. & Guidetti, R. (2024). Actual checklist of Tardigrada species (2009–2024, Ver. 43: 05–07–2024). https://doi.org/10.25431/11380_1178608
DeMilio, E., Lawton, C., & Marley, N. J. (2016). Tardigrada of Ireland: A review of records and an updated checklist of species including a new addition to the Irish fauna. *ZooKeys, 616*, 77–101. https://doi.org/10.3897/zookeys.616.8222
Doyère, M.L. (1840). Mémoire sur les Tardigrades. *Annales des Scienzes Naturelles, Série 2, Tome 14-Zoologie*, 269–361. http://www.biodiversitylibrary.org/item/47974
Du Bois-Reymond Marcus, E. (1952). On South American Malacopoda. *Boletim Da Faculdade De Filosofia, Ciencias e Letras Da Universidade De Sao Paulo, Serie Zoologia, 17*, 189–209.
Dujardin, F. (1851). Sur les Tardigrades et sur une espèce a longs pieds dans l'eau de mer. *Annales des Scienzes Naturelles, 15*, 161–166.
Ehrenberg, C. G. (1853). Diagnoses novarum formarum. *Verhandlungen der Königlich Preussische Akademie der Wissenschaften Zu Berlin, 8*, 526–533.
Ehrenberg, C.G. (1859). Beitrag zur Bestimmung des stationären mikroskopischen Lebens in bis zu 20,000 Fuß Alpenhöhe. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, 427–456.
Englisch, H. (1936). Über die lateralen Darmanhangsdrüsen (Vasa malphigii) und die Wohnpflanzen der Tardigraden. *Zoologische Jahrbücher 68, Abteilung für Systematik, Ökologie und Systematik der Tiere*, 325–352.
Gąsiorek, P., & Vončina, K. (2023). Atlas of the Echiniscidae (Heterotardigrada) of the World— 63 part I: West Palaearctic *Echiniscus* species. *Zootaxa, 5344*(1), 1–72.
Gąsiorek, P., Stec, D., Morek, W., & Michalczyk, Ł. (2017). An integrative redescription of *Echiniscus testudo* (Doyère, 1840), the nominal taxon for the class Heterotardigrada (Ecdysozoa: Panarthropoda: Tardigrada). *Zoologischer Anzeiger, 270*, 107–122.
Gąsiorek, P., Morek, W., Stec, D., & Michalczyk, Ł. (2019a). Untangling the *Echiniscus* Gordian knot: Paraphyly of the "arctomys group" (Heterotardigrada: Echiniscidae). *Cladistics, 35*, 633–653.
Gąsiorek, P., Stec, D., Morek, W., & Michalczyk, Ł. (2019b). Deceptive conservatism of claws: Distinct phyletic lineages concealed within Isohypsibioidea (Eutardigrada) revealed by molecular and morphological evidence. *Contributions to Zoology, 88*, 78–132.
Goeze, J.A.E. (1773). 2. Beobachtung: Über den kleinen Wasserbären. In: *Herrn Karl Bonnets Abhandlungen aus der Insektologie, aus dem Französischen übersetzt und mit einigen Zusätzen herausgegeben von Joh. August Ephraim Goeze, Pastor bei der St. Blasii Kirche in Quedlinburg*. JJ Gebauers Wittwe und Joh Jacob Gebauer, Halle (pp 367–355).
Grabowski, B. (1995). Ökologische Untersuchungen an moosbewohnenden Bärtierchen (Tardigrada) mit einem Bericht über drei neue Arten für Deutschland. *Acta Biologica Benrodis, 7*, 77–98.
Greef, R. (1866). Untersuchungen über den Bau und die Naturgeschichte der Bärthierchen. *Archiv Für Mikroskopische Anatomie, 2*, 102–131.
Grell, K. G. (1936). Beiträge zur Kenntnis von *Actinarctus doryphorus* E. Schulz nebst Bemerkungen zur Tardigraden Fauna des Helgoländer Skitt-Gatts. *Zoologischer Anzeiger, 117*, 143–154.
Greven, H. (1972). Tardigraden des nördlichen Sauerlandes. *Zoologischer Anzeiger, 189*, 368–381.
Greven, H. (1976). Some ultrastructural observations on the midgut Epithelium of *Isohypsibius augusti* (Murray, 1907) (Eutardigrada). *Cell and Tissue Research, 166*, 339–351.
Greven, H. (2007). Comments on the eyes of tardigrades. *Arthropod Structure & Development, 36*, 401–407. https://doi.org/10.1016/j.asd.2007.06.003
Greven, H., & Blom, H. J. (1977). *Isohypsibius granulifer* Thulin 1928 – ein neuer Tardigrade für Deutschland. *Decheniana (Bonn), 130*, 128–130.
Greven, H., & Grohé, G. (1975). Die Feinstruktur des Integumentes und der Muskelansatzstellen von *Echiniscoides sigismundi* (Heterotardigrada). *Helgoländer Wissenschaftliche Meeresuntersuchungen, 27*, 450–460.
Greven, H., & Kristensen, R. M. (2001). Some Aspects of Spermiogenesis and Spermatozoan Ultrastructure in *Echiniscoides sigismundi* (Heterotardigrada: Echiniscoididae). *Zoologischer Anzeiger, 240*, 331–339. https://doi.org/10.1078/0044-5231-00040
Greven, H., & Kuhlmann, D. (1972). Die Struktur des Nervengewebes von *Macrobiotus hufelandi* C.A.S. Schultze (Tardigrada). *Zeitschrift Für Zellforschung und Mikroskopische Anatomie, 132*, 131–146.
Greven, H., & Peters, W. (1986). Localization of Chitin in the cuticle of Tardigrada using wheat germ agglutinin-gold conjugate as a specific electrondense marker. *Tissue & Cell, 2*, 297–304.
Greven, H. (2018). From Johann August Ephraim Goeze to Ernst Marcus: A Ramble Through the History of Early Tardigrade Research (1773 Until 1929). *In R. O. Schill (Ed.), Water Bears: The Biology of Tardigrades* (pp 1-55). Springer, Cham.
Guidetti, R. (1998). Two new species of Macrobiotidae (Tardigrada: Eutardigrada) from the United States of America, and some taxonomic considerations of the genus *Murrayon*. *Proceedings of the Biological Society of Washington, 111*(3), 663–673.
Guidetti, R., Rebecchi, L., & Bertolani, R. (2000). Cuticle structure and systematics of the Macrobiotidae (Tardigrada, Eutardigrada). *Acta Zoologica (Stockholm), 81*, 27–36.
Guidetti, R., Jönsson, K. I., & Kristensen, R. M. (2015). Tardigrades of Sweden; an updated checklist. *Zootaxa, 3981*(4), 491–507. https://doi.org/10.11646/zootaxa.3981.4.2
Guidetti, R., Schill, R. O., Giovannini, I., Massa, E., Goldoni, S. A., Ebel, C., Förschler, M. I., Rebecchi, L., & Cesari, M.

(2021). When DNA sequence data and morphological results fit together: Phylogenetic position of *Crenubiotus* within Macrobiotoidea (Eutardigrada) with description of *Crenubiotus ruhesteini* sp. nov. *Journal of Zoological Systematics and Evolutionary Research, 59*, 576–587. https://doi.org/10.1111/jzs.12449

Guidetti, R., Cesari, M., Giovannini, I., Ebel, C., Förschler, M. I., Rebecchi, L., & Schill, R. O. (2022). Morphology and taxonomy of the genus *Ramazzottius* (Eutardigrada; Ramazzottiidae) with the integrative description of *Ramazzottius kretschmanni* sp. nov. *The European Zoological Journal, 38*(1), 339–363. https://doi.org/10.1080/24750263.2022.2043468

Guidetti, R., Giovannini, I., Del Papa, V., Ekrem, T., Nelson, D. R., Rebecchi, L., & Cesari, M. (2022). Phylogeny of the asexual lineage Murrayidae (Macrobiotoidea, Eutardigrada) with the description of Paramurrayon gen. nov. and Paramurrayon meieri sp. nov. *Invertebrate Systematics, 36*(12), 1099–1117.

Hansen, J.G., Jørgensen, A., Kristensen, R.M. (2001). Preliminary Studies of the Tardigrade Fauna of the Faroe Bank. *Zoologischer Anzeiger, 240*, 385–393. http://www.urbanfischer.de/journals/zoolanz

Heinis, F. (1908). Tardigraden der Schweiz. *Zoologischer Anzeiger, 32*(22), 633–638.

Heinis, F. (1910). Systematik und Biologie der moosbewohnenden Rhizopoden, Rotatorien und Tardigraden der Umgebung von Basel mit Berücksichtigung der übrigen Schweiz. *Archiv Für Hydrobiologie, 5*(89–166), 217–256.

Hofmann, I., & Eichelberg, E. (1986). Faunistisch-ökologische Untersuchungen zur Habitatpräferenz moosbewohnender Tardigraden. *Zoologische Beiträge N.F., 31*, 61–76.

Hofmann, I. (1987). Habitat preference of the most frequent moss-living Tardigrada in the area of Giessen (Hessen). *In: R. Bertolani (ed.), Biology of Tardigrades. Selected Symposia and Monographs U.Z.I.,1, Modena, Mucchi Editore*, 211 –216.

Hohberg, K. (2006). Tardigrade species composition in young soils and some aspects on life history of *Macrobiotus richtersi* J. Murray, 1911. *Pedobiologia, 50*, 267–274.

Hohberg, K., & Traunspurger, W. (2005). Predator-prey interaction in soil food web: Functional response, size-dependent foraging efficiency, and the influence of soil texture. *Biology and Fertility of Soils, 41*, 419–427. https://doi.org/10.1007/s00374-005-0852-9

Hohberg, K., Russel, D. J., & Elmer, M. (2011). Mass occurence of algal-feeding tardigrade *Apodibius confusus*, in the young soils of a post-minig site. *Journal of Zoological Systematics and Evolutionary Research, 49*(Suppl. 1), 62–65.

Iharos, G. (1966). Neue Tardigraden-Arten aus Ungarn. *Acta Zoologica Academiae Scientiarum Hungaricae, XII, 1–2*, 111–122.

Kaczmarek, Ł, Michalczyk, Ł, & McInnes, S. J. (2014). Annotated zoogeography of non-marine Tardigrada. *Part I: Central America. Zootaxa, 3763*(1), 001–062. https://doi.org/10.11646/zootaxa.3763.1.1

Kaczmarek, Ł, Kayastha, P., Gawlak, M., Mioduchowska, M., & Roszkowska, M. (2022a). An Integrative Redescription of *Echiniscus quadrispinosus quadrispinosus* Richters, 1902 (Heterotardigrada, Echiniscidae) from the terra typica in Taunus Mountain Range (Europe; Germany). *European Journal of Taxonomy, 823*, 102–124. https://doi.org/10.5852/ejt.2022.823.1819

Kaczmarek, Ł, Kayastha, P., Roszkowska, M., Gawlak, M., & Mioduchowska, M. (2022). Intergrative redescription of the *Minibiotus intermedius* (Plate, 1888) – The type species of the genus *Minibiotus* R.O. Schuster, 1980. *Diversity, 14*(5), 365. https://doi.org/10.3390/d14050356

Kristensen, R. M., & Hallas, T. E. (1980). The Tidal Genus *Echiniscoides* and Its Variability, with Erection of Echiniscoididae. *Zoologica Scipta, 9*, 113–127.

Kristensen, R.M. (1982). New aberrant Eutardigrades from homothermic Springs on Disko Island, West Greenland. *Proceedings of the Third International Symposium on the Tardigrada, East Tennessee State University Press*, 203–220.

Marcus, E. (1927). Zur Anatomie und Ökologie mariner Tardigraden. *Zoologische Jahrbücher, Abteilung Für Systematik, Ökologie und Geographie der Tiere, 53*, 487–558.

Marcus, E. (1928). Bärtierchen (Tardigrada). *Die Tierwelt Deutschlands, Jena, 12*, 1–230.

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

Marcus, E. (1936). Tardigrada. *Das Tierreich, 66.Lieferung. Berlin und Leipzig*, 1–340.

Maucci, W. (1973). Tardigradi muscicola della Turchia. *Memorie del Museo Civico di Storia Naturale, XX*, 169–221.

Meier, T. (2017). A checklist of Norwegian Tardigrada. *Fauna Norvegica, 37*, 25–42. https://doi.org/10.5324/fn.v37i0.2269

Michalczyk, Ł, Wełnicz, W., Frohme, M., & Kaczmarek, Ł. (2012). Redescriptions of three *Milnesium* Doyère, 1840 taxa (Tardigrada: Eutardigrada: Milnesiidae), including the nominal species for the genus. *Zootaxa, 3154*, 1–20.

Morek, W., Suzuki, A. C., Schill, R. O., Georgiev, D., Yankova, M., Marley, N. J., & Michalczyk, Ł. (2019). Redescription of *Milnesium alpigenum* Ehrenberg, 1853 (Tardigrada: Apochela) and a description of *Milnesium inceptum* sp. nov., a tardigrade laboratory model. *Zootaxa, 4586*(1), 35–64.

Murray, J. (1905b). The Tardigrada of the Fourth Valley. *The Annals of Scottish Natural History, 53*, 160–164.

Murray, J. (1906a). Scottish alpine Tardigrada. *The Annals of Scottish Natural History, 57*, 25–30.

Murray, J. (1906b). The Tardigrada of the Fourth Valley. *The Annals of Scottish Natural History, 57*, 214–217.

Murray, J. (1907a). The Encystment of Macrobiotus. *The Zoologist, 11*, 4–11.

Murray, J. (1907b). Arctic tardigrada, collected by Wm. S. Bruce. *Transactions of the Royal Society of Edinburgh, 45*, 669–681.

Murray, J. (1907c). Scottish Tardigrada collected by the Lake Survey. *Transactions of the Royal Society of Edinburgh, 45*, 641–668.

Murray, J. (1907d). Some South African Tardigrada. *Journal of the Royal Microscopical Society, 12*, 515–524.

Murray, J. (1911). Arctiscoida. *Proceedings of the Royal Irish Academy, 31*, 1–16.

Murray, J. (1905a). The Tardigrada of the Scottish Lochs. *Transactions of the Royal Society of Edinburgh, Vol.41, Part III (No 27)*, 677–698.

Murray, J. (1906c). Scottish National Antarctic Expedition: Tardigrada of the South Orkneys. *Transactions of the Royal Society of Edinburgh, Vol.45, Part II. (No 12)*, 323–338.

Pilato, G. (1977). *Macrobiotus willardi*, a new species of Tardigrada from Canada. *Canadian Journal of Zoology, 55*, 628–630.

Pilato, G. (1998). Microhypsibiidae, new family of eutardigrades, and description of the new genus *Fractonotus* (Tardigrada). *Spixiana, 21*(2), 129–134.

Pilato, G., Bertolani, R., & Binda, M. G. (1982). Studio degli *Isohypsibius* del Gruppo elegans (Eutardigrada, Hypsibiidae) con descrizione di due specie. *Animalia, 9*(1/3), 185–198.

Pilato, G., Binda, M. G., Napolitano, A., & Moncada, E. (2000). The specific value of *Macrobiotus coronatus* De Barros 1942, and description of two new species of the *harmsworthi* group (Eutardigrada). *Bollettino Delle Seduté Dell'accademia Gioenia di Scienze Naturali in Catania, 33*(358), 103–120.

Pilato, G. (1969a). Su un interessante Tardigrado esapodo delle dune costiere siciliane: *Hexapodibius micronyx* n. gen. n. sp. *Bollettino delle seduté dell'Accademia Gioenia di Scienze naturali in Catania. Ser. IV, Vol. IX, 9*, 618–622.

Pilato, G. (1969b). Schema per una nuova sistemazione delle famiglie e dei generi degli Eutardigrada. Bollettino delle seduté della Accademia Gioenia di Scienze naturali in Catania. Ser. IV, Vol. X, 9, 180–193.

Plate, L. H. (1888). Beiträge zur Naturgeschichte der Tardigraden. *Zoologische Jahrbücher, Abteilung Für Anatomie und Ontogenie der Tiere, 3*, 487–550.

Pogwizd, J., & Stec, D. (2020). New records of *Dactylobiotus parthenogeneticus* Bertolani, 1982 provide insight into its genetic variability and geographic distribution. *Folia Biologica (Kraków), 68*(2), 57–72.

Pollock, L. W. (1971). On some British marine Tardigrada, including two new species of *Batillipes*. *Journal of the Marine Association of the United Kingdom, 51*, 93–103.

Pollock, L. W. (1982). *A closer look at some marine Heterotardigrada* (pp. 193–202). East Tennessee State University Press.

Rahm, G. (1924). Beitrag zur Kenntnis der Moostierwelt der preussischen Rheinlande. *Diss. Nicolaische Verlbh. R. Stricker*.

Rahm, G. (1925). Beitrag zur Kenntnis der Moostierwelt der preussischen Rheinlande. *Archiv für Naturgeschichte, Berlin, 90*, 153–159 und 187–193.

Rahm, G. (1931). Tardigrada of the South of America (Esp. Chile). *Revista Chilenda de Historia Natural*, 118–141.

Ramazzotti, G. (1962). Il Phylum Tardigrada. *Memorie Dell'istituto Italiano di Idrobiologia, 14*, 1–595.

Ramazzotti, G. & Maucci, W. (1983). Il Phylum Tardigrada. III edizione riveduta e aggiornata. *Memorie dell'Istituto Italiano di Idrobiologia, 41*, 1–1012. (English translation by Clark W. Beasley, 1995, McMurry University, Abilene, Texas, 79697, U.S.A.).

Remane, A. (1924). Neue aberrante Gastrotrichen I: *Macrodasys buddenbrocki* nov. gen. nov. spec. *Zoologischer Anzeiger, 61*, 289–297.

Renaud-Debyser, J. (1959). Sur quelques Tardigrades du bassin D'Arcachon. *Vie Et Milieu, Tome x, Fasc., 2*, 134–146.

Renaud-Mornant, J. (1980). Description de trois espèces nouvelles du genre Tanarctus Renaud-Debyser, 1959, et création de la sous-famille des Tanarctinae, subfam. nov. (Tardigrada, Heterotardigrada). *Bulletin du Muséum national d'histoire naturelle, Paris, 4 sér., 2, section A, no 1*, 129–141.

Reukauf, E. (1912a). Ein neuer Wasserbär, *Macrobiotus ferdinandi* (Reukauf). *Zoologischer Anzeiger, 39*, 352–353.

Reukauf, E. (1912b). Über das Simplexstadium und die Mundwerkzeuge der Macrobioten. *Zoologischer Anzeiger, 39*, 369–372.

Reukauf, E. (1912). Ein Verderber des Wasserbären *Macrobiotus lacustris* Duj., *Macrobiotophthora vimariensis* (Reukauf). *Centralblatt für Bakteriologie Parasitenkunde und Infektionskrankheiten. Abteilung, 63*(46), 390–393.

Richters, F. (1903). Nordische Tardigraden. *Zoologischer Anzeiger, 27*(5), 168–172.

Richters, F. (1904a). Beitrag zur Verbreitung der Tardigraden im südlichen Skandinavien und an der mecklenburgischen Küste. *Zoologischer Anzeiger, 28*, 347–352.

Richters, F. (1904b). Arktische Tardigraden. *Fauna Arctica, Band III, Lieferung, 3*, 495–508.

Richters, F. (1907a). Zwei neue *Echiniscus*-Arten. *Zoologischer Anzeiger, 31*(7), 197–202.

Richters, F. (1907b). Die Fauna der Moosrasen des Gaussbergs und einiger südlicher Inseln. *Deutsche Südpolar-Expedition, 9*(4), 259–302.

Richters, F. (1908). Marine Tardigraden. *Zoologischer Anzeiger, 33*, 77–85.

Richters, F. (1900). Beiträge zur Kenntnis der Fauna der Umgegend von Frankfurt a. M. *Bericht der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main*, 21–44. http://www.biodiversitylibrary.org/item/36149

Richters, F. (1902). Beiträge zur Kenntnis der Fauna der Umgebung von Frankfurt a. M. *Bericht der Senckenbergischen Naturforschenden Gesellschaft in Frankfurt am Main, II. Teil*, 3–21.

Richters, F. (1909a). Die Tardigraden der Kieler Bucht. *Bericht der Senckenbergischen Naturforschenden Gesellschaft, 40, II. Teil*, 35–40.

Richters, F. (1909b). Süßwasser-Makrobioten. *Bericht der Senckenbergischen Naturforschenden Gesellschaft, 40, II. Teil*, 28–34.

Richters, F. (1911). Tardigrades. *Campagne artique de 1907, Faune des mousses*, 1–19.

Richters, F. (1926). Tardigrada. *In Handbuch der Zoologie; Kükemthal, W., Krumbach, T., Eds.; Walter de Gruyter & Co, Berlin, Vol. 3*, 58–61.

Riemann, F. (1966). Die interstitielle Fauna im Elbe-Aestuar Verbreitung und Systematik. *Archiv für Hydrobiologie, Supplement XXXI (Elbe-Aestuar III), 1/2*, 223–226.

Rudescu, L. (1964). Tardigrada. *Fauna Republicii Populare Romîne, Vol. IV, 7*, 1–400.

Russel, D. J., Dastych, H., Zeller, U., Kratzmann, M., & Alberti, G. (1994). Zur Mesofauna des Bodens der Sandhausener Dünen. *Beihefte Zu Den Veröffentlichungen Für Naturschutz und Landschaftspflege Baden-Württemberg, 80*, 325–348.

Sands, C. J., McInnes, S. J., Marley, N. J., Goodall-Copestake, W. P., Convey, P., & Linse, K. (2008). Phylum Tardigrada: An "individual" approach. *Cladistics, 24*, 1–11.

Schill, R. O., & Steinbrück, G. (2007). Identification and differentiation of Heterotardigrada and Eutardigrada species by riboprinting. *Journal of Zoological Systematics and Evolutionary Research, 45*(3), 184–190. https://doi.org/10.1111/j.1439-0469.2007.00409.x

Schmidt, P. (1971a). Organisation und Fortpflanzung von Tardigraden. Institut für den wissenschaftlichen Film, Göttingen, C 1062/1971.

Schmidt, P. (1971b). *Milnesium tardigradum* (Tardigrada) Organisation und Fortpflanzung. Encyclopaedia Cinematographica, Institut für den wissenschaftlichen Film, Göttingen, E1659/1971.

Schmidt, P. (1971c). *Hypsibius dujardini* (Tardigrada) Organisation und Fortpflanzung. Encyclopaedia Cinematographica, Institut für den wissenschaftlichen Film, Göttingen, E1658/1971.

Schultze, C.A.S. (1834a). *Macrobiotus hufelandii*, animal e crustaceorum classe novum etc. Apud Carolus Curths, Berolini.

Schultze, C.A.S. (1834b). Über *Macrobiotus Hufelandii*. Okens Isis, Heft 6/7: 708–710. http://www.biodiversitylibrary.org/item/87984

Schultze, M. (1865). *Echiniscus sigismundi*, ein Arctiscoide der Nordsee. *Archiv für mikroskopische Anatomie, 1*, 428–436. http://www.biodiversitylibrary.org/item/49502

Schulz, E. (1935). *Actinarctus doryphorus* nov. gen. nov. spec., ein merkwürdiger Tardigrad aus der Nordsee. *Zoologischer Anzeiger, 111*, 285–292.

Schulz, E. (1951). Über *Stygarctus bradypus* n. g. n. sp., einen Tardigraden aus dem Küstengrundwasser, und seine phylogenetische Bedeutung. *Kieler Meeresforschungen, 8*(1), 86–97.

Schulz, E. (1953). *Orzeliscus septentrionalis* nov. spec., ein neuer mariner Tardigrad an der deutschen Nordseeküste. *Zoologischer Anzeiger, 111*, 285–288.

Schuster, R. (1999). A new species of the genus *Diphascon* (Tardigrada) from Germany. *Acta Biologica Benrodis, 10*, 21–25.

Schuster, R. (2003b). Faunistische und ökologische Untersuchungen an Tardigraden des Schwarzwalds (Deutschland). *Acta Biologica Benrodis, 12*, 147–192.

Schuster, R. (2021). *Minibiotus bernhardi* sp. n. (Eutardigrada, Macrobiotidae), a new Tardigrade species from the Black Forest (Baden-Württemberg). *Entomologie Heute, 32*, 121–131.

Schuster, R. O., Nelson, D. R., Grigarick, A. A., & Christenberry, D. (1980). Systematic criteria of the Eutardigrada. *Transactions of the American Microscopical Society, 99*(3), 284–303.

Schuster, R. & Greven, H. (2007). A long-term study of population dynamics *of tardigrades in the moss Rhytidiadelphus squarrosus (Hedw) Warnst. Proceedings of the Tenth International Symposium on Tardigrada, Journal of Limnology, 66 (Suppl.1), 141–151.* https://doi.org/10.4081/jlimnol.2007.s1.141

Schuster, R. & Greven, H. (2013). Reproductive traits of *Macrobiotus hufelandi* during a long-term field study with notes on *Paramacrobiotus richtersi* and *Diphascon pingue* (Eutardigrada). *Journal of Limnology, 72(sl)*, 166–174. https://doi.org/10.4081/jlimnol.2013.s1.e21.

Schuster, R. (2003). Faunistische und ökologische Untersuchungen an moosbewohnenden Tardigraden. *Dissertation Universität Düsseldorf*, 1–163.

Scourfield, D.J. (1897). Contributions to the Non-Marine Fauna of Spitsbergen. Part I. Preliminary notes, and report on the Rhizopoda, Tardigrada, Entomostraca. *Proceedings of the zoological Society of London*, 784–792.

Stec, D., Morek, W., Gąsiorek, P., Blagden, B., & Michalczyk, Ł. (2017). Description of *Macrobiotus scoticus* sp. nov. (Tardigrada: Macrobiotidae: Hufelandi Group) from Scotland by means of integrative Taxonomy. *Annales Zoologici, 67*(2), 181–197.

Stec, D., Morek, W., Gąsiorek, P., & Michalczyk, Ł. (2018). Unmasking hidden species diversity within the *Ramazzottius oberhaeuseri* complex, with an integrative redescription of the nominal species for the family Ramazzottiidae (Tardigrada: Eutardigrada: Parachela). *Systematics and Biodiversity, 16*(4), 357–376.

Stec, D., Vecchi, M., Maciejowski, W., & Michalczyk, Ł. (2020). Resolving the systematics of Richtersiidae by multilocus phylogeny and an integrative redescription of the nominal species for the genus *Crenubiotus* (Tardigrada). *Scientific Reports, 10*, 19418. https://doi.org/10.1038/s41598-020-75962-1

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*(2), 207–266.

Tumanov, D. V., & Tsvetkova, A. Y. (2023). Some have drops and some do not, but can we rely on that? Re-investigation of *Diphascon tenue* (Tardigrada: Eutardigrada) with discussion of the phylogeny and taxonomy of the superfamily Hypsibioidea. *Zoosystematica Rossica, 32*, 50–74.

Urbanowicz, C. (1925). Sur la variabilité de „*Macrobiotus oberhaeuseri*“. *Bulletin Biologique De La France Et De La Belgique, 49*, 124–142.

Vuori, T., Massa, E., Calhim, S., & Vecchi, M. (2020). Tardigrades of Finland: New records and annotated checklist. *Zootaxa, 4851*(3), 477–521.

Walz, B. (1979). The Morphology of Cells and Cell organelles in the Anhydrobiotic Tardigrade, *Macrobiotus hufelandi*. *Protoplasma, 99*, 19–30. 10.0033-183X/79/0099/0019/802.40

Węglarska, B. (1959). Die Tardigraden (Tardigrada) Polens I. Tardigraden der Woiwodschaft Kraków. *Acta Zoologica Cracoviensia, Tom IV, 13*, 1–47.

Węglarska, B. (1973). Tardigrada in High Tatra localities bare of snow with description of *Itaquascon pawlowskii* sp.n. *Vestnik Ceskoslovenske Spolecnosti Zoologicke, 27*, 150–154.

Wenck,W. v. (1914). Entwicklungsgeschichtliche Untersuchungen an Tardigraden (*Macrobiotus lacustris* Duj.). *Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere, XXXVII*, 492–505.