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An illustrated identification key to the eutardigrade species (Tardigrada, Eutardigrada) presently known from European soils

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Abstract

The present paper aims at providing a practical identification tool for soil zoologists. It shall facilitate taxonomic examination of tardigrade communities in order to encourage further investigations and by this expand our scarce knowledge on soil tardigrades. From faunistic studies on soil tardigrades a list of the eutardigrade species presently known from European soils was gathered comprising 22 genera, 58 species, 3 species groups. Based on the most important standard works and on up-to-date nomenclature an illustrated key to the eutardigrade genera of European soils was created. Genus descriptions and identification keys to the soil species were added while those genera that hold only one or two soil species were accomplished with short species descriptions. Additional information is given on the relevant determination features, such as claws and bucco-pharyngeal apparatus. Difficulties in tardigrade identification and taxonomy are discussed. Due to the comparably small number of studies that so far exist on soil tardigrades, the key will most likely not cover all species present in European soils, but shall provide a basis to facilitate further research.

Keywords Eutardigrada | Identification key | Soil tardigrades

1. Introduction

Terrestrial tardigrades successfully inhabit mosses, lichens and leaf litter (Marcus 1929). That soil pore systems also represent a significant habitat for tardigrades was long doubted. During the last 50 years, however, a few intensive investigations of soil zoologists (e.g., Hallas & Yeates 1972, Anderson et al. 1984, Briones et al. 1997, Stark & Kristensen 1999, Ito & Abe 2001, Harada & Ito 2006, Hohberg 2006, Hohberg et al. 2011, Nelson & Bartels 2013) brought proof that tardigrades inhabit soils and that especially young, but also mature soils, may host tardigrades in high to massive numbers and with many species. Present research continues to concentrate on tardigrade communities of moss cushions and lichens, and we still know comparably little of the soil inhabiting tardigrade communities, their ecological demands and vice versa their impact on the ecosystem.

It is certainly not lack of interest that led to tardigrades being so far neglected in soil zoological studies, but rather the difficulties that accompany ecologists that try to become acquainted with tardigrade taxonomy. Tardigrades of the class Eutardigrada, the taxon group that is found in soils, are especially difficult to determine. Most of the rather few determination characters are tiny differences in the structure of the claws, the feeding apparatus and the structure of the cuticle, that should be investigated using differntial interference or phase contrast.

An important work was and still is the monograph of Ramazzotti & Maucci (1983) that contains 531 species descriptions and both, a key to the genera and a number of species keys including limno-terrestrial and marine tardigrades. Although the descriptions of more recent species are missing, no publication of comparable extent on species level has been published yet. Also Dastych (1988) provided a helpful species key to the

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Tardigrades of Poland. But since the 1980s, there have been many taxonomic revisions (e.g., Guidetti et al. 2009, Marley et al. 2011, Bertolani et al. 2014a, Vecchi et al. 2016) and numerous new genera and species have been introduced (e.g., Pollock 1995, Fontoura et al. 2009, Lisi 2011, Fujimoto et al. 2012, Bertolani et al. 2014b, Guil et al. 2015, Hansen et al. 2017) rising tardigrade species number to more than 1200 (Guidetti & Bertolani 2005, Degma & Guidetti 2007, Degma et al. 2017). Pilato & Binda (2010) already took into account many changes, describing the properties of the eutardigrade genera, but do not provide a species key. In some cases, these are provided in publications on genera (e.g., Bertolani & Rebecchi 1993, Dastych 2011, Hansen et al. 2017) or have to be gathered from original species descriptions. All this combined makes it rather difficult to begin working with tardigrades.

The aim of the present paper is to provide an illustrated key for those tardigrade species of the class Eutardigrada that have been reported so far from European soils. Species like *Itaquascon placophorum* that until now have only been found in leaf litter were not included. We are aware that some of these leaf litter species might be able to migrate into soil. But as for other soil animal groups there will also be a high number of definite litter layer species, which like moss species are not included in strict soil studies, where the leaf litter and moss is removed before soil extraction. As heterotardigrades are rare or absent in soils (Nelson et al. 2015), they are not considered in this key. The intention of this work is a practical and user-friendly approach to taxonomy that allows a fast and reliable identification of the genera and additional species keys for more detailed determination. This is achieved by focusing on obvious features rather than on systematic relationships. Due to the comparably small number of soil studies that considered tardigrades, the key will most likely not cover all species present in soil, but provides a basis for further research. The present paper is thought as a tool for soil zoologists to facilitate taxonomic examination of tardigrade communities in soil studies in order to encourage investigations and by this expand our knowledge on this soil animal group.

2. Material and methods

First, a list of the tardigrade species presently known from European soils was prepared. For the creation of this species list, various publications on soil tardigrade studies were gathered, some of which in Italian and German language. For three Spanish studies we refer to a soil species list given in Guil et al. (2015).

The 'Actual checklist of Tardigrada species' was considered the standard for taxonomy and nomenclature (Guidetti & Bertolani 2005, Degma & Guidetti 2007, Degma et al. 2017).

If not stated differently, the description of tardigrade features and taxonomic characters as well as the general genus descriptions base on Pilato & Binda (2010), Bertolani et al. (2014), Nelson et al. (2015). For species descriptions we used preferably the many original publications in combination with Ramazzotti & Maucci (1983) and Dastych (1988). Also, the online key of the Great Smoky Mountain National Park was taken into account to gather information on tardigrade species (Bartels & Nelson 2010).

3. Soil eutardigrades of Europe

The distribution of soil tardigrades within the Tardigrada was analyzed, showing that tardigrade species that have been reported from European soils appear in both eutardigrade orders (Apochela and Parachela), eight of thirteen families and 22 genera (Tab. 1).

4. Eutardigrade identification features

Tardigrades are small, often colorless animals with a bilaterally symmetrical body and four pairs of legs (Fig. 1A). Eutardigrades have only few morphological characters that allow for taxonomic differentiation. One is claw morphology (Fig. 1B). Eutardigrades share the presence of two claws on each leg. In few genera the claws are lacking on the fourth pair of legs (*Hexapodibius*) or are even absent on all legs (*Apodibius* and *Necopinatum*).

An eutardigrade claw always comprises of a primary and a secondary branch, further features may be the presence and shape of spines, lunules and cuticular thickenings (Fig. 1B). The shape of the claws is an important feature in eutardigrade identification. There are different claw types that vary in symmetry and arrangement of the primary (1) and secondary branches (2).

4.1. Claw symmetry

With respect to the median plane of the leg, claws may be either 'asymmetrically arranged' (conventionally described as: 2121) or 'symmetrically arranged' (conventionally described as: 2112) (Pilato & Binda 2010).

Table 1. List of tardigrade species presently reported from European soils. a) Ramazzotti (1959), b) Manicardi & Bertolani (1987), c) Bertolani et al. (1987), d) Bertolani et al. (1994), e) Bertolani & Rebecchi (1996), f) Pilato et al (2005), g) Dastych (1988), h) Guil et al. (2014), i) Mihelcic (1949), j) Mihelcic (1954), k) Mihelcic (1958), l) Mihelcic (1972), m) Mihelcic (1963), n) Hallas & Yeates (1972), o) Morgan (1980), p) Hohberg (2006), q) Hohberg et al. (2011), r) Iharos, (1977); AT: Austria, DE: Germany, DK: Denmark, ES: Spain, HU: Hungary, IS: Iceland, IT: Italy, PL: Poland.

	synonyms used in reference	country	reference
Apochela Schuster, Nelson, Grigarick & Christenberry, 1980			
Milnesiidae Ramazzotti, 1962			
Milnesium Doyère, 1840			
Milnesium asiaticum Tumanov, 2006		ES	h
Milnesium tardigradum tardigradum Doyère, 1840		AT	l
Parachela Schuster, Nelson, Grigarick & Christenberry, 1980			
Eohypsibioidea Bertolani & Kristensen, 1987			
Eohypsibiidae Bertolani & Kristensen, 1987			
Eohypsibius Kristensen, 1982			
Eohypsibius nadjae Kristensen, 1982		IT	c,e
Hypsibioidea Pilato, 1969			
Hypsibiidae Pilato, 1969			
Diphasconinae Dastych, 1992			
Diphascon Plate, 1888			
Diphascon alpinum Murray, 1906		DK	n
Diphascon higginsi Binda, 1971		DE, IT	b,e,p,q
Diphascon mariae (Mihelčič, 1951)	*Hypsibius* (*Diphascon*) *mariae*	AT	l
Diphascon nelsonae Pilato, Binda, Bertolani & Lisi, 2005		ES	h
Diphascon nobilei (Binda, 1969)		DE, IT	c,e,f,p
Diphascon pingue (Marcus, 1936)		DE, IT, ES	c,e,h,p
Diphascon platyungue Pilato, Binda, Bertolani & Lisi, 2005		IT	f
Diphascon stappersi Richters, 1911		DK	n
Hypsibiinae Pilato, 1969			
Hypsibius Ehrenberg, 1848			
Hypsibius convergens (Urbanowicz, 1925)		AT, DE, IT, ES	a,l,h,p,q
Hypsibius dujardini (Doyère, 1840)		AT, DK, DE, ES, IS	l,h,n,o,p
Hypsibius pallidus Thulin, 1911		AT, DE, ES, IT	e,l,i,p
Hypsibius pedrottii Bertolani, Manicardi & Gibertoni, 1987		IT	e
Hypsibius pradellii Bertolani & Rebecchi, 1996		IT	e
Itaquasconinae Bartoš in Rudescu, 1964			
Adropion Pilato, 1987			
Adropion belgicae (Richters, 1911)	*Diphascon* (*Adropion*) *belgicae*	IT	c
Adropion prorsirostre (Thulin, 1928)	*Diphascon* (*A.*) *prorsirostre*	IT	b,c,d,e
Adropion scoticum scoticum (Murray, 1905)	*Diphascon* (*A.*) *scoticum*	AT, DK, IS, IT	b,c,d,e,l,n,o
Astatumen Pilato, 1997			
Astatumen trinacriae (Arcidiacono, 1962)	*Itaquascon trinacriae*	DE	p
Mesocrista			
Mesocrista spitzbergensis (Richters, 1903)		IS	o
Sarascon			
Sarascon hortensiae Guil, Rodrigo & Machordom, 2014		ES	h
Pilatobiinae Bertolani, Guidetti, Marchioro, Altiero, Rebecchi & Cesari, 2014			
Pilatobius Bertolani, Guidetti, Marchioro, Altiero, Rebecchi & Cesari, 2014			
Pilatobius brevipes (Marcus, 1936)	*Diphascon* (*Diphascon*) *brevipes*	IT	c
Pilatobius bullatus (Murray, 1905)	*Diphascon* (*D.*) *bullatum*, *Hypsibius bullatus*	AT, DK, DE, IT	a,l,n,p
Pilatobius granifer (Greven, 1972)	*Diphascon granifer*	IT	b,c,e
Pilatobius patanei (Binda & Pilato, 1971)	*Diphascon* (*D.*) *patanei*	IT	c,e
Pilatobius rugosus (Bartoš, 1935)		DE	p
Pilatobius secchii (Bertolani & Rebecchi, 1996)	*Diphascon* (*D.*) *secchii*	IT	e

Table 1 continued.

	synonyms used in reference	country	reference
Ramazzottiidae Sands, McInnes, Marley, Goodall-Copestake, Convey & Linse, 2008			
Ramazzottius Binda & Pilato, 1986			
Ramazzottius oberhaeuseri (Doyère, 1840)	*Hypsibius oberhaeuseri*	AT, DE	l,q
Isohypsibioidea Sands, McInnes, Marley, Goodall-Copestake, Convey & Linse, 2008			
Hexapodibiidae Cesari, Vecchi, Palmer, Bertolani, Pilato, Rebecchi & Guidetti, 2016			
Hexapodibius Pilato, 1969			
Hexapodibius bindae Pilato, 1982		ES	h
Hexapodibius christenberryae Pilato & Binda, 2003		ES	h
Hexapodibius cf. *micronyx*		DE	q
Hexapodibius pseudomicronyx Robotti, 1972		IT	b,c
Parhexapodibius Pilato, 1969			
Parhexapodibius pilatoi (Bernard, 1977)		IT	b,c
Parhexapodibius ramazzottii Manicardi & Bertolani, 1987		IT	b
Isohypsibiidae Sands, McInnes, Marley, Goodall-Copestake, Convey & Linse, 2008			
Apodibius Dastych, 1983			
Apodibius confusus Dastych, 1983		DE	q
Doryphoribius Pilato, 1969			
Doryphoribius doryphorus (Binda & Pilato, 1969)		ES	h
Doryphoribius flavus (Iharos, 1966)		ES	h
Doryphoribius macrodon Binda, Pilato & Dastych, 1980		IT	c
Eremobiotus Biserov, 1992			
Eremobiotus alicatai (Binda, 1969)		DE	p,q
Isohypsibius Thulin, 1928			
Isohypsibius asper (Murray, 1906)	*Isohypsibius tetradactyloides* (Richters, 1907)	ES	h
Isohypsibius dastychi Pilato, Bertolani & Binda, 1982		DE	p,q
Isohypsibius franzi (Mihelčič, 1951)	*Hypsibius franzi*	AT, IT, ES	a,l,i
Isohypsibius lunulatus (Iharos, 1966)		IT	b,c,d,e
Isohypsibius mihelcici (Iharos, 1964)		HU	r
Isohypsibius prosostomus Thulin, 1928	*Hypsibius prosostomus*	AT, DK	l,n
Isohypsibius ronsisvallei Binda & Pilato, 196		IT	c,d
Isohypsibius sattleri (Richters, 1902)	*Hypsibius sattleri*	AT, HU, IT	d,e,l,r
Isohypsibius schaudinni (Richters, 1909)		HU	r
Isohypsibius tuberculoides (Mihelčič, 1951)		ES	i,k
Isohypsibius tuberculatus-group	*Hypsibius tuberculatus*	AT, DE, ES, IT	a, l,m,k,p,q
Macrobiotoidea Thulin, 1928 in Marley et al. 2011			
Macrobiotidae Thulin, 1928			
Macrobiotus C.A.S. Schultze, 1834			
Macrobiotus crenulatus Richters, 1904	*Macrobiotus dentatus* Binda, 1974	IT	b
Macrobiotus echinogenitus Richters, 1904		AT	l
Macrobiotus hufelandi-group		AT, DK, ES, HU, IT	a,l,m,i,k,n,r
Macrobiotus terricola Mihelčič, 1951		AT, ES	i,k
Mesobiotus Vecchi, Cesari, Bertolani, Jönsson, Rebecchi & Guidetti, 2016			
Mesobiotus harmsworthi-group	*Macrobiotus harmsworthi*	AT, DK, DE, ES	l,h,j,n,p
Minibiotus R.O. Schuster, 1980			
Minibiotus intermedius (Plate, 1888)		AT, ES	l,m,h,k
Paramacrobiotus Guidetti, Schill, Bertolani, Dandekar & Wolf, 2009			
Paramacrobiotus richtersi (Murray, 1911)	*Macrobiotus richtersi*	AT, DE, HU, IT, PL, ES	a,b,c,g,l,h, p,q,r
Xerobiotus Bertolani & Biserov, 1996			
Xerobiotus pseudohufelandi (Iharos, 1966)	*Macrobiotus pseudohufelandi*	IT, ES	c,h
Xerobiotus xerophilus (Dastych, 1978)		ES	h
incertae sedis			
Necopinatidae Ramazzotti & Maucci, 1983			
Necopinatum Pilato, 1971			
Necopinatum mirabile Pilato, 1971		IT	c

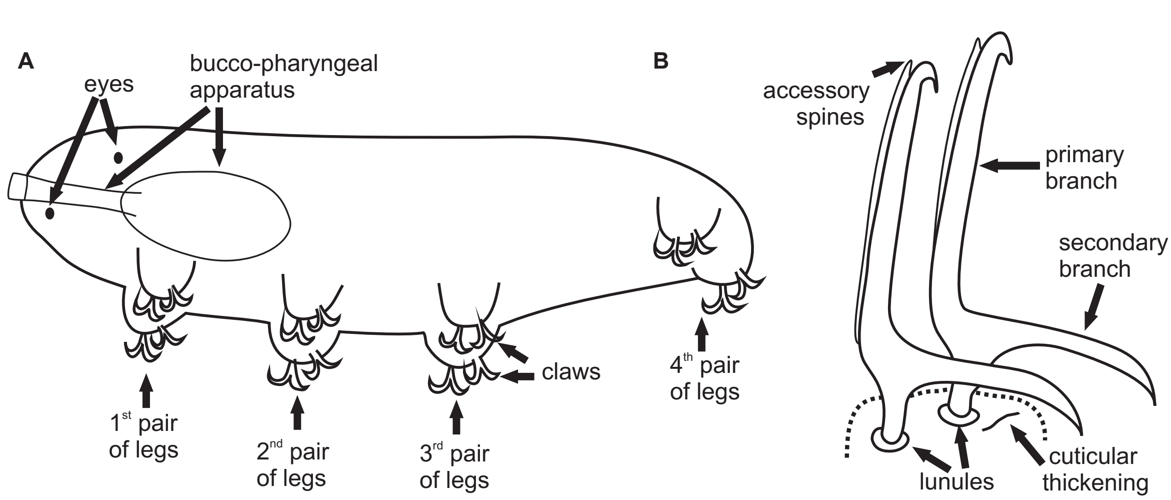


Figure 1. Generalized eutardigrade schematics (**A**) whole body in ventrolateral view, (**B**) claw structure.

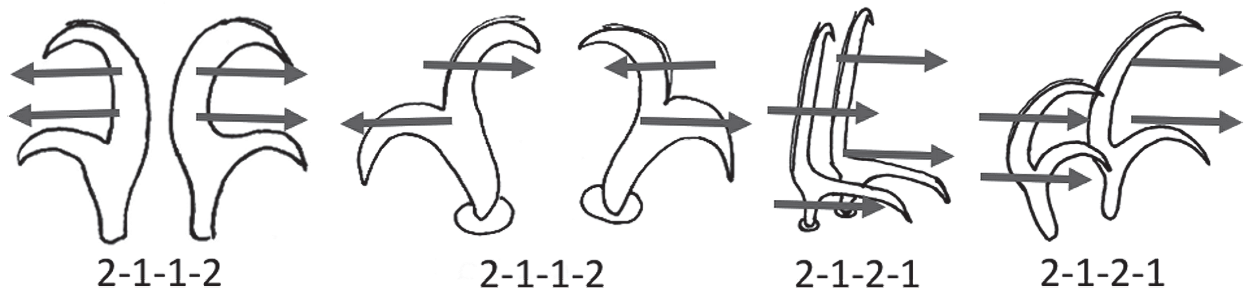


Figure 2. Claw symmetry of eutardigrades. 1 = primary branch, 2 = secondary branch. There are different claw types that vary in symmetry and arrangement of the primary (1) and secondary (2) branches; claw schemata redrawn from Bertolani (1982).

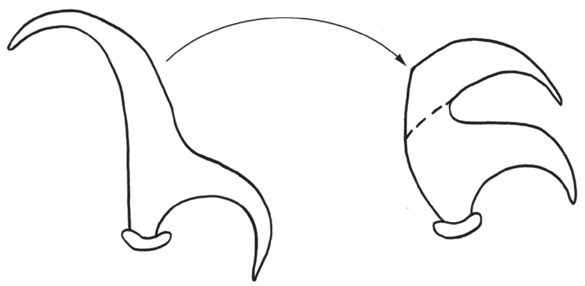


Figure 3. Inversion of the primary branch of the *Isohypsibius* type claw, making it look like a *Hypsibius* type of claw. Such folds happen during the process of embedding probably due to mechanical forces.

To describe it more visually: while in the 2121 (asymmetric) constitution both branches of both claws point in the same direction, in the 2112 (symmetric) constitution the two primary, and the two secondary branches, respectively, point in opposite directions (Fig. 2).

It must be mentioned, however, that claw symmetry may also lead to misidentification, as during the process of embedding the branches of the claws tend to fold and thus point into unnatural directions. Also, it may happen that a whole claw is inverted. This happens especially with claws of the Eohypsibiidae type, where a 180° rotation of the internal claws results in a symmetric arrangement of the actual asymmetric constitution (Pilato & Binda 2010).

While studying a variety of embedded specimens of different *Isohypsibius* species we came to notice that a number of specimens showed 'folded' claw branches. Particularly, the primary branch of the inner claw tends to be inverted and pressed into a position that is different from the natural (Fig. 3). This probably happens during the process of embedding, due to mechanical forces applied. In the example of *Isohypsibius* (Fig. 3) claws resembled at first sight the *Hypsibius*-type (Fig. 4C), but other features like cuticular thickenings did not match the genus of *Hypsibius*. At second examination the fold (broken line in Fig. 3) was visible and we decided on *Isohypsibius* type with twisted claws. It is thus advisable to check a specimen with all claws of all legs and also to compare the diagnosis with other genera specific features.

4.2. Claw types of eutardigrade genera used in the present identification key

The *Milnesium* type

The primary and secondary branch are, in contrast to the other here described (Parachelan) claw types, clearly separated with some distance between. Primary branch is long and straight with only the tips slightly curved inwards (Fig. 4A).

The *Isohypsibius* type

The two claws of each leg are very similar in size and shape. Both branches are about straight with only the tips curved slightly inwards. The angles between the basal sections and the secondary branches are close to a right angle. Branches of one claw can point in the same or in opposite directions. 2121 symmetry (Fig. 4B).

The *Hypsibius* type

The two claws of each leg are very different in size and shape. In some cases, the primary branch is almost straight with only the tip curled slightly inwards in other cases both branches can be curled inwards. The secondary branches are always curled inwards and form a continuous curve with the basal section. Branches of one claw can point in the same or in opposite directions. 2121 symmetry (Fig. 4C).

The *Ramazzottius* (= *oberhaeuseri*) type

The two claws of each leg are very different in shape and size. Short and stout inner claws. Basal section of outer claw is long with small curved secondary and very long and slender primary branch. There is a constriction between basal tract and primary branch. 2121 symmetry (Fig. 4D).

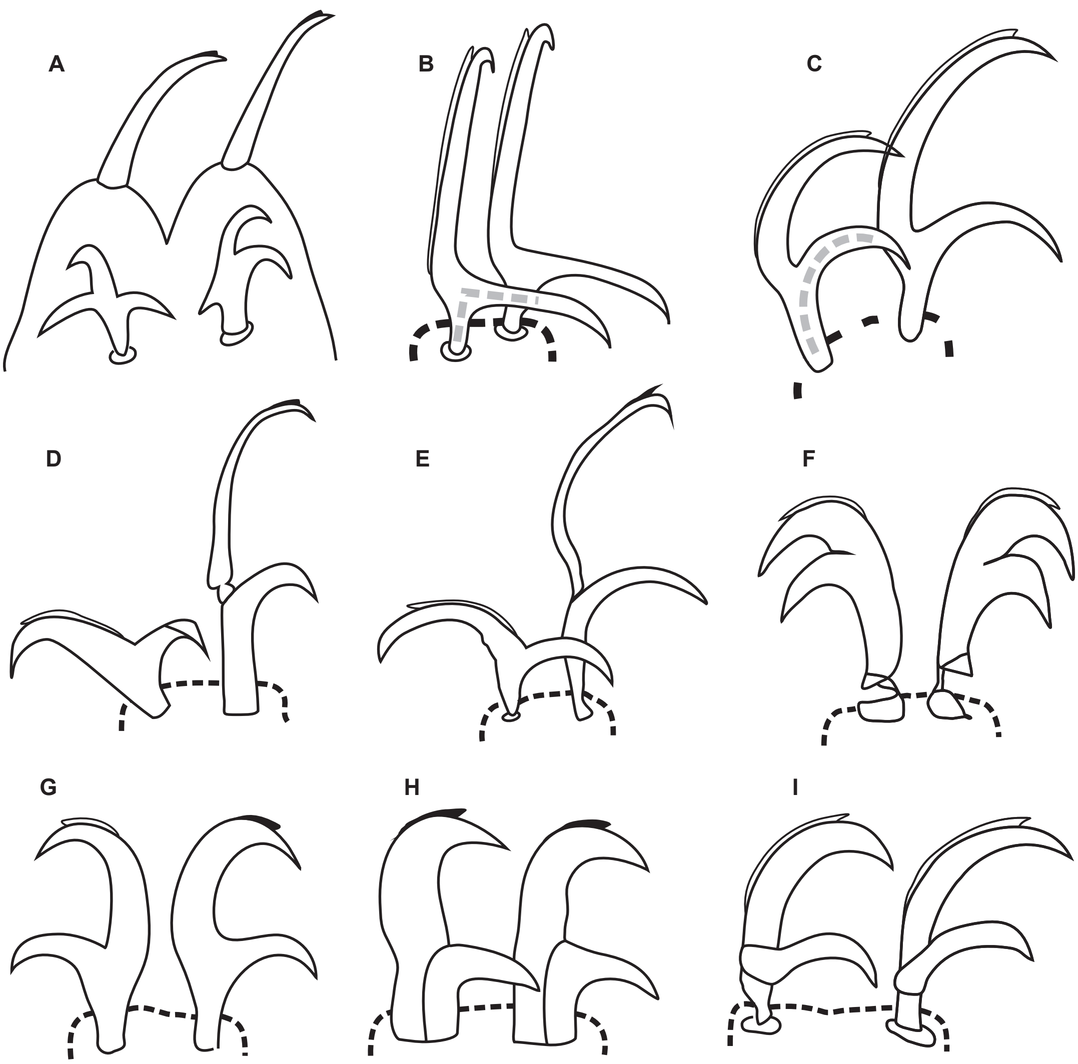


Figure 4. Claw types of different eutardigrade genera. (**A**) *Milnesium*, (**B**) *Isohypsibius*, (**C**) *Hypsibius*, (**D**) *Ramazzottius*, (**E**) *Sarascon*, (**F**) *Macrobiotus*, (**G**) *Xerobiotus*, (**H**) *Hexapodibius*, (**I**) Eohypsibiidae (=*Bertolanius)*; broken grey lines illustrate angles between the basal section and the secondary claw branch, rather rectangular in *Isohypsibius* (**B**) and a continuous curve in *Hypsibius* (**C**); (**A**), (**B**), (**C**) & (**I**) redrawn from Bertolani (1982); (**D**), (**E**), (**F**) & (**H**) redrawn from Pilato & Binda (2010).

The *Sarascon* type

The two claws of each leg are very different in shape and size and, similarly to *Ramazzottius* type, express a variant of the *Hypsibius* type where the primary branches of the outer claws are extremely long and slender. In contrast to *Ramazzottius* type, however, there is no constriction between the basal tract and the primary branch. 2121 symmetry (Fig. 4E).

The *Macrobiotus* type (= *hufelandi*)

The two claws of each leg are very similar in size and shape. Curved primary and secondary branch of similar size unite in a rigid common tract. The common tract is separated by a septum from a poorly sclerified section and a thin and flexible stem at the base of the claw. 2112 symmetry (Fig. 4F).

The *Xerobiotus* type

The two claws of each leg are very similar in size and shape. Curved primary and secondary branch of similar size unite in a rigid common tract. In contrast to the *Macrobiotus* type there is no stem or poorly sclerified part. 2112 symmetry (Fig. 4G).

The *Hexapodibius* type

The two claws of each leg are very similar in size and shape. Primary and secondary branch are joined in a broad basal tract with a suture (dividing line) between primary and secondary branch. The primary branch is straight with only the tip slightly curved, while secondary branch is slightly curved in its entire length. Secondary branch may be reduced to a small spur or absent. 2121 symmetry (Fig. 4H).

The Eohypsibiidae type (= *Bertolanius* type)

The two claws of each leg are similar in size and shape. The primary and the secondary branch are joined rigidly and distinct claw sections (primary branch, secondary branch, basal section) can be distinguished that are separated by septa. 2121 symmetry (Fig. 4I).

4.3. Bucco-pharyngeal apparatus

Several features of the bucco-pharyngeal apparatus are important characters in identifying Eutardigrada (Fig. 5): The most obvious features are probably the structure and provision of the pharynx, e.g. the presence, number, size and shape of placoids and the structure of the buccal tube and whether it passes over into a flexible part pharyngeal tube or not (Fig. 5A). Other specific characters concern the shape of the stylet furca and the apophyses for the insertion of the stylet muscle (AISM, Fig. 5). The AISM are located at the front end of the buccal tube, below the buccal crown (Fig. 5). In genera with a ventral lamina, there is only a ventral apophysis, merged with the subsequent ventral lamina. The ventral lamina serves as reinforcement for the buccal tube (Fig. 5A, B). In genera without a ventral lamina, there is a ventral apophysis and a dorsal apophysis, the shape of which becomes visible only in lateral view (Fig. 5C, D).

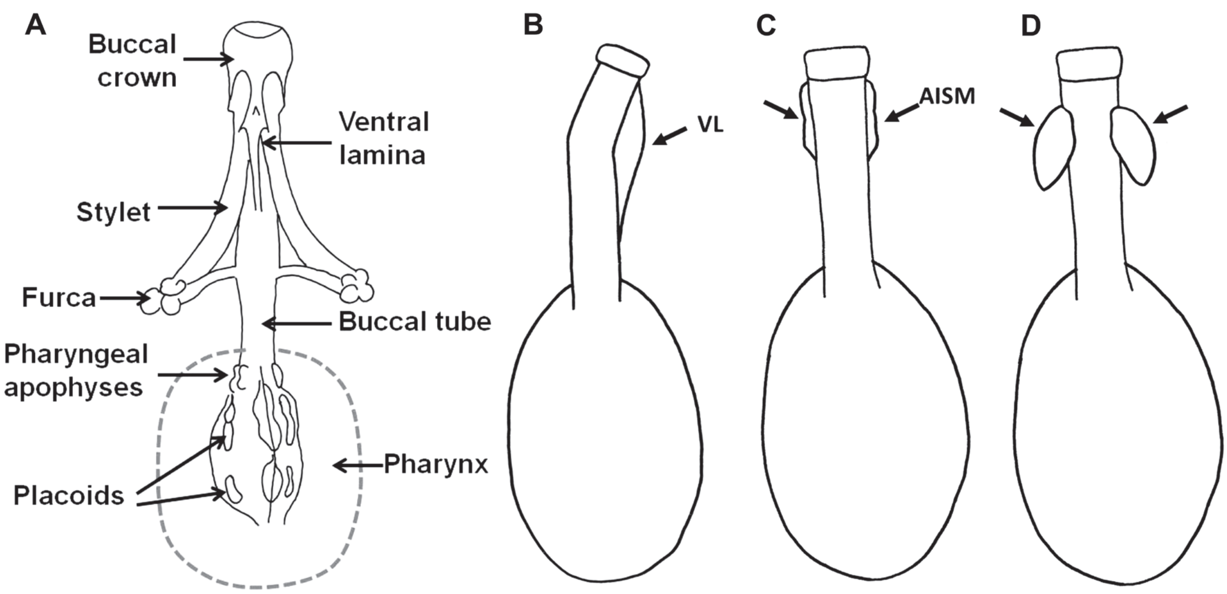


Figure 5. Bucco-pharyngeal apparatus of Eutardigrada. (**A**) General ventral view (**B**–**D**) Different types of bucco-pharyngeal strengthenings in lateral view. (**B**) with ventral lamina (**C**) with ridge shaped apophyses (**D**) with hook shaped apophyses; **VL**: ventral lamina, **AISM**: apophyses for the insertion of the stylet muscle.

5. Key to the genera

1a) two cephalic (cp) and six peribuccal papillae (ppi) present, *Milnesium* type claws (for details see claw description above), placoids never present .... *Milnesium*

1b) no cephalic and peribuccal papillae present 2

2a) all legs without claws, ventral lamina present .... *Apodibius*

2b) all legs without claws, instead legs I-III may have minute (ca. 2 µm) sclerified forcep-like structures (fls); ventral lamina absent .... *Necopinatum*

2c) legs IV without claws, legs I–III with claws of *Hexapodibius* type (Fig. 4H) .... *Hexapodibius*

2d) all legs with claws, claws normally developed 3

3a) flexible pharyngeal tube with spiral thickenings and of variable length subsequent to rigid buccal tube 4

3b) no flexible pharyngeal tube, only rigid buccal tube 10

4a) no or only one undivided placoid present 5

4b) more than one placoid present 6

5a) buccal tube barely longer than apophyses for the insertion of the stylet muscles (AISM), no stylet supports .... *Astatumen*

5b) buccal tube is clearly longer than apophyses for the insertion of the stylet muscles (AISM), slender stylet supports (ss) that are often hardly visible ...... *Itaquascon*

6a) thickening, often drop-shaped, between buccal tube and pharyngeal tube 7

6b) no such thickening 8

7a) always three macroplacoids in a straight row and a microplacoid and/or septulum may be present...... .... *Diphascon*

7b) always two macroplacoids in a curved row and a septulum .... *Pilatobius*

8a) pharyngeal tube longer than buccal tube, both long and rather narrow, typically shaped furca .... *Adropion*

8b) pharyngeal tube clearly shorter than buccal tube, furca of *Eohypsibius* type, claws of Eohybisibiidae type (Fig. 4I) .... *Eohypsibius*

8c) pharyngeal tube same length or slightly longer/shorter than buccal tube, both wide and rather short, furca not typically shaped, claws of *Hypsibius*-type (Fig. 4C) 9

9a) microplacoid present, pharyngeal tube same length or slightly longer than buccal tube, furca of *Mesocrista* type .... *Mesocrista*

9b) no microplacoid present, pharyngeal tube same length or slightly shorter than buccal tube, furca of *Platicrista* type .... *Platicrista*

10a) claws of *Macrobiotus* type 11

10b) claws of *Isohypsibius* type 13

10c) claws of *Hypsibius* type .... *Hypsibius*

10d) claws of *Ramazzottius* type .... *Ramazzottius*

10e) claws of *Xerobiotus* type .... *Xerobiotus*

10f) claws of *Sarascon* type .... *Sarascon*

10g) claws of the *Hexapodibius* type .... *Parhexapodibius*

11a) no peribuccal lamellae, often posterior bend in buccal tube, ten peribuccal papulae present .... *Minibiotus*

11b) peribuccal lamellae present, no posterior bend in buccal tube, no peribuccal papulae 12

12a) microplacoid close to rearmost macroplacoid; 2 or 3 macroplacoids .... *Macrobiotus/Mesobiotus*

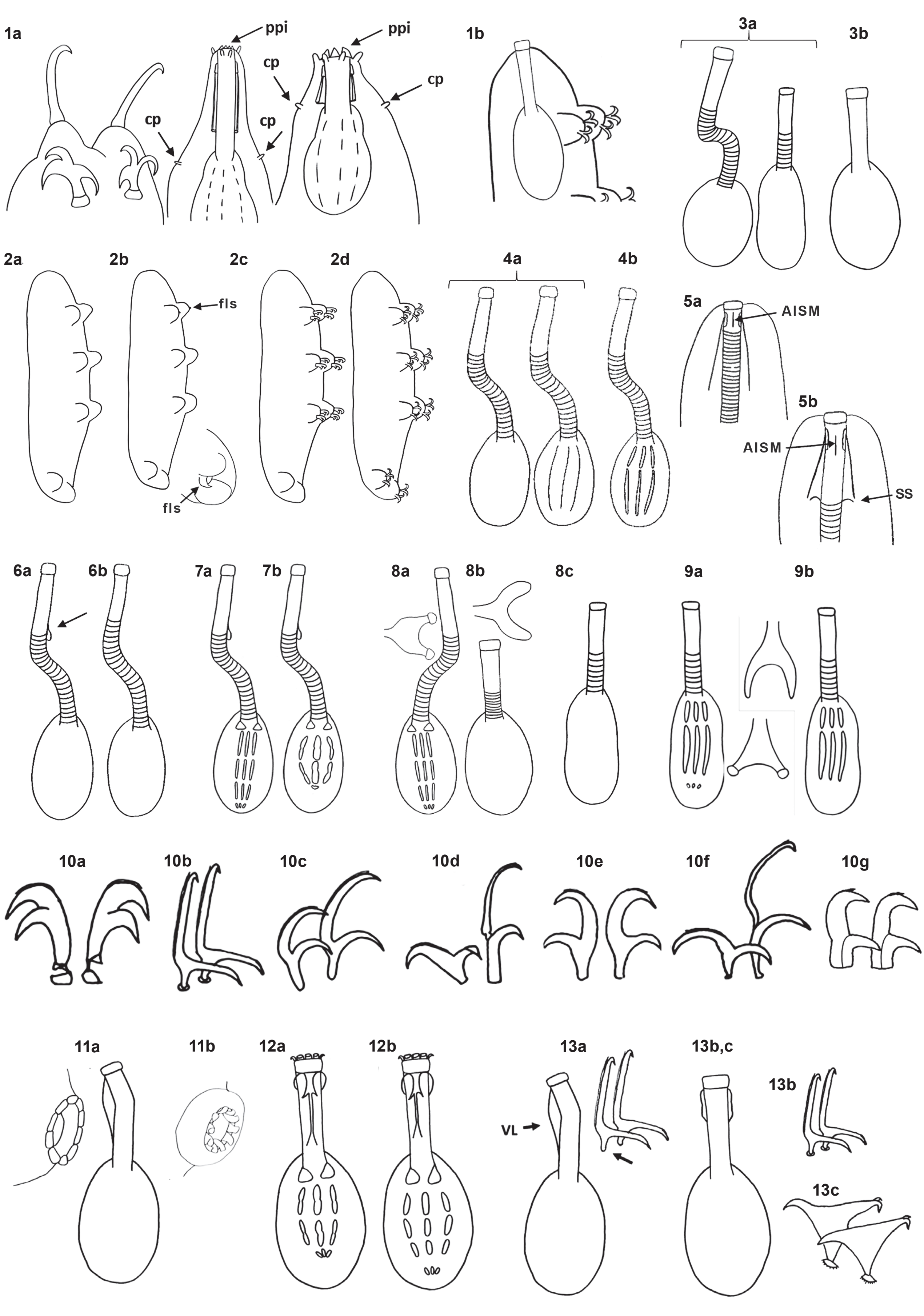
12b) microplacoid, if present clearly further than its own length away from the rearmost macroplacoid, 3 macroplacoids .... *Paramacrobiotus*

13a) ventral lamina present .... *Doryphoribius*

13b) ventral lamina absent .... *Isohypsibius*

13c) ventral lamina absent, fourth pair of legs with modified claws .... *Eremobiotus*

The genera printed in grey color have not yet been reported for European soils, but as they are very similar to other genera enlisted and have been reported in soils outside Europe, they were added to the key to allow comparison and prevent misidentification. The following figures are numbered according to key theses/antitheses which refer to these figures.


1a
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4a
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5a
AISM
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AISM
SS
6a
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7a
7b
8a
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8c
9a
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10a
10b
10c
10d
10e
10f
10g
11a
11b
12a
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6. Characterization of the genera and species reported from soil

AISM: Apohyses for the insertion of the stylet muscle

Adropion Pilato, 1987

Formerly subgenus of *Diphascon*, raised to genus level by Bertolani et al. (2014a)

Claws: *Hypsibius*-type
Lunules: absent
Furca: typically shaped
AISM: semilunar hooks
Peribuccal lamellae: absent
Peribuccal papulae: absent
Peribuccal lobes: 6

Bucco-pharyngeal apparatus: flexible pharyngeal tube subsequent to rigid buccal tube, no cuticular thickening between buccal tube and pharyngeal tube, pharyngeal tube longer than buccal tube, both long and rather narrow; ventral lamina absent; pharyngeal apophyses small or absent; macroplacoids present, microplacoid may be present, septulum may be present; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Diphascon scoticum* Murray, 1905
Currently 18 species and two subspecies belong to the genus. So far two species and one subspecies were reported from European soils.

1a) two macroplacoids present .... *A. belgicae*
1b) three macroplacoids present, microplacoid and septulum present or absent 2
2a) microplacoid present, septulum present .... *A. scoticum scoticum*
2b) microplacoid absent, septulum absent .... *A. prorsirostre*

Apodibius Dastych, 1983

Claws: absent on all legs
Lunules: absent
Furca: typically shaped
AISM: asymmetrical, due to presence of a ventral lamina
Peribuccal lamellae: absent
Peribuccal papulae: 6
Peribuccal lobes: 6
Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina present; pharyngeal apophyses present; macroplacoids present, septulum absent; stylet supports present
Eggs: unknown
Type species: *Apodibius confusus* Dastych, 1983
Currently three species belong to the genus. So far only *Apodibius confusus* was reported from European soils.

Apodibius confusus Dastych, 1983

Species-specific characters according to Dastych (1983) supplemented by Dastych (1988):
Body length 245–330 µm, original description was prepared from three possibly juvenile specimens.
Body color: white to yellow-white
Cuticle smooth
Eyes present
Anterior edge of mouth tube surrounded by narrow wreath of tiny roundish thickenings
Buccal cavity smooth (no ridges, no granulation)
Mouth tube with strengthening bar and apophyses
Pharynx: widely oval with two macroplacoids, no microplacoids, with first macroplacoid longer and restricted in middle

Astatumen Pilato, 1997

Claws: *Hypsibius*-type
Lunules: absent
Furca: *Astatumen*-type
AISM: shape of wide and flat ridges
Peribuccal lamellae: absent
Peribuccal papulae: probably absent
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: flexible pharyngeal tube subsequent to rigid buccal tube, no cuticular thickening between buccal tube and pharyngeal tube, pharyngeal tube longer than buccal tube, buccal tube barely longer than AISM; ventral lamina absent; pharyngeal apophyses absent; placoids absent or only one undivided, septulum absent; stylet supports absent
Eggs: smooth, laid in exuvia
Type species: *Itaquascon trinacriae* Arcidiacono, 1962
Currently four species belong to the genus. So far only *A. trinacriae* was reported from European soils.

Astatumen trinacriae (Arcidiacono, 1962)

Originally described as *Itaquascon trinacriae.*

Species-specific characters according to Arcidiacono (1962) and Dastych (1988):
Body length: up to 650 µm

Body color: white, occasionally with brown pigment
Cuticle smooth
Eyes absent
Pharynx: oval, 1 long undivided placoid
Cuticular bars at the base of inner claws (legs II-III), 'but these are sometimes poorly visible'

Diphascon Plate, 1888

Claws: *Hypsibius*-type
Lunules: absent
Furca: typically shaped
AISM: semilunar hooks
Peribuccal lamellae: absent
Peribuccal papulae: absent
Peribuccal lobes: 6

Bucco-pharyngeal apparatus: flexible pharyngeal tube subsequent to rigid buccal tube, cuticular thickening between buccal tube and pharyngeal tube - often drop-shaped, in *D. higginsi* small and flat-, pharyngeal tube longer than buccal tube, both long and rather narrow; ventral lamina absent; pharyngeal apophyses present; three macroplacoids present, microplacoid may be present, septulum may be present; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Diphascon chilenense* Plate, 1888
Currently 40 species belong to the genus. So far eight species were reported from European soils. *D. mariae* does not appear in this key, as it has two macroplacoids, but the key to the genera differentiates between *Pilatobius* and *Diphascon* by the number of placoids (three and two, respectively). Also we are uncertain about the details of the first descriptions regarding the presence of a microplacoid or a septulum (see discussion).

1a) septulum present 2
1b) septulum absent 4
2a) base of the claws is expanded and dentate .... *D. higginsi*
2b) base of the claws is not dentate 3
3a) buccal tube very narrow (1 µm), macroplacoid row about 50 % of the length of the buccal tube .... *D. alpinum*
3b) buccal tube narrow (1.2–1.8 µm), macroplacoid row about 65 % of the length of the buccal tube .... *D. pingue group*
4a) base of the claws is expanded and dentate 5
4b) base of the claws is not dentate 6
5a) claws longer: ratio of posterior claw of leg IV to buccopharyngeal tube ca. 62 % ..... *D. nobilei*
5b) claws shorter: ratio of posterior claw of leg IV to buccopharyngeal tube ca. 41–42 % .... *D. platyungue*
6a) buccal tube very narrow (1 µm), macroplacoids very short, in the shape of granules or short rounded rods .... *D. stappersi*
6b) buccal tube broader (2.7 µm), macroplacoids longer, rod-shaped .... *D. nelsonae*

For more details on the *D. pingue* group, which is species rich and rather difficult to discern, see Pilato & Binda (1999) and subsequent descriptions of new species from the group.

Doryphoribius Pilato, 1969

Claws: *Isohypsibius*-type
Lunules: reduced or absent
Furca: typically shaped
AISM: asymmetrical, due to presence of a ventral lamina
Peribuccal lamellae: absent
Peribuccal papulae: 6
Peribuccal lobes: 6

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina present; pharyngeal apophyses present; two or three macroplacoids present, microplacoid probably absent, septulum absent; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Hypsibius doryphorus* Binda & Pilato, 1969
Currently 38 species belong to the genus. So far three species were reported from European soils.

1a) cuticular gibbosities present on legs, reticular design at dorsal cuticle .... *D. flavus*
1b) no cuticular gibbosities present on legs 2
2a) buccal cavity with numerous teeth, one large dorsal median tooth, buccal tube >3.0 µm wide .... *D. macrodon*
2b) buccal cavity without teeth, buccal tube <3.0 µm wide .... *D. doryphorus*

For a detailed key on the genus *Doyphoribius* see Michalczyk & Kaczmarek (2010).

Eremobiotus Biserov, 1992

Claws: *Isohypsibius*-type with modified claws on the fourth pair of legs
Lunules: present
Furca: typically shaped
AISM: crest-shaped, according to Biserov (1992)
Peribuccal lamellae: absent
Peribuccal papulae: 6
Peribuccal lobes: 6

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina absent; pharyngeal apophyses present; two macroplacoids present, microplacoid absent, septulum absent (Lisi et al. 2016); stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Eremobiotus ovezovae* Biserov, 1992
Currently three species belong to the genus, for which Lisi et al. (2016) published a diagnostic table. So far, only *E. alicatai* was reported from European soils.

***Eremobiotus alicatai* (Binda, 1969)**
Originally described as *Isohypsibius alicatai* Binda, 1969

Species-specific characters according to Bertolani (1982), Ramazzotti & Maucci (1983) and Dastych (1988):
Body length: up to 300 µm
Body color: white
Cuticle smooth
Eyes absent
Mouth opening: antero-ventrally, mouth tube short
Pharynx: round to oval (1.1–1.5 longer than broad) with apophyses, two macroplacoids, with first macroplacoid longer and restricted in middle, no microplacoids
Cuticular bars long and thin, at the base of inner claws (legs I-III), bars show tiny teeth at edges
Lunules: dentated

Hexapodibius Pilato, 1969

Claws: *Hexapodibius*-type, no claws on the fourth pair of legs
Lunules: absent
Furca: typically shaped
AISM: asymmetrical, due to presence of a ventral lamina
Peribuccal lamellae: absent
Peribuccal papulae: 6
Peribuccal lobes: 6

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina present; pharyngeal apophyses present; two or three macroplacoids present, microplacoid absent, septulum absent (Pilato 1969, Bernard 1977, Pilato & Binda 2003); stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Hexapodibius micronyx* Pilato, 1969
Currently six species belong to the genus. For differential diagnosis of all six species see Pilato & Binda (2003). So far four species were reported from European soils.

1a) two macroplacoids present .... *H. christenberryae*
1b) three macroplacoids present 2
2a) adult animal larger (up to 341 µm), buccal tube wide (3.5–6 µm) .... *H. micronyx*
2b) adult animal smaller (about 220–235 µm), buccal tube narrower (about 2.3–2.9 µm) 3
3a) legs I – III with dorsal gibbosity .... *H. pseudomicronyx*
3b) legs I – III without dorsal gibbosity.......... *H. bindae*

Hypsibius Ehrenberg, 1848

Claws: *Hypsibius*-type
Lunules: absent or present but difficult to see
Furca: typically shaped
AISM: hook shaped
Peribuccal lamellae: absent
Peribuccal papulae: absent
Peribuccal lobes: 6

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina absent; pharyngeal apophyses present; two or three macroplacoids present, microplacoid present or absent, septulum present or absent; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Macrobiotus dujardini* Doyère, 1840
Currently 42 species belong to the genus. So far five species were reported from European soils, of which all contained only two macroplacoids.

1a) cuticle sculptured with small tubercles (ca. 1 µm) .... *H. pradellii*
1b) cuticle smooth.. 2
2a) septulum present .... *H. dujardini*
2b) septulum and microplacoids absent 3
3a) claws small, with outer claws of 4th pair of legs 7 µm long (in a 150 µm long specimen), which is 34–38 % of its buccal tube length (Bertolani et al. 1987) .... *H. pedrottii*

3b) claws larger, with outer claws of 4th pair of legs 15–18 µm long (in a 300 µm long specimen), which is ca. 70 % of its buccal tube length (Dastych 1988) 4
4a) macroplacoids longer: 1st is 4–5 µm long, and ratio 1st / 2nd macropl. >1.4 .... *H. convergens*
4b) macroplacoids shorter: 1st is 2–3 µm long, and ratio 1st / 2nd macropl. <1.4 .... *H. pallidus*

Isohypsibius Thulin, 1928

Claws: *Isohypsibius*-type
Lunules: present or absent
Furca: typically shaped
AISM: ridge shaped
Peribuccal lamellae: absent
Peribuccal papulae: absent
Peribuccal lobes: 6

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina absent; pharyngeal apophyses present; two or three macroplacoids present, microplacoid present or absent, septulum absent; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Isohypsibius prosostomus* Thulin, 1928
Currently 129 species belong to the genus. So far five species and one species group were reported from European soils.

1a) three macroplacoids present, microplacoid may be present 2
1b) two macroplacoids present, microplacoid absent 4
2a) massive body with short legs, up to 400–500 µm long; macroplacoids of increasing size and in the shape of short rods, microplacoid always absent; internal diameter of buccal tube about 1 µm .... *I. asper*
2b) more slender body, macroplacoids in the shape of (oval) granules, microplacoid usually present; internal diameter of buccal tube about 3 µm 3
3a) mouth-opening terminally located; first and second macroplacoid about the same length, third longer than first and second together, macroplacoids in the shape of rather elongated granules, first macroplacoid in contact with apophyses, microplacoid always present; cuticular bars on legs I – III always present .... *I. prosostomus*
3b) mouth-opening anterio-ventrally located; macroplacoids of increasing size and in the shape of oval granules, microplacoid is small may be present or absent; cuticular bars on legs I-III might be absent .... *I. schaudinni*
4a) no gibbosities on body, placoids in the shape of granules, first constricted .... *I. dastychi*
4b) body with gibbosities 5
5a) large number of gibbosities in 20 dorsal transverse rows .... *I. tubercoloides*
5b) 10 or less dorsal transverse rows of gibbosities .... *tuberculatus* group: *I. mihelcici*, *I. sattleri*, *I. franzi*, *I. lunulatus*, *I. ronsisvallei*

Regarding the *tuberculatus* group it is unkown which exact species were accounted as such in other studies. As the gibbosities, and especially their shape or number, are difficult to identify in embedded animals we decided to summarize all species with gibbosities, with the exception of *I. tubercoloides,* which may be clearly discerned from all other species by having 20 rows of gibbosities compared to a maximum of ten. A key considering all species of the *tuberculatus* group together with reliable characters is unfortunately still missing.

Itaquascon de Barros, 1939

Claws: *Hypsibius*-type
Lunules: absent
Furca: *Itaquascon*-type
AISM: wide and flat ridges
Peribuccal lamellae: absent
Peribuccal papulae: probably absent
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: flexible pharyngeal tube subsequent to rigid buccal tube, no cuticular thickening between buccal and pharyngeal tube, both long and rather narrow, buccal tube considerably longer than AISM; ventral lamina absent; pharyngeal apophyses absent; placoids absent or only one undivided present, septulum absent; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Itaquascon umbellinae* de Barros, 1939
Currently twelve species belong to the genus. So far, no species were reported from European soils, but as the genus is very similar to *Astatumen* it was added to prevent misinterpretation. Five species were reported from soils worldwide.

Macrobiotus C.A.S. Schultze, 1834
Mesobiotus Vecchi, Cesari, Bertolani, Jönsson, Rebecchi & Guidetti, 2016

Vecchi et al (2016) erected the new genus *Mesobiotus* including the former *Macrobiotus harmsworthi* group and the *Macrobiotus furciger* group. As the genera are phenotypically very similar, we decided to make one key for both *Macrobiotus* and *Mesobiotus*.

Claws*: Macrobiotus/hufelandi*-type
Lunules: present
Furca: typically shaped
AISM: asymmetrical, due to presence of a ventral lamina
Peribuccal lamellae: 10
Peribuccal papulae: absent
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina present; pharyngeal apophyses present; two or three macroplacoids present, microplacoid present or absent, if present close to the macroplacoids, septulum absent; stylet supports present
Eggs: laid freely, processes/ornamentation on egg shells
Type species: *Macrobiotus hufelandi* C. A. S. Schultze, 1834 / *Macrobiotus harmsworthi* Murray, 1907
Currently 100 species belong to the genus *Macrobiotus*. So far three species and one species group were reported from European soils. Currently 58 species belong to the genus *Mesobiotus* and species from one group (*harmsworthi*) were reported from European soils.
As the different species of both *Macrobiotus hufelandi* and *Mesobiotus harmsworthi* group are very difficult to distinguish without eggs, the present identification key will not go into further detail, but see Bertolani & Rebecchi (1993) for a diagnostic key to the species of the *Macrobiotus hufelandi* group.

1a) two macroplacoids and microplacoid present......... 2
1b) three macroplacoids and microplacoid present 4
2a) body smooth and without pores; lunules on all legs large and strongly dentate; macroplacoids of about equal length .... *Macrobiotus echinogenitus*
2b) body smooth with pores; lunules on all legs small or of medium size with more or less crenate or dentate margin, at least on leg IV; first macroplacoid longer than second 3
3a) cuticle with big, pit-like pores; lunules well developed with twelve long teeth on all legs .... *Macrobiotus crenulatus*
3b) cuticle with small, round pores; lunules small or of medium size, smooth or at least on leg IV lightly crenate/dentate .... *Macrobiotus hufelandi* group
4a) buccal tube straight; eyespots usually present; macroplacoids in the shape of short rounded rods; length almost equal (third may be slightly longer), row of placoids in a bent arch; large microplacoid close to the third macroplacoid .... *Mesobiotus harmsworthi* group
4b) buccal tube curved right after the buccal opening, then straight; eyespots absent; macroplacoids of increasing size .... *Macrobiotus terricola*

Mesocrista Pilato, 1987

Claws: *Hypsibius*-type
Lunules: absent
Furca: *Mesocrista*-type
AISM: wide and flat ridges
Peribuccal lamellae: absent
Peribuccal papulae: probably present
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: flexible pharyngeal tube subsequent to rigid buccal tube, no cuticular thickening between buccal and pharyngeal tube, both rather short and wide, buccal tube considerably longer than AISM, pharyngeal tube same length or slightly longer than buccal tube; ventral lamina absent; pharyngeal apophyses absent; two macroplacoids present, microplacoid present, septulum absent; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Diphascon spitzbergense* Richters, 1903
Currently two species belong to the genus. So far, only *M. spitzbergensis* was reported from European soils.

Mesocrista spitzbergensis (Richters, 1903)
Originally described as *Diphascon spitzbergense* Richters, 1903

Species-specific characters according to Richters (1903) supplemented by Ramazzotti & Maucci (1983) and Dastych (1988):
Body length: up to 650 µm
Body color: white
Cuticle smooth
Eyes absent
Mouth tube wide
Pharynx: oval, almost twice as long as broad, two long macroplacoids, with 2nd macroplacoid 2–3x longer than second, microplacoids present and distinct

Cuticular bars: small and difficult to see, at the base of inner claws (legs I-III), and between bases of inner and outer claws

Milnesium Doyère, 1840

Claws*: Milnesium*-type
Lunules: absent
Furca: *Milnesium*-type
AISM: very short and flat ridges
Peribuccal lamellae: 4 or 6
Peribuccal papulae: absent
Peribuccal lobes: absent

Head with two cephalic sensory papillae and six peribuccal papillae
Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube, broad buccal tube; ventral lamina absent; pharyngeal apophyses absent; placoids absent; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Milnesium tardigradum* Doyère, 1840
Due to the unique morphology of *Milnesium*, the comparably small morphological diversity within the genus was not taken seriously for 150 years. Until a second species, *Milnesium tetralamellatum* Binda & Pilato 1990, was described, all records of *Milnesium* were assessed to *M. tardigradum*. Currently 34 species belong to the genus. So far, only two species were reported from European soils, *M. tardigradum* and *M. asiaticum* Tumanov, 2006. The records of the first may be considered exact genus determinations, but might belong to another species than *M. tardigradum* sensu stricto.
Discrimination of the 34 *Milnesium* species is difficult due to the small number of distinguishing characters, which often are difficult to discern, like for example the number of small accessory points on the claws' main and secondary branches. Because of these difficulties and also due to the abovementioned uncertainties (what really lays hidden behind the soil records of *M. tardigradum*) we decided to end here at the genus level. For those keen to go further to the species level, we suggest to consult Michalczyk et al. (2012) who present a key to the species of *Milnesium*.

Minibiotus R.O. Schuster, 1980

Claws*: Macrobiotus/hufelandi*-type
Lunules: present
Furca: typically shaped
AISM: asymmetrical, due to presence of a ventral lamina
Peribuccal lamellae: absent
Peribuccal papulae: 10
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina present; pharyngeal apophyses present; two or three macroplacoids present, microplacoids present or absent (e.g. Binda & Pilato 1995, Meyer & Domingue 2011), septulum absent; stylet supports present
Eggs: laid freely, processes/ornamentation on egg shells
Type species: *Macrobiotus intermedius* Plate, 1888
Currently 47 species belong to the genus. So far, only *M. intermedius* was reported from European soils, but these records likely concern more species.

Minibiotus intermedius **(Plate, 1888)**
Originally described as *Macrobiotus intermedius*

Species-specific characters according to Ramazzotti & Maucci (1983) and Dastych (1988):
Body length: up to 350 µm, more often smaller
Body color: white, sometimes with greyish-brown pigment
Cuticle: without pores
Eyes present, large and in a rather posterior position, or small and indistinct (Ramazzotti & Maucci 1983)
Mouth opening anterio-ventrally
Mouth tube: only 1 µm in diameter
Pharynx: almost spherical with large apophyses, three roundish macroplacoids, equal in length, microplacoid present
Egg processes: characteristic, each process looking like 'the head of a screw enclosed in a transparent capsule' (Ramazzotti & Maucci 1983)

Necopinatum Ramazzotti & Maucci, 1983

Claws: absent or severely reduced to minute (ca. 2 µm) sclerified structures, in the shape of small forceps that may occur on leg I and also on legs II and III
Legs: short, terminally with two roundish lobes
Lunules: absent
Furca: typically shaped
AISM: symmetrical in the shape of ridges
Peribuccal lamellae: absent
Peribuccal papulae: not known
Peribuccal lobes: not known

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina absent; pharyngeal apophyses present; two macroplacoids present, microplacoid absent, septulum absent; stylet supports present.
Eggs: smooth, laid in the exuvia (Bertolani et al. 2014a)
Type species: *Necopinatum mirabile* Pilato 1971
Currently one species, *N. mirabile*, belongs to the genus and was reported from European soils. The phylogenetic position of *Necopinatum* is still unclear.

Necopinatum mirabile **Pilato, 1971**

Species-specific characters according to Bertolani et al. (1987, 2014a), supplemented by Ramazzotti & Maucci (1983) and Pilato & Binda (2010).
Body length up to 210 µm
Body color: white
Cuticle smooth
Eyes absent
Buccal tube: short and rigid, ends dorsally with a thick drop-like structure (Pilato & Binda 2010)
Pharynx: widely oval with two macroplacoids, no microplacoids, with first macroplacoid longer than second
A rare species, first description from moss at the volcano Etna in Sicily, Italy, second finding from Italian soil samples by Bertolani et al. (1987).
Future findings should also consider molecular analyses in order to clarify the phylogenetic position of the genus and its only species.

Parhexapodibius **Pilato, 1969**

Claws: Hexapodibius-type
Lunules: absent
Furca: typically shaped
AISM: asymmetrical, due to presence of a ventral lamina
Peribuccal lamellae: absent
Peribuccal papulae: 6
Peribuccal lobes: 6

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina present; pharyngeal apophyses present; two or three macroplacoids present, microplacoids present or absent, septulum absent; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Parhexapodibius lagrecai* Binda & Pilato, 1969

Currently five species belong to the genus. So far, two species were reported from European soils.

1a) claws of 4th pair of legs reduced to a single doubleclaw per leg, macroplacoids ellipsoidal-shaped and slender .... *P. pilatoi*
1b) claws of 4th pair of legs slightly smaller but otherwise like legs I-III, macroplacoids rod-shaped and wide …... *P. ramazzottii*

Parhexapodibius pilatoi **Bernard, 1977**

Species-specific characters according to Bernard (1977), supplemented by Ramazzotti & Maucci (1983)
Body length up to 350 µm
Body color: white or light yellow
Cuticle smooth
Eyes absent, only in the holotype they are present (Bernard 1977)
Buccal tube: narrow (width only 6–8 % of tube length)
Pharynx: widely oval with three macroplacoids, and no microplacoids. Shape and size of the macroplacoids are given differently: While Bernard (1977) describes the macroplacoids with 1st and 2nd about equal in length and both ellipsoidal, the 3rd longer (1.3 times as long), Ramazzotti & Maucci (1983) state that the 1st macroplacoid is a roundish granule, while only the 2nd and 3rd are slightly elongated. Both agree, however, that the 3rd macroplacoid is longer than the 2nd.
Claws: The claws of 4th pair of legs are reduced to a single double claw per leg.

Parhexapodibius ramazzottii **Manicardi & Bertolani, 1987**

Species-specific characters according to Manicardi & Bertolani (1987).
Body length up to 270 µm
Body color: white
Cuticle smooth
Eyes present
Buccal tube: narrow (width only 9 % of tube length)
Pharynx: widely oval (length to width ratio: 1.25) with well developed apophyses, three rod-shaped macroplacoids, and no microplacoids. 1st and 2nd of similar length, the 3rd longer (1.2 times as long).
Claws: The claws of the 4th pair of legs are slightly smaller, external claws being 6.4 µm

instead of 7 µm in the holotype (body length: 264 µm), but otherwise like the claws of the first three pairs of legs.

Paramacrobiotus Guidetti, Schill, Bertolani, Dandekar & Wolf, 2009

Claws*: Macrobiotus/ hufelandi*-type
Lunules: present
Furca: typically shaped
AISM: asymmetrical, due to presence of a ventral lamina
Peribuccal lamellae: 10
Peribuccal papulae: absent
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina present; pharyngeal apophyses present; three macroplacoids present, microplacoid present or absent, if present further away from macroplacoids than its own length; stylet supports present
Eggs: laid freely, processes/ornamentation on egg shells
Type species: *Macrobiotus richtersi* Murray, 1911
Currently 33 species belong to the genus. So far, only *Paramacrobiotus richtersi* was reported from European soils. It is very likely that the findings include other species, as the reliable identification of species within this genus, like in *Macrobiotus* and *Mesobiotus*, requires observations of eggs.

***Paramacrobiotus richtersi* (Murray, 1911)**
Originally described as *Macrobiotus richtersi*.

Species-specific characters according to Ramazzotti & Maucci (1983) and Dastych (1988):
Body length: up to 1000 µm, often smaller than 800 µm
Body color: white, older specimens often with brown pigment
Cuticle: smooth, without pores
Eyes usually absent, seldom present
Mouth opening anterio-ventrally
Mouth tube wide, diameter at least 1/5 of tube length
Pharynx: oval with apophyses, three macroplacoids, 1st and 2nd equal in length, 3rd longest, microplacoid present, distance to nearest macroplacoid is longer than length of microplacoid
Eggs free with conical processes, often with flattened tips, egg diameter (inclusive processes 80–100 µm), surface of processes netlike (0.5 µm meshes), egg surface between processes with coarse-meshed structures (crown of unsculptured areolae around each process).

A wide spread species, common in moss and soil.

Pilatobius Bertolani, Guidetti, Marchioro, Altiero, Rebecchi & Cesari, 2014

Claws*: Hypsibius*-type
Lunules: absent, rarely present
Furca: typically shaped
AISM: semilunar hooks
Peribuccal lamellae: absent
Peribuccal papulae: absent
Peribuccal lobes: 6

Bucco-pharyngeal apparatus: flexible pharyngeal tube subsequent to rigid buccal tube, cuticular thickening between buccal tube and pharyngeal tube, often drop-shaped, pharyngeal tube longer than buccal tube, both long and rather narrow; ventral lamina absent; pharyngeal apophyses present; always two macroplacoids and a septulum present, microplacoid may be present; stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Diphascon bullatum* Murray, 1905
Currently 23 species belong to the genus. So far, six species were reported from European soils.

1a) body with gibbosities 2
1b) body without gibbosities 3
2a) cuticle with polygonal sculpture, gibbosities always on the whole dorsum .... *P. patanei*
2b) cuticle with sculpture of rounded granules, rows of gibbosities sometimes reduced to two caudal rows .... *P. bullatus*
3a) cuticle smooth 4
3b) cuticle with granulation 5
4a) smaller claws, primary branch of leg IV about 10 µm .... *P. brevipes*
4b) bigger claws, primary branch of leg IV about 13 µm .... *P. secchii*
5a) uniform granulation on dorsum from cephalic to caudal end .... *P. granifer*
5b) extremely fine granulation on cuticle, in caudal region larger and more distinct .... *P. rugosus*

Platicrista Pilato, 1987

Claws: *Hypsibius*-type
Lunules: generally absent (reported only in hind legs of one species)
Furca: *Platicrista*-type
AISM: wide and flat ridges
Peribuccal lamellae: absent
Peribuccal papulae: probably present
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: flexible pharyngeal tube subsequent to rigid buccal tube, no cuticular thickening between buccal and pharyngeal tube, both rather short and wide, buccal tube considerably longer than AISM, pharyngeal tube same length or slightly shorter than buccal tube; ventral lamina absent; pharyngeal apophyses absent; macroplacoids present, microplacoid absent, septulum absent (Pilato 1987); stylet supports present
Eggs: smooth, laid in exuvia
Type species: *Diphascon angustatum* Murray, 1905
Currently six species belong to the genus. So far, no species were reported from European soils, but as the genus is very similar to *Mesocrista* it was added to prevent misinterpretation. Two species were reported in soils worldwide.

Ramazzottius Binda & Pilato, 1986

Claws*: Ramazzottius*-type
Lunules: present, very small and reduced, or absent
Furca: typically shaped
AISM: blunt hooks
Peribuccal lamellae: absent
Peribuccal papulae: absent
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina absent; pharyngeal apophyses present; macroplacoids present, microplacoids absent, septulum absent (Binda & Pilato 1986); stylet supports present
Eggs: laid freely, processes/ornamentation on egg shells
Type species: *Macrobiotus oberhaeuseri* Doyère, 1840
Currently 27 species belong to the genus. So far, only *R. oberhaeuseri* was reported from European soils.

Ramazzottius oberhaeuseri (Doyère, 1840)

Originally described as *Macrobiotus oberhaeuseri*.

Species-specific characters according to Ramazzotti & Maucci (1983) and Dastych (1988):
- Body length: up to 500 µm, but usually smaller than 300 µm
- Body color: juveniles white, adults pigmented light to reddish brown, pigment usually arranged in longitudinal bands
- Cuticle: with small regular granulation (1.0–1.5 µm), clearest posteriorly, but some completely smooth
- Eyes absent, but two elliptical organs are present in their position, a generic character (Pilato & Binda 2010)
- Mouth tube narrow, inner diameter only 1 µm
- Pharynx: round to oval (1.3–1.8x longer than broad), two round macroplacoids, with 1st only slightly longer, apophyses large, microplacoids absent
- Egg processes: hemispheric, variable in shape

Sarascon Guil, Rodrigo & Machordom, 2014

Claws*:* external claws of the *Hypsibius* type with extremely long and slender primary branch; internal claws of the *Isohypsibius* type
Lunules: present
Furca: *Itaquascon*-type
AISM: flat ridges
Peribuccal lamellae: absent
Peribuccal papulae: absent
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina absent; pharyngeal apophyses absent; placoids absent, septulum absent; stylet support present
Eggs: unknown
Type species: *Sarascon hortensiae* Guil, Rodrigo & Machordom, 2014
Currently only one species, *Sarascon hortensiae,* belongs to the genus, which was described from soil samples in Spain.

Sarascon hortensiae Guil, Rodrigo & Machordom, 2014

Species-specific characters according to Guil et al. (2014):
- Body length: up to 290 µm
- Body color: white

Cuticle: smooth without pores or other structure
Eyes absent
Mouth tube narrow, inner diameter ca. 2 µm
Pharynx: lacking apophyses and placoids

Xerobiotus Bertolani & Biserov, 1996

Claws: *Xerobiotus*-type, cuticular bars absent (Pilato et al. 2011)
Lunules: present only on 4th pair of legs
Furca: typically shaped
AISM: asymmetrical, due to presence of a ventral lamina
Peribuccal lamellae: 10
Peribuccal papulae: absent
Peribuccal lobes: absent

Bucco-pharyngeal apparatus: no flexible pharyngeal tube subsequent to rigid buccal tube; ventral lamina present; pharyngeal apophyses present; two macroplacoids present, microplacoid present, septulum absent (Pilato et al. 2011); stylet supports present
Eggs: laid freely, processes/ornamentation on egg shells
Type species: *Macrobiotus pseudohufelandi* Iharos, 1966
Currently three species belong to the genus, for which Pilato et al. (2011) published a diagnostic table.

The two *Xerobiotus* species, *X. pseudohufelandi* and *X. xerophilus*, that are presently known to occur in European soils are especially difficult to distinguish from each other. Dastych (1988) giving short descriptions of the species, by then *Macrobiotus pseudohufelandi* and *Parhexapodibius xerophilus,* had no need to directly compare the characters of the two species since the two species then belonged to different genera. The only obvious differences in his descriptions are the claw type: with *M. pseudohufelandi* having claws of the *Macrobiotus type* and *P. xerophilus* of the by then *Calohypsibius* type (with a broad basal stem, but see Dastych & Alberti 1990). *Xerobiotus* and the respective claw type, an in-between of the two above claw types, was not described by then. Introducing the new genus, Bertolani and Biserov (1996) give one distinguishing feature, when they discuss the generally reduced size of the claws within the genus:

1a) claws of 4th pair of legs are largest .... *X. pseudohufelandi*
1b) claws of 4th pair of legs are smallest .... *X. xerophilus*

Xerobiotus pseudohufelandi **(Iharos, 1966)**
Originally described as *Macrobiotus pseudohufelandi*.

Species-specific characters according to Ramazzotti & Maucci (1983) and Dastych (1988):
Body length: up to 500 µm, more often smaller than 400 µm
Body color: white
Cuticle: smooth
Eyes present
Mouth tube 4 µm wide, mouth opening surrounded by lamellae
Pharynx: oval with large apophyses, two macroplacoids, 1st macroplacoid being constricted and 1.5–2.0x longer than 2nd, microplacoid present
Egg processes: conical with flattened tips

Xerobiotus xerophilus **(Dastych, 1978)**
Originally described as *Hexapodibius xerophilus*.

Species-specific characters according to Ramazzotti & Maucci (1983) and Dastych (1988):
Body length: up to 500 µm
Body color: white
Cuticle: smooth
Eyes present, usually large
Mouth tube 4 µm wide, with well developed strengthening bar.
Pharynx: oval, with large apophyses, two macroplacoids, 1st macroplacoid being constricted and 1.5–2.0x longer than 2nd, microplacoid present

7. Discussion

As studies on tardigrades in soils are still underrepresented, the current list and thus the key cannot be considered complete. In some cases this key will not lead to a result, or uncertainties will remain.We then recommend considering the publications of Pilato & Binda (2010) and Degma (2010) on genus level and additional species keys as given above.

The present key focuses on strict soil species. It may be questioned, if terrestric habitats, i.e. soil, leaf litter, lichens and moss are really separable in terms of tardigrades. From a soil biologist view, soils end with the AH-layer (Bardgett 2005) and during sampling all loose and undecomposed organic material (fresh litter) as well as moss and lichens are removed. Fresh litter of course, is a species rich habitat for tardigrades as is moss and lichen. When these substrates fall dry some of the species will probably migrate downwards into the soil and may then be considered as litter and soil species. But this has not been investigated yet, nor do we know which species are restricted to the litter layer. We accordingly decided to list only those species that derive from soil examinations. Still we cannot exclude in all cases, e.g. Mihelcic (1949, 1958) that leaf litter was included in the soil sample. However, examinations on pure leaf litter, e.g. Mihelcic (1965), Guidetti et al. (1999) and Guidetti & Bertolani (2001) were not included in the present study.

In the last years there have been many revisions of tardigrade taxonomy. It seems that within this process some irregularities have occured, which complicate the preparation of identification keys. For example, Bertolani et al. (2014a) split the genus *Diphascon* and established the new genus *Pilatobius*. Bertolani et al. (2014a) define the genus *Diphascon* with always three macroplacoids, but e.g. *Diphascon mariae* has only two macroplacoids and is still associated within the genus *Diphascon*. On the other hand, *D. mariae* having a microplacoid but according to Ramazzotti and Maucci (1983) no septulum, does also not fit into the new genus *Pilatobius*, which requires not only two macroplacoids but also a septulum. If still existing, the type material may be informative to review whether the microplacoid of *D. mariae* might as well be a septulum. At the time of the description of the species the septulum was often confused with the microplacoid. The best example is *Hypsibius dujardini*, for many years described with a microplacoid but in reality having a septulum. Due to these complications we decided to exclude *D. mariae* from the key.

Claw type and symmetry are both important features for the identification of eutardigrade genera, but they also bear some difficulties. For claws of the Eohypsibiidae-type Pilato & Binda (2010) stated that the internal claws have the tendency to rotate on their base by 180° thus ‘imitating’ a symmetrical 2-1-1-2 arrangement. During our own work with embedded tardigrades we made similar experiences: Some specimens contradictorily seemed to have both, claws of the *Hypsibius*-type, but also cuticular thickenings. Additionally, some of the claws did not look the same even on the same pair of legs. Another interpretation for these animals seemed to be claws in the shape of *Bertolanius*-type, only that they did not show the characteristic separation of the three sections (Fig. 3I). With the assumption that possibly the branches of the claws tend to be twisted (Fig. 6), we were able to identify the claws as *Isohypsibius*-type. Indeed, going through literature we found various examples of *Isohypsibius* drawings, where the claws of each leg were drawn differently, some with both branches pointing in the same direction and some pointing in different directions (e.g. *Isohypsibius* species in Dastych, 1988). Tardigrade novices should thus keep in mind that single claw branches may be twisted during tardigrade preparation and that it is appropriate to check all the claws of a specimen before deciding on the claw type.

Genera expressing reduced or even lacking claws have evolved independently and seem to be especially frequent in soil habitats (e.g. Dastych 1983, Bertolani & Biserov 1996). Hohberg et al. (2011) found large quantities of *Apodibius confusus*, accompanied by *Hexapodibius* cf. *micronyx*, in soil and therefore conclude that claws are not needed for survival and reproduction in soil habitats.

While the presence or absence of eyespots is a feature frequently used for identification on species level, some inconsistencies remain. There are reports of specimens of the same species, some with and some without eyespots, e.g. *Paramacrobiotus richtersi*, *Pilatobius bullatus* as well as several species of *Hexapodibius* (see Dastych, 1988). Also, in identification literature terms such as ‘eyes usually present’ are frequent, e.g. *Hypsibius dujardini* and *Hypsibius pallidus* in Ramazzotti and Maucci (1983). While these findings may as well be due to misinterpretation or misidentification, there has not been much research about the topic. A general investigation is missing, if in these cases really no eyes are present, or if the eyes are just lacking pigment (personal communication with Hartmut Greven, University Düsseldorf, Germany). Due to this unresolved issue, we refrained from using the presence and absence of eyes as a determination character.

We hope that this illustrated key will serve as a helpful tool both, for young tardigradologists and for soil zoologist not yet experienced with tardigrades and that it may lead to tardigrades being more often considered in soil biological investigations. With every new record the list of tardigrade species known from European soils will naturally grow larger. The usability of the key presented here will thus depend on regular updates derived by information and suggestions received from tardigradologists and soil zoologists. We explicitly encourage amendments to and improvement of the present key and are looking forward to receiving new records.

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