

Bergtrollus dzimbowski gen. n., sp. n.,
a remarkable new tardigrade genus and species
from the nival zone of the Lyngen Alps, Norway
(Tardigrada: Milnesiidae)

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(with 51 figures)

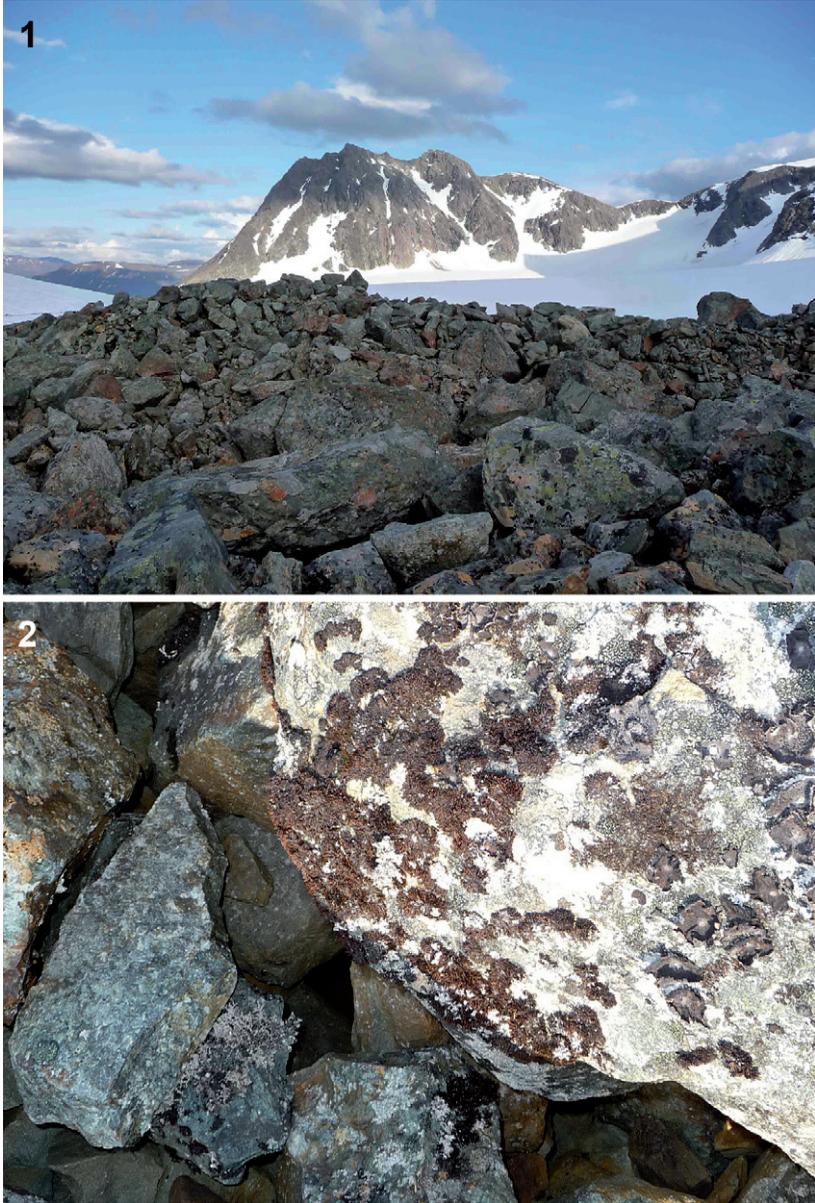
Abstract

Bergtrollus dzimbowski gen. n., sp. n., a new genus and species of Tardigrada (the Milnesiidae) from moss in the nival zone of the Lyngen Alps (Norway), is described. This is the second milnesiid genus, apart from *Milnesium* Doyère, 1840, known to occur in the Northern Hemisphere. The new tardigrade is characterized by a strikingly long and protrusible proboscis ('snout') formed by the prolonged mouth region. A similar organ in Eutardigrada has also been reported in *Milnesioides exsertum* Claxton, 1999 and in the recently discovered *Limmenius porcellus* Horning *et al.*, 1978 (see Claxton 1999) (both Milnesiidae). These species are known from limited records in New Zealand and Australia. The shape and length of the buccal tube in *Bergtrollus* gen. n. is intermediate between those of *Milnesioides* and *Limmenius*, but the mouth cavity is similar to *Milnesium*. Diagnostic morphological characters and identification key for all four genera of the Milnesiidae are presented and the phylogenetic status of the new taxon within the family is discussed.

Key words: Tardigrada, taxonomy, *Bergtrollus dzimbowski* gen. n., sp. n., nival zone, the Lyngen Alps, Norway, the Arctic.

Introduction

Milnesium tardigradum Doyère, 1840 is one of the first described, still valid, worldwide recorded and commonly known tardigrades. The species represents well-separated phyletic branch within Eutardigrada defined by Schuster *et al.* (1980) as the order Apochela. The order consists of the sole family Milnesiidae Ramazzotti, 1962 with the three genera, *Milnesium* Doyère, 1840, *Limmenius* Horning *et al.*, 1978 and *Milnesioides* Claxton, 1990. Within *Milnesium* more than 16 nominal species have been described in recent years (for a check-list see *e.g.*, Guidetti & Bertolani 2005, Degma & Guidetti 2007). Two remaining genera are monospecific and represented by *Limmenius porcellus* Horning, Schuster & Grigarick, 1978 and *Milnesioides exsertum* Claxton, 1999. These species, in particular *L. porcellus*, are characterized by a very long buccal tube, as compared to *Milnesium*. Moreover,



Figs 1-2. The type locality of *Bergtrollus dzimbowski* gen. n., sp. n.: general (1) and detailed (2) view. In the background E slope of the subsummit of Mt. Steindalstinden.

the uppermost part of the head and mouth region in *M. exsertum* form a characteristic, extremely long 'snout' (Claxton 1999), a structure not known in other Eutardigrades. The presence of the snout (= proboscis) has also been discovered recently in the originally poorly described *Limmenius* (see Claxton, *l.c.*). While the members of *Milnesium* are common and distributed worldwide, those of *Limmenius* and *Milnesioides* have been recorded very rarely and only from the Southern Hemisphere. *L. porcellus* is known from a few localities in New Zealand (Horning *et al.* 1978) and from a single specimen from Tasmania (Claxton 1999), while *M. exsertum* has been reported only from Australia, including Tasmania (Claxton, *l.c.*).

When recently processing bryophytes from the Lyngen Alps (Northern Norway), several milnesiid tardigrades intermediate in their morphology between *Limmenius* and *Milnesioides* were encountered. Analysis of the material brought to light a new and remarkable tardigrade genus and species and also the first record of the second genus of the family Milnesiidae in the Northern Hemisphere. The paper describes the new tardigrade, compares it with other milnesiid genera and discusses its phylogenetic status within the family. Furthermore, a diagnostic key for these genera is provided.

Material and Methods

The new tardigrade were found in a small sample of moss (ca 7-10 cm²) collected in the nival zone of the Lyngen Alps, Norway (for details see "type locality" below). The moss was placed in a paper bag and air-dried. After seven months the sample was soaked in distilled water and kept overnight at the temperature of 0 °C. Tardigrades were extracted by the method described by Dastyč (1985), with some living individuals being observed under a stereo-microscope. The animals were fixed for SEM examination with hot Bouin's medium, dehydrated, critical-point-dried and carbon-coated or, for light microscope study, killed with hot water and mounted in a Faure's medium as permanent microslide preparations. One specimen (holotype) was fixed in a mixture of methanol and acetic acid (3:1), stained with aceto-lactic orcein (see e.g. Bertolani 1971) and mounted after examination, like other specimens, in Faure's medium.

Measurements were taken with *PHC*. The body length was measured without legs IV, mostly with retracted proboscis ('snout'). The proboscis was fully extended in only two preserved individuals (one mounted for SEM: Figs 3, 11). However, as these animals represent *simplex*-stage, their lamellar operculum and peribuccal papillae are torn away (Figs 15-17). Consequently, the proboscis was measured without these structures (slide no. 1982A, Table 1, column "b": 80.1 µm). The length of the organ, when available, was obtained indirectly from the remaining individuals ($n = 3$, holotype included), *i.e.* through adding lengths of retracted pseudosegments of the proboscis and that of lamellar operculum. The distance between the (upper) edge of the base of the cephalic papilla and the apex of the mouth region was considered as the length of the snout.

The length of the bucco-pharyngeal and buccal apparatus includes peribuccal lamellae. The term 'buccal apparatus' includes mouth cavity, buccal tube and associated structures; the 'bucco-pharyngeal apparatus' embraces additionally the pharynx. The mouth cavity (= 'mouth ring' by Dewel & Clark 1973, in part) was measured with and



without the lamellae. The (external) diameter of the mouth cavity was taken at the bases of the peribuccal lamellae, immediately below their perpendicular striation. The mouth cavity length (that without lamellae) is the distance between the upper (strongly sclerotized) edge of the stylet sheaths and the level of the bases of peribuccal lamellae, just below their striation (comp. Claxton 1999). The length of the buccal tube was measured from the upper edge of the stylet sheaths up to the posterior edge of the tube, including terminal apophyses. The length of the buccal tube is made up of two units, *i.e.* that from the upper edge of the stylet sheaths up to the anterior edge of the stylet support insertion (= *SSA* unit; = *pt ss* index in Tumanov 2006, based on Pilato 1981) and that from the anterior (fore) edge of the stylet support insertion up to the posterior edge of the tube, including its terminal apophyses (= *SSB* unit). The (external) diameter of the tube is taken just above the insertion of the stylet supports. Two specimens (slide no. T1985c and T1982d) had on the left and right side of the tube different (aberrant) length of the unit *SSB*. The unit sides measured 58.3 vs. 63.0 and 61.1 vs. 64.8 μm , respectively. Arbitrarily, the higher values of these lengths have been considered for calculations.

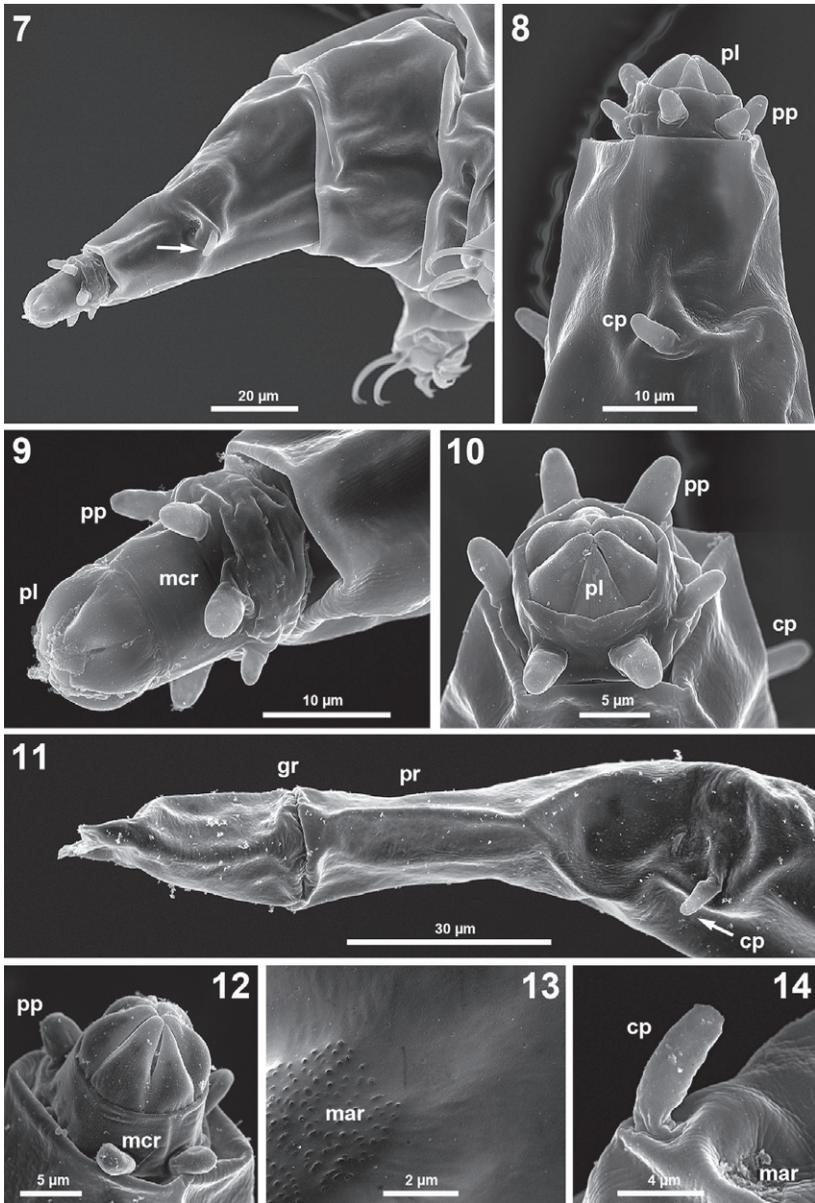
The whole length of the primary (= main) branch of the claw was measured from the apex of accessory spines up to the external edge of the arch-like cuticular bar (*mbb*: Figs 30, 31), which bar is located dorsally and laterally at the finger-like base of the branch. The length of sclerotized unit of the primary branch was measured from the apex of accessory spines up to very proximal termination of its sclerotized component (= "main branch length" in Tumanov 2006: Fig. 1). The length (height) of the remaining (*i.e.* basal) part of claw (= 'basal claw': Fig. 29: *bc*) includes lunula (= 'basal thickening': *e.g.* Tumanov 2006) and is the distance between the tip of the secondary branch and the posterior edge of the lunula. An additional measurement of the basal claw excludes the lunula. The width of lunula is a diameter of the structure.

The morphometric indices applied are defined in Dastych (2006, 2011). For calculation of the hind claw base index ("*HBI*") only the sclerotized part of the claw main branch was considered [the length (height) of hind basal claw, lunula excluded x 100 / sclerotized unit of the hind claw main branch]. Furthermore, the following new morphometric indices have been introduced:

- 1) the **snout / body index** ("*SBI*") *i.e.*, the (percent) ratio between the length of the snout (proboscis) and the body;
- 2) the **mouth cavity index** ("*MCAVI*") which describes the shape of the mouth cavity [the length of mouth cavity, peribuccal lamellae excluded x 100 / mouth cavity width];
- 3) the **hind claw lunula index** ("*HLI*") which defined the size of the hind lunula (the hind claw lunula width x 100 / the basal claw length, lunula included).

Microphotographs were taken with ZEISS 'Fotomikroskop III', *SEM* micrographs with LEO 1525. Figures 19, 23, 24, 34 come from the holotype of the new taxon, the other images represent paratypes.

Figs 3-6. *Bergtrollus dzimbowski* gen. n., sp. n., animal in *simplex*-stage. **3.** habitus: latero-dorsally, **4-6:** apex of the proboscis ('snout') in latero-dorsal, latero-ventral and lateral view, respectively (peribuccal lamellae and papillae torn out). (Scale bars for Figs 5-6: 10 μm . Other explanations in text).



Figs 7-14. *Bergtrollus dzimbowski* gen. n., sp. n. **7.** head region, proboscis partly retracted: lateral view, **8.** head, proboscis retracted: latero-dorsally, **9.** mouth region, apex of proboscis: laterally (comp. Fig. 7), **10.** mouth region: frontoventrally, **11.** proboscis in *simplex*-stage: laterally, **12.** mouth region: ventro-laterally, **13.** head region: cuticle, pores at the muscle attachment, **14.** cephalic papilla and muscle attachment: dorsally. (Explanations in text).

The new tardigrade has been compared with *Milnesium tardigradum* Doyère, 1848 from Norway (Jotunheimen, Fig. 41 and Glomfjell). Moreover, four paratypes of *Milnesioides exsertum* [borrowed from the Australian Museum, Sydney: microslides No. KS 41615 (see Fig. 51), KS 41616-617 (Figs 44, 45), KS 41618] and four paratypes of *Limmenius porcellus* have been examined. The latter came from the National Museum of New Zealand Te Papa Tongarewa, Wellington [two microslides: No. NZ 23 (Fig. 43), NZ 378 (Figs 47, 49, 50)] and from the Bohart Museum, University of California, Davis [two slides, No. NZ 8 (Fig. 46), NZ 221 (Fig. 48)].

Abbreviations used are:

ar - artefact

bc - basal claw

bt - buccal tube

cp - cephalic (head) papilla

DIC - differential interference contrast

ey - eye dot

gr - groove

HBI - the hind claw base index

LM - light microscope

lu - lunula

mar - muscle attachment region

mbb - main branch bar

MCAVI - mouth cavity index

mc - mouth cavity

mcra - mouth cavity range

n.a. - not applicable

ov - ovocyte

pb - primary (main) branch

ph - pharynx

PHC - phase contrast

pl - peribuccal lamella

pp - peribuccal papilla

pr - proboscis (snout)

PT - whole buccal tube indices (Pilato 1981; = *WTI* indices: Dastych 2006)

PUI - posterior tube unit indices

qa - quaternary branch

r^2 , *r squared* - coefficient of determination

se - secondary branch

SBI - snout / body index

SD - standard deviation

SEM - scanning electron microscope

sh - stylet sheath

ss - stylet support

SSA - buccal tube anterior unit (the distance between stylet sheaths and stylet support insertion)

SSB - buccal tube posterior unit (the distance between stylet support and terminal apophyses)

st - stylet

tb - transversal bar

te - tertiary branch

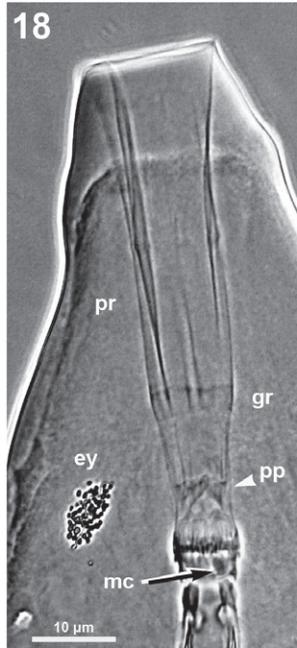
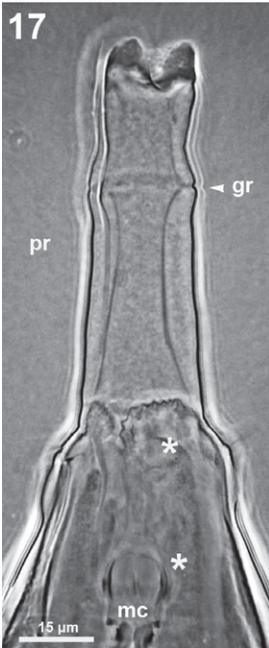
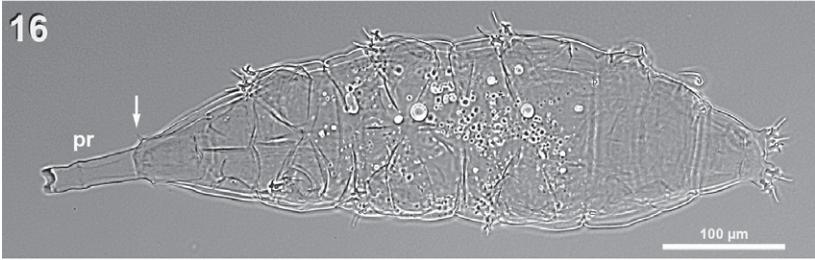
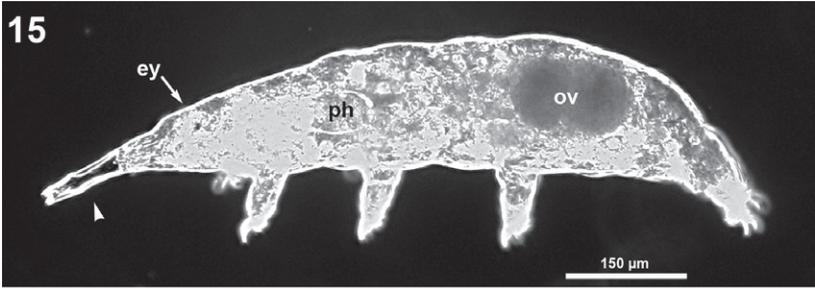
WTI - whole buccal tube indices (= *pt* indices, Pilato, 1981)

WT SSA - stylet supports "anterior" index (= *pt ss*: Tumanov 2006, based on Pilato 1981)

V - coefficient of variability

ZMH - Zoologisches Museum Hamburg

\bar{x} - (arithmetic) mean.



Description of new genus

Class: Eutardigrada (Richters, 1926) *emend.* Marcus, 1927

Order: Apochela Schuster *et al.*, 1980

Family: Milnesiidae Ramazzotti, 1962

Bergtrollus gen. n.

DIAGNOSIS: Semiterrestrial, medium- to large-sized milnesiids with a very long, telescopically protrusible tubular proboscis ('snout'). Mouth cavity short. Buccal tube long, flexible, smooth (*i.e.*, without net- /spiral-like strengthening), stylets thin and long. The claw system of *Milnesium*-type.

TYPE SPECIES: *Bergtrollus dzimbowski* sp. n. by monotypy.

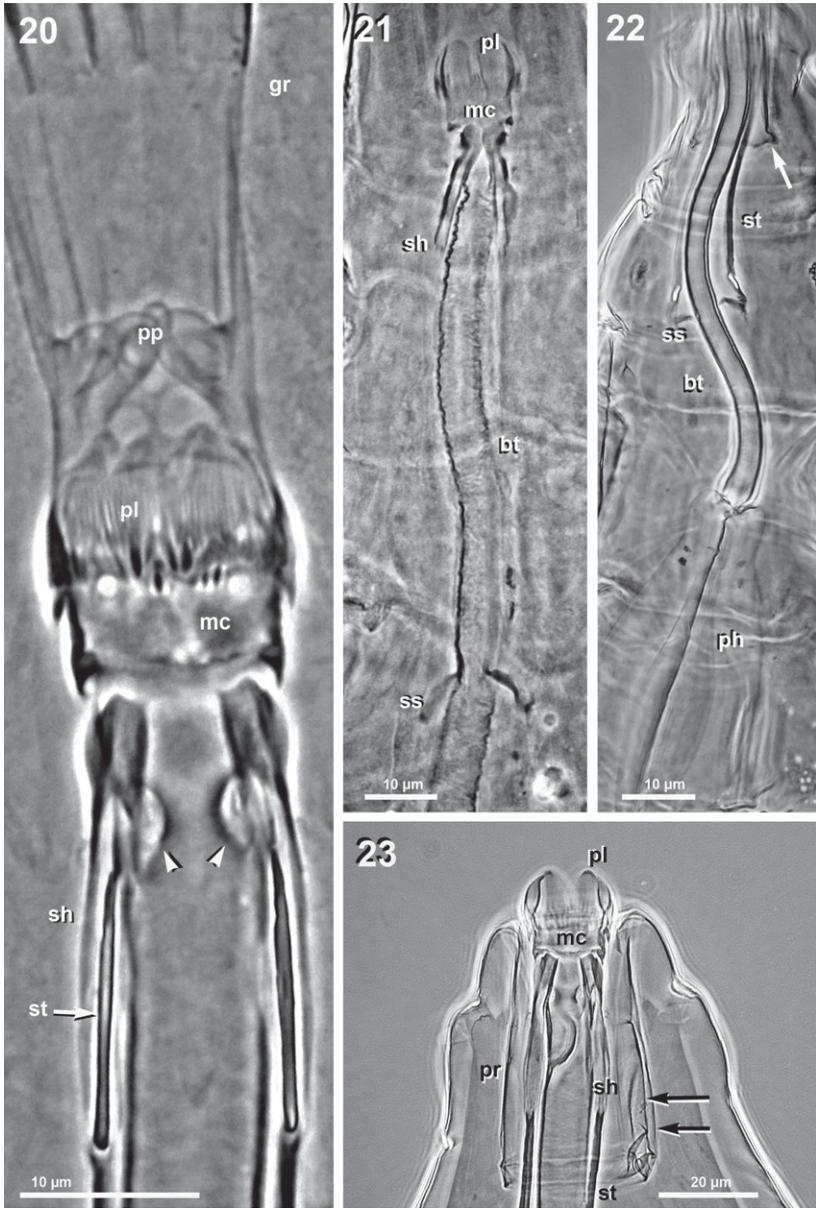
Included taxa: A single species, *Bergtrollus dzimbowski* sp. n.

ETYMOLOGY: *Bergtrollus* = mountain troll. The new genus is named after the mystic creatures, trolls, thought to inhabit Scandinavia (*Berg* = mountain: German, Norwegian).

REMARKS: *Bergtrollus* gen. n. is the third of four known genera of the Milnesiidae with strikingly long, protrusible proboscis ('snout'), this organ being absent in *Milnesium* itself. The proboscis is in all these taxa of *ca.* 10-20 % of their body length [SBI index for the new genus: $\bar{x} = 15.08 \pm 1.56$ (13.8-17.3) ($n = 4$), *Milnesioides*: 9.7 and 15.8, *Limmenius*: $\bar{x} = 18.20 \pm 3.92$ (13.3-22.8) % ($n = 4$)].

The buccal tube length of the new genus is intermediate between that of the genera *Milnesioides* and *Limmenius*, as is also the width of the tube (comp. Figs 42-44). The shortest and the widest tube (Fig. 41) in the family have members of *Milnesium*. In *Bergtrollus* gen. n. the mouth cavity is short and wide [MCAVI index: $\bar{x} = 37.60 \pm 6.13$ (31.3-50.0) ($n = 8$)] resembling that of *Milnesium* [$\bar{x} = 33.5 \pm 7.04$ (26.9-40.9) ($n = 4$)] but is different in shape and size from the cavity of the genera reported from the Southern Hemisphere, *i.e.*, *Milnesioides* and *Limmenius*. The latter taxa, particularly *Limmenius*, have the mouth cavity distinctly narrower and longer [MCAVI: $\bar{x} = 105.80 \pm 16.0$ (93.8-129.4) ($n = 4$) and $\bar{x} = 157.60 \pm 21.09$ (128.7-178.0) ($n = 4$), respectively; see also Figs 41-44].

Figs 15-19. *Bergtrollus dzimbowski* gen. n., sp. n. (15-17: animal in *simplex*-stage): **15.** habitus, water-mounted ♀; 'empty' proboscis (*arrowhead*), mouth appendages torn out: lateral view, **16.** habitus (*arrow*: cephalic papilla): ventrally, **17.** proboscis in a late *simplex*-stage: the mouth region and buccal apparatus retracted (*asterisks*, respectively) and in a process of formation: dorsal view, **18.** head region: strongly retracted proboscis and such anterior part of buccal apparatus: dorsally, **19.** greatly retracted, telescopically arranged proboscis (*arrows*) and bucco-pharyngeal apparatus: dorso-ventrally. (All PHC. Other explanations in text).



The insertion of the stylet supports in *Bergtrollus* gen. n. is similar to that in *Milnesium* and *Limmenius* and the supports in these genera are inserted at ca. 60 % of the buccal tube length [WTSSA (= *pt* ss) index in the new genus: 60.6-62.2 ($n = 3$), *Milnesium*: $\bar{x} = 63.2 \pm 3.3$ (59.6-67.6) ($n = 4$), *Limmenius*: $\bar{x} = 59.78 \pm 3.73$ (55.3-62.9) ($n = 4$)]. In *Milnesioides* the supports are inserted much more caudally, at ca. 80 % of the tube length ($\bar{x} = 77.03 \pm 1.81$ (75.4-79.6) % ($n = 4$)). It should be noted that the insertion of the supports (the index values) is more similar in genera with different type of buccal tube (*Milnesium* vs. *Limmenius*) but is distinctly different in genera where the buccal apparatus is more similar, i.e., *Milnesium* vs. *Milnesioides* (Figs 41-44).

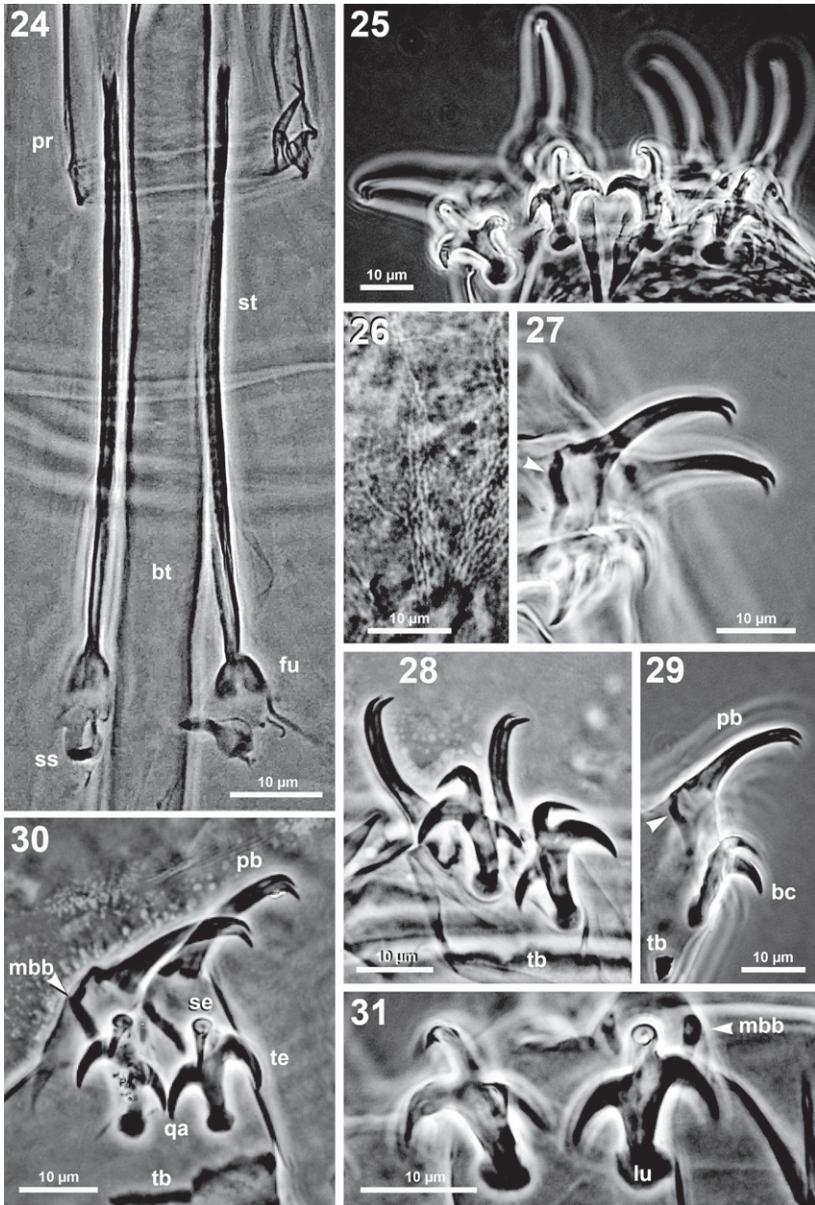
The claw system of *Bergtrollus* gen. n. is of the same type as that of other milnesiids, indicating its conservative character within the whole family.

The mouth and head appendages and the type of claws place *Bergtrollus dzimbowski* gen. n., sp. n. without doubt in the family Milnesiidae. However, the phylogenetic position of this taxon within the family is not clear and at present can be only a subject of speculation.

As inferring from the presence of proboscis and the morphology of its buccal tube, the new genus could be considered as an intermediate form between genera *Milnesioides* and *Limmenius*. Consequently, it could be placed as a "missing link" in such a position within prearranged series of the three remaining milnesiid genera, as illustrated but not commented by Claxton (1999: Fig. 10a-c). *Milnesioides* has a broader but shorter mouth tube than *Bergtrollus* gen. n. but is somehow similar to the tube of *Milnesium*. On the other hand, in *Limmenius* the tube is very long, narrower and much more flexible than in the new genus. Moreover, in *Limmenius* the tube is provided with a net-/spiral-like strengthening. The organ is within the Milnesiidae the most advanced. The tube of the latter genus resembles such independently evolved organ of e.g., the genus *Diphascon* (the order Parachela, the Diphasconidae).

The mouth cavity in *Bergtrollus* gen. n. is very short and wide and resembles that in *Milnesium*. The cavity differs markedly from those present in the both Southern Hemisphere genera, *Milnesioides* and *Limmenius*. Because of this, one can also hypothesise that the new taxon originated not within the southern (Gondwanan?) lineage to which *Milnesioides* and *Limmenius* might belong, but evolved independently from *Milnesium*-like ancestors within the northern (Laurasian) region.

Figs 20-23. *Bergtrollus dzimbowski* gen. n., sp. n. **20.** mouth region and anterior part of buccal apparatus in greatly retracted proboscis (comp. Fig. 18): dorsally, **21.** developing buccal apparatus, the late *simplex*-stage: dorsally (comp. Fig. 17), **22.** bucco-pharyngeal apparatus, proboscis retracted (arrow): dorsally, **23.** mouth region and anterior part of buccal apparatus; proboscis telescopically arranged, retracted (arrows): dorsally. (All PHC. Other explanations in text).



Figs 24-31. *Bergtrollus dzimowski* gen. n., sp. n. **24.** fragment of buccal apparatus: dorso-ventrally, **25.** claws IV, **26.** fragment of the cuticle above legs IV: dorsally, **27.** claws IV (arrowhead: main branch cuticular bar, *mbb*): laterally, **28.** claws I: laterally, **29.** claw II, **30.** claws III, **31.** basal claws IV. (All *PHC*. Other explanations in text).

Apart from scarce information on *Milnesium*, there is no molecular data concerning other milnesiid genera. Data on their morphology, biology and distribution are very rare. Further studies might thus help to understand better evolutionary processes within the family Milnesiidae and phyletic relation within its genera.

The diagnostic key for the Milnesiidae genera is provided after the species description.

DISTRIBUTION: Known only from the type locality in the Lyngen Alps, Northern Norway (the Arctic zone).

Description of the species

Bergtrollus dzimbowski sp. n.

(Figs 3-40, 42)

TYPE MATERIAL. Holotype. – (Figs 19-23, 24, 34). Female, 666 μm long, coll. H. Dastyh, 13 Sept 2009. Stained with lactic orcein, mounted in Faure's medium. The microslide (No. T1985j, slide No. 1) is deposited in the Zoologisches Museum Hamburg (ZMH Acc. No. A28/11).

Type locality. – (Figs 1-2). Northern Norway, Troms, the Lyngen Alps. Upper region of the glacier Steindalsbreen. A small pass between Steindal- and Goverdal Valley, at SW ridge of the Nállangáisi-Massiv (N 69° 23' 48.6" + E 019° 49' 52.2", ca. 1000 m a.s.l.). A scree field on the pass at the base of a small semi-nunatak Sfinxen. The rock moss *Andreaea rupestris* Hedw. (Andreaeaceae) on a gabbro (silicate) boulder, not shaded, exposed SE; 13 Sept. 2009, coll. H. Dastyh.

Paratypes. – Locality data as above. Altogether 10 females. Eight animals mounted in Faure's medium on five slides (Nos 2-6: ZMH Acc. No. A29/11). One paratype is deposited at the Zoological Museum Bergen, Norway (slide No. 4), the Australian Museum, Sydney (slide No. 2), and the National Museum of New Zealand Te Papa Tongarewa, Wellington (slide No. 3). The remainder of type specimens is lodged in the ZMH, including two paratypic individuals mounted on SEM stubs (ZMH Acc. No. A30/11).

The species co-occurred in the sample with *Echiniscus wendti* Richters, 1903, *Hebesuncus conjungens* (Thulin, 1911), *Macrobotus* cf. *islandicus* Richters, 1904, *Milnesium eury stomum* Maucci, 1991 and *Mil.* cf. *tardigradum* Doyère, 1840.

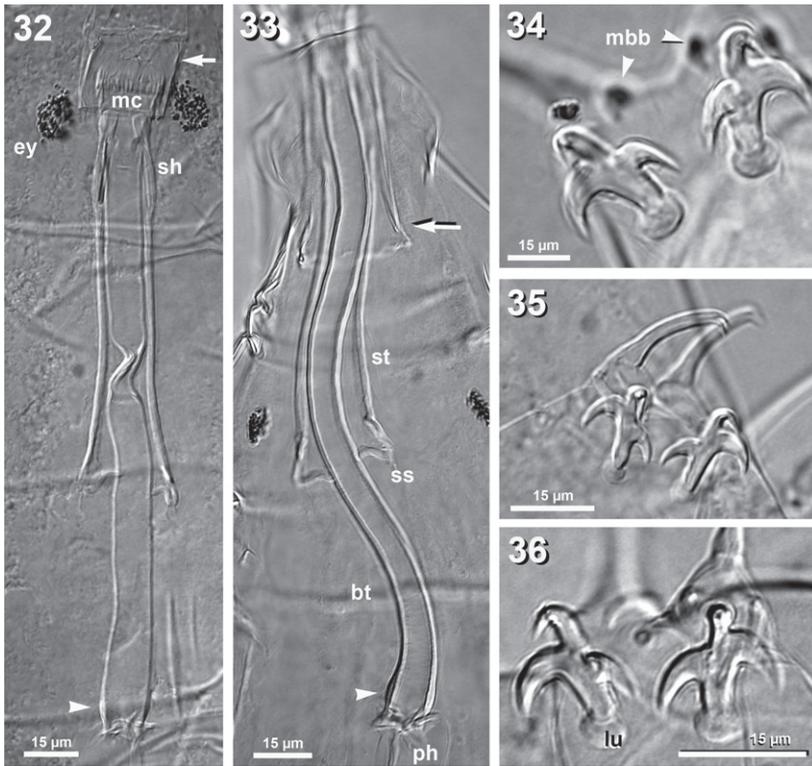
ETYMOLOGY. – The specific name is in honour of my fellow climber and friend, Hans-Jochen Dzimbowski (Deutscher Alpenverein, Hamburg), the organizer of our trips to the Norwegian mountains.

DIAGNOSIS. – As for genus.

DESCRIPTION. – Body 492-736 (holotype 666) μm long, light-brown or yellow-brownish, with darker pigmented areas in its rear. Cuticle smooth (Fig. 13), sometimes in small areas slightly folded (Fig. 26). Eye-dots relatively large (Figs 18, 32, 33), composed of irregularly shaped and differently sized pigment granules.

Mouth region located on a long, protrusible tubular proboscis ('snout') (Figs 3, 11, 16-18: *pr*; Fig. 15: *arrowhead*), more or less retracted in preserved specimens (e.g., Figs 7, 8, 10, 19). A small but distinct vertical ring-like groove around anterior part of the proboscis, at its ca. 1/3 distal length (Figs 4-6, 11, 17, 18, 20: *gr*). The groove divides the proboscis externally in two differently long pseudosegments (Fig. 17) when the 'snout' is fully extended or retracted. The tubular proboscis retracts mostly in the form of a usually telescopically closely arranged, two or three shorter subunits (Figs 19, 22, 23, 33: *arrows*). When fully extended, it is ca. 15 % of the body length ($SBl = 13.8-17.3\%$, $n = 4$). Two cephalic papillae symmetrically are located at the basal part of the proboscis (Figs 7, 10: *cp*).

Bucco-pharyngeal apparatus large, almost half of the body length. Mouth cavity small, buccal tube markedly long, flexible (Figs 19, 20, 21, 32, 33: *bt*). Pharynx large, pear-shaped (Figs 15, 19: *ph*).



Figs 32-36. *Bergtrollus dzimbowski* gen. n., sp. n. **32-33:** buccal apparatus, **34.** basal claw IV, **35.** claws I, **36.** basal claws IV. (All DIC. Other explanations in text).

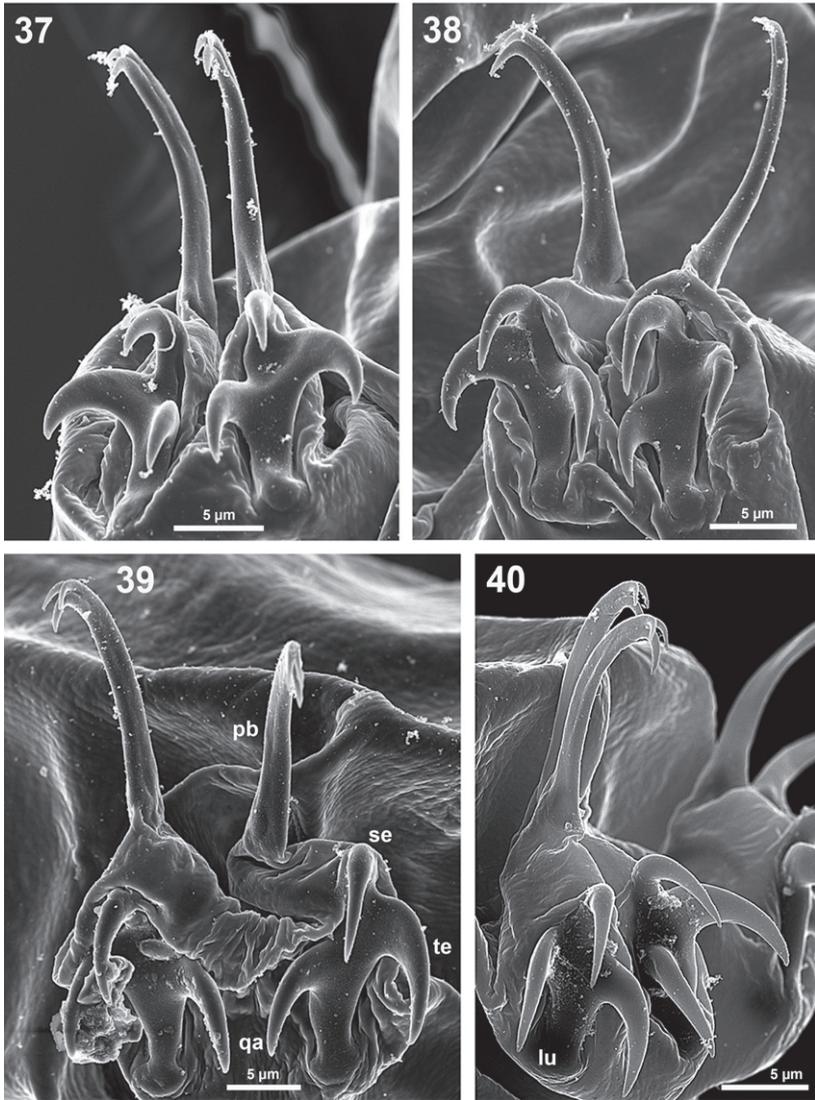
Mouth opening surrounded by six finger-like peribuccal papillae (Figs 8, 9, 18, 20: *pp*) and covered by an operculum composed of six peribuccal lamellae. The lamellae triangular, elongated (8-10, 23: *pl*), with a fine vertical striation, visible in *LM* (Fig. 20) and partly in *SEM*. Mouth cavity small, short, its lining strongly sclerotized (Figs 18, 20, 23, 32: *mc*), its wall smooth, without discernible armature (teeth or granules). The openings of stylet sheaths leading into the mouth cavity small, their location strongly sclerotized (Figs 18, 20, 23). The posterior part of sheaths weakly sclerotized, shaped as a long and delicate cuticular tubes (Figs 20, 23, 32: *sh*). Just below the strongly sclerotized (anterior) units of the stylet sheaths two small, roundish, differently light-defracting fields. These areas are lighter and less sclerotized than the surrounding wall of the buccal tube (Fig. 20: *arrowhead*, 42). The structures represent a part of the pharyngeal organs (see note in § "Remarks").

Buccal tube very long, relatively wide and flexible (Figs 19, 22, 33: *bt*). The tube wall smooth, *i.e.* without net- /spiral-like strengthening. The tube slightly thickened at its posterior end, thus forming small and flat terminal apophyses (Figs 32, 33: *arrowhead*). As in other milnesiids, the tube is located (disembogues) just at the uppermost anterior edge of the pharynx. No placoids in the pharynx lumen. Stylets long, markedly thin (Figs 22, 32, 33: *st*), with a broad, flat spade-like furca (Fig. 24: *fu*). Stylet supports located in *ca.* 62 % of the tube length (Figs 22, 33: *ss*). One specimen (microslide No. 6) in the *simplex*-stage was in a process of development of its buccal apparatus, which was thus weakly sclerotized. The buccal tube remained there 'soft', its wall being distinctly folded (Fig. 21).

Claws of *Milnesium*-type. Each claw composed of an apical unit, *i.e.* the primary (= main) branch (Figs 30, 39: *pb*) and well separated remaining part, the basal unit (Fig. 29: *bc*). The primary branch short, slightly thickened, with distinct accessory spines (Figs 28, 40). The branch base dorsally and laterally with an arch-like cuticular bar (Figs 30, 31, 34: *mbb*). The basal unit of the claw (= basal claw: Fig. 29: *bc*) composed of three branches, *i.e.* the secondary, tertiary and the lowest, quaternary branch (Figs 30, 39: *se*, *te*, *qa*, respectively). The latter branch has also been termed as 'basal spur': *e.g.*, Tumanov 2006). The branches relatively long, their number (3) on particular claw constant. The proximal part of the basal claw (*i.e.*, its foot) with a roundish structure, the lunula (Figs 31, 40: *lu*), particularly well formed on legs IV. (The latter called also 'basal thickening': *e.g.*, Pilato & Binda 2010, Tumanov *l.c.*). Below basal claws I-III occurs ventrally a transversal cuticular bar (Figs 29, 30: *tb*).

Claws I not modified, indicating thus all animals examined as females.

Eggs unknown.



Figs 37-40. *Bergtrollus dzimbowski* gen. n., sp. n. 37. claws I, 38. claws II, 39. claws IV, 40. claws IV. (Explanations in text).

Morphometric data

Measurements are in μm , all indices in %. Their values are presented as follows:

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

$\bar{x} \pm \text{SD}$ (min-max) [n] * V / r2 (for indices).

For the abbreviations and definitions of indices see § "Material and methods" and Dastych (2006, 2011). The morphometrics of the holotype (666 μm long) is separated from other data by a dot (•) and marked in **bold**. Not measured (unfavourably positioned) structures in the holotype are marked with " / - ".

A) Measurements (μm)

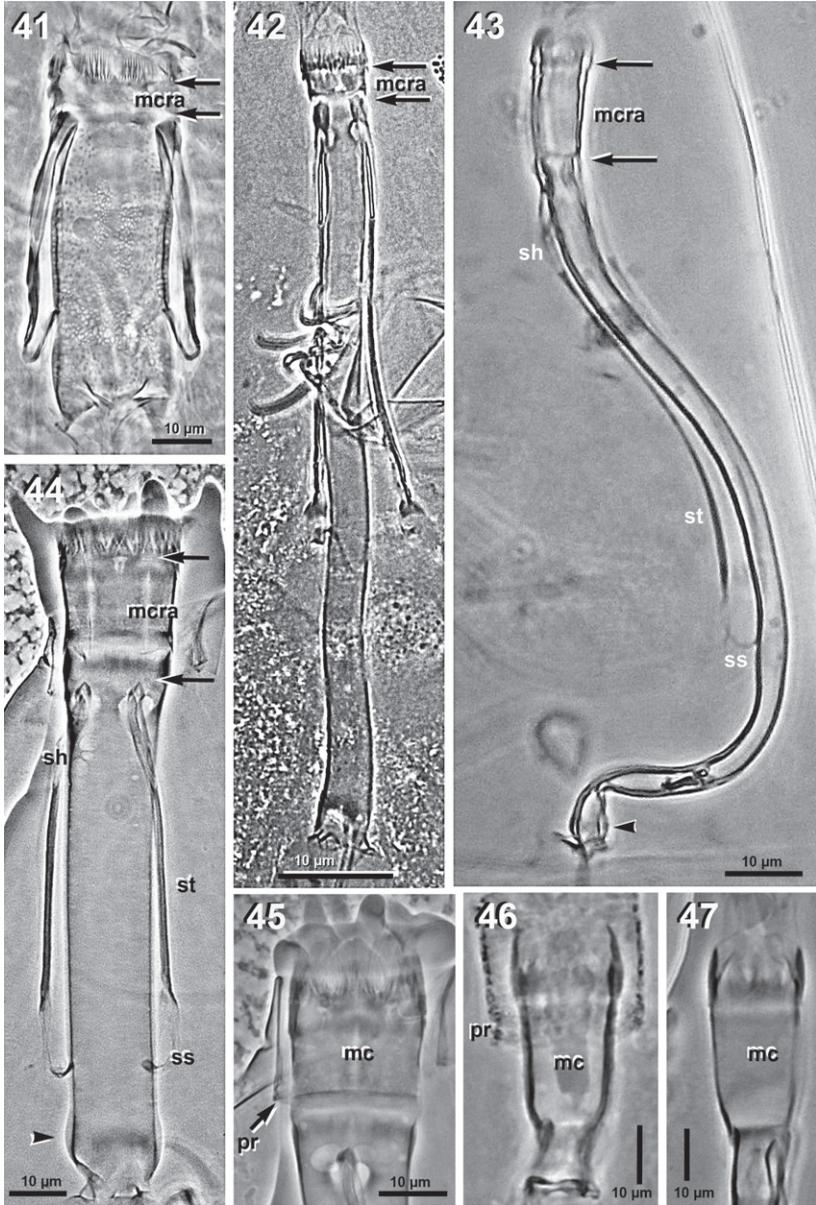
a. Body length	592.70 \pm 78.78 (492.8-736.4) [9] * 13.3 • 666.4
b. Proboscis ('snout') length	95.98 \pm (80.1-106.7) [4] * 13.1 • 91.8
c. Peribuccal papilla length	<i>n.a.</i> (5.4, 6.3) [2] * <i>n.a.</i> / -
d. Cephalic papilla length	6.48 \pm 0.75 (5.4-7.2) [5] * 11.6 • 5.4
e. Bucco-pharyngeal apparatus length	278.20 \pm 36.87 (231.0-330.0) [5] * 13.3 • 330.0
f. Pharynx length	108.90 \pm 11.11 (90.9-123.2) [8] * 10.2 • 123.2
g. Pharynx width	55.86 \pm 10.48 (45.0-77.0) [8] * 18.8 • 77.0
h. Mouth cavity length (+lamellae)	13.28 \pm 1.25 (10.8-14.4) [8] * 9.42 • 14.4
i. Mouth cavity length (-lamellae)	4.85 \pm 1.03 (4.1-7.2) [8] * 21.3 • 4.5
j. Mouth cavity (ext.) width	12.94 \pm 1.86 (10.8-16.2) [8] * 14.4 • 14.4
k. Stylet sheaths length	27.00 \pm 2.55 (24.3-29.7) [5] * 9.4 • 29.7
l. Buccal tube length	<i>n.a.</i> (153.0-171.9) [3] * <i>n.a.</i> • 171.9
m. SSA length (tube above stylet supports)	<i>n.a.</i> (92.7-103.5) [3] * <i>n.a.</i> • 103.5
n. SSB length (tube below stylet supports)	62.74 \pm 6.05 (49.5-67.5) [7] * 9.7 • 65.7
o. Buccal tube (ext.) width	8.35 \pm 1.37 (6.8-9.9) [8] * 16.4 • 9.9
p. Ext. claw 1 whole main branch length	20.80 \pm 2.93 (16.2-22.5) [9] * 9.3 • 22.5
q. Ext. claw 1 sclerot. main branch length	17.50 \pm 1.80 (13.5-19.8) [9] * 10.3 • 19.8
r. Ext. claw 1 basal unit (+lunula) length	14.60 \pm 1.54 (11.7-16.2) [9] * 10.6 • 16.2
s. Ext. claw 1 basal unit (-lunula) length	12.50 \pm 1.49 (9.0-13.1) [8] * 12.0 • 13.5
t. Ext. claw 1 lunula width	3.32 \pm 0.41 (2.7-3.6) [8] * 12.3 • 3.6
u. Hind claw whole main branch length	22.95 \pm 1.55 (21.6-25.2) [4] * 6.8 • / -
v. Hind claw sclerot. main branch length	19.44 \pm 0.49 (18.9-19.8) [5] * 2.5 • 18.9
w. Hind claw basal unit (+lunula) length	15.63 \pm 1.72 (12.6-18.0) [7] * 11.2 • 18.0
x. Hind claw basal unit (-lunula) length	13.28 \pm 1.50 (10.8-15.3) [6] * 11.3 • 15.3
y. Hind claw lunula width	5.11 \pm 0.36 (4.5-5.4) [6] * 7.0 • 5.4

For a list of measurements taken from each type specimen see Appendix 1.

B) Indices

1) *WTI* (the whole tube length indices) (= "pt indices": Pilato 1981).

<i>WT</i> proboscis ('snout') length	<i>n.a.</i> (53.4-69.7) [3] * <i>n.a.</i> / 84.0 • 53.4
<i>WT</i> cephalic papilla length	<i>n.a.</i> (3.1, 4.1) [2] * <i>n.a.</i> / - • 3.1
<i>WT</i> buccal apparatus length	<i>n.a.</i> (180.6-192.0) [3] * <i>n.a.</i> / 95.7 • 192.0
<i>WT</i> pharynx length	<i>n.a.</i> (71.6-74.1) [3] * <i>n.a.</i> / 91.7 • 71.6
<i>WT</i> pharynx width	<i>n.a.</i> (32.8-44.8) [3] * <i>n.a.</i> / 24.7 • 44.8



<i>WT</i> mouth cavity length (+lamel.)	<i>n.a.</i> (8.4-9.4) [3] * <i>n.a.</i> / - • 8.4
<i>WT</i> mouth cavity length (- lamel.)	<i>n.a.</i> (2.6-4.5) [3] * <i>n.a.</i> / 12.5 • 2.6
<i>WT</i> mouth cavity (ext.) width	<i>n.a.</i> (8.4-10.6) [3] * <i>n.a.</i> / 72.6 • 8.4
<i>WT</i> stylet sheaths length	<i>n.a.</i> (17.3-18.8) [3] * <i>n.a.</i> / 27.4 • 17.3
<i>WT</i> SSA length (tube above stylet supports)	<i>n.a.</i> (60.6-62.2) [3] * <i>n.a.</i> / 90.8 • 60.2
<i>WT</i> SSB length (tube below stylet supports)	<i>n.a.</i> (38.2-41.2) [3] * <i>n.a.</i> / 77.3 • 38.2
<i>WT</i> buccal tube (ext.) width	<i>n.a.</i> (5.8-6.5) [3] * <i>n.a.</i> / < 0.1 • 5.8
<i>WT</i> ext. claw 1 whole main branch length	<i>n.a.</i> (13.1-14.7) [3] * <i>n.a.</i> / < 0.1 • 13.1
<i>WT</i> ext. claw 1 sclerot. main branch length	<i>n.a.</i> (11.1-11.8) [3] * <i>n.a.</i> / 77.3 • 11.5
<i>WT</i> ext. claw 1 basal unit (+ lunula) length	<i>n.a.</i> (9.4-10.6) [3] * <i>n.a.</i> / < 0.1 • 9.4
<i>WT</i> ext. claw 1 basal unit (- lunula) length	<i>n.a.</i> (7.9-8.8) [3] * <i>n.a.</i> / - • 7.9
<i>WT</i> ext. claw 1 lunula width	<i>n.a.</i> (2.1-2-2) [3] * <i>n.a.</i> / 72.6 • 2.1
<i>WT</i> hind claw whole main branch length	<i>n.a.</i> (13.9, 16.5) [2] * <i>n.a.</i> / - • -
<i>WT</i> hind claw sclerot. main branch length	<i>n.a.</i> (11.0-12.9) [3] * <i>n.a.</i> / 72.6 • 11.0
<i>WT</i> hind claw basal unit (+ lunula) length	<i>n.a.</i> (10.0-10.6) [3] * <i>n.a.</i> / 77.3 • 10.5
<i>WT</i> hind claw basal unit (- lunula) length	<i>n.a.</i> (8.6-8.9) [3] * <i>n.a.</i> / 95.1 • 8.9
<i>WT</i> hind claw lunula width	<i>n.a.</i> (3.1-3.5) [3] * <i>n.a.</i> / < 0.1 • 3.1

2) *PUI* (the posterior tube unit indices)

<i>PU</i> proboscis ('snout') length	159.50 ± 13.56 (139.7-169.4) [4] * 8.5 / 54.5 • 139.7
<i>PU</i> peribuccal papilla length	<i>n.a.</i> (8.5-9.6) [2] * <i>n.a.</i> / <i>n.a.</i> • -
<i>PU</i> cephalic papilla length	10.60 ± 1.72 (8.2-12.7) [5] * 16.2 / 0.2 • 8.2
<i>PU</i> buccal apparatus length	452.20 ± 42.18 (401.9-502.3) [4] * 9.3 / 20.5 • 502.3
<i>PU</i> pharynx length	174.5 ± 14.30 (155.6-191.4) [6] * 8.2 / 0.5 • 187.5
<i>PU</i> pharynx width	88.45 ± 18.53 (69.4-117.2) [6] * 21.0 / 1.8 • 117.2
<i>PU</i> mouth cavity length (+lamel.)	21.05 ± 1.72 (19.2-22.9) [6] * 8.2 / 19.1 • 21.9
<i>PU</i> mouth cavity length (- lamel.)	7.77 ± 1.95 (6.3-11.4) [6] * 25.1 / 48.5 • 6.8
<i>PU</i> mouth cavity (ext.) width	20.60 ± 3.55 (16.4-25.7) [6] * 17.2 / 53.6 • 21.9
<i>PU</i> stylet sheaths length	45.43 ± 6.86 (37.5-54.2) [4] * 15.1 / 0.4 • 54.2
<i>PU</i> buccal tube (ext.) width	13.57 ± 2.11 (11.0-15.7) [6] * 15.8 / 8.8 • 15.1
<i>PU</i> ext. claw 1 whole main branch length	33.00 ± 2.10 (29.3-35.7) [7] * 6.4 / 62.3 • 34.2
<i>PU</i> ext. claw 1 sclerot. main branch length	27.49 ± 1.91 (24.7-30.1) [7] * 7.0 / 59.5 • 30.1
<i>PU</i> ext. claw 1 basal unit (+ lunula) length	23.21 ± 2.28 (18.7-25.7) [7] * 9.8 / 31.6 • 24.7
<i>PU</i> ext. claw 1 basal unit (- lunula) length	20.10 ± 1.22 (18.4-21.4) [6] * 6.1 / 81.4 • 20.5
<i>PU</i> ext. claw 1 lunula width	5.48 ± 0.20 (5.1-5.7) [6] * 3.7 / 87.4 • 5.5
<i>PU</i> hind claw whole main branch length	<i>n.a.</i> (32.9-40.0) [3] * <i>n.a.</i> / <i>n.a.</i> • -
<i>PU</i> hind claw sclerot. main branch length	30.08 ± 1.06 (28.8-31.4) [4] * 3.5 / - • 28.8
<i>PU</i> hind claw basal unit (+ lunula) length	24.87 ± 2.12 (21.3-27.4) [6] * 8.5 / 46.1 • 27.4
<i>PU</i> hind claw basal unit (- lunula) length	21.62 ± 1.43 (19.4-23.3) [5] * 6.6 / 70.2 • 23.3
<i>PU</i> hind claw lunula width	8.42 0.46 (7.9-9.1) [5] * 5.4 / 86.2 • 8.2

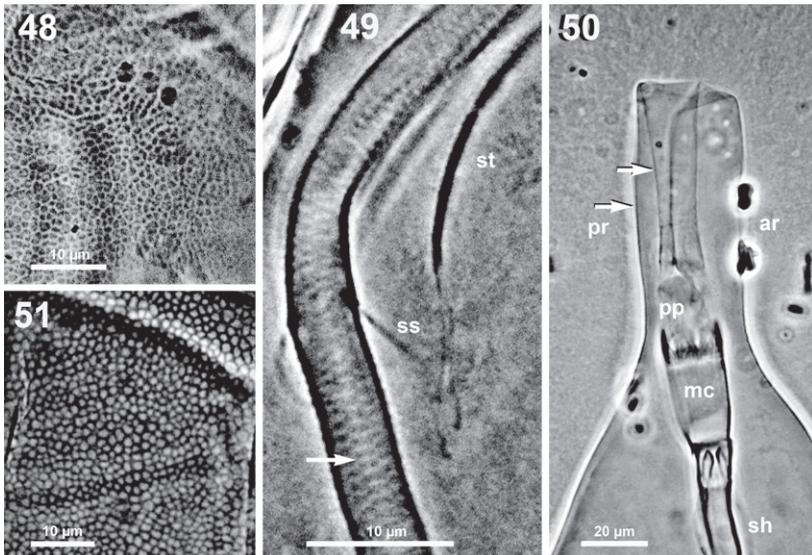
Figs 41-47. Types of the buccal apparatus in the Milnesiidae. **41.** *Milnesium tardigradum* Doyère, **42.** *Bergtrollus dzimbowski* gen. n., sp. n., **43.** *Limmenius porcellus* Horning *et al.*, **44-45:** *Milnesioides exsertum* Claxton, buccal apparatus and its anterior part, respectively, **46-47:** *L. porcellus*, anterior part of buccal apparatus: dorso-ventral and lateral view, respectively. (All *PHC*. The range of mouth cavity (*mcra*) is marked by arrows. Paratypes used for Figs 42-47 are indicated in § "Material and methods". Other explanations in text).

C) Other indices

Snout / body index (<i>SBI</i>)	15.03 ± 1.56 (13.8-17.3) [4] * 10.4 / 45.5 • 13.8
Mouth cavity index (<i>MCAVI</i>)	37.60 ± 6.13 (31.3-50.0) [8] * 16.3 / 31.4 • 31.3
Hind claw base index (<i>HBI</i>)	71.88 ± 6.14 (68.2-81.0) [4] * 8.6 / 61.0 • 81.0
Hind claw lunula index (<i>HLI</i>)	29.40 ± 2.72 (29.4-35.7) [6] * 8.4 / 54.8 • 30.0

VARIABILITY. – The individuals of *B. dzimbowski* sp. n. examined are characterized by a relatively low intra-specific variability of their qualitative features. As the morphometric data of the new species are based only on few available measurements ($n = 2-9$), the results of descriptive statistics have often only an approximate character. The coefficient of determination of the *WT SSA (= pt ss)* index is high, with *r squared* value equalling 90.8 % ($n = 3$). It indicates a high degree of correlation between the length of the buccal tube and *SSA* unit. The index is considered as of high diagnostic importance (Pilato 1981) and already standardized for eutardigrades. In the new species it ranges between 60.6-62.2 % ($n = 3$).

REPRODUCTION MODE AND PLOIDY. – Only females have been found among all (11) specimens of *B. dzimbowski* sp. n. examined. It is therefore too early to try to define the reproduction mode in the species. In all genera



Figs 48-51. *Limenius porcellus* Horning et al. (48-50): **48.** cuticular pattern at the body rear: dorso-laterally, **49.** net-/spiral-like structure of the buccal tube, **50.** anterior part of the head region, proboscis (arrows) and buccal apparatus partly retracted: dorso-ventrally, **51.** *Milnesioides exsertum* Claxton, cuticular pattern at the body rear: dorso-laterally. (All *PHC*. Paratypes used for Figs 48-51 are indicated in § "Material and methods". Other explanations in text).

of the Milnesiidae the bisexual mode prevails and occurs at least in several species of *Milnesium*. This mode has also been reported for *Milnesioides exsertum* (see Claxton 1999). In the present study three males were found among examined paratypes of *Limmenius porcellus* (slides Nos. NZ 8, 23, 378), indicating bisexual reproduction in this genus also (unpublished). The ploidy in *B. dzimbowski* sp. n. is not known.

BIOLOGY AND DISTRIBUTION. – The limited biological information on the new species can only be partly inferred from data on its type locality in the Lyngen Alps (Figs 1, 2). *B. dzimbowski* sp. n. has been found in a nival zone of the Norwegian continental Arctic, in a small patch of rock moss, *Andreaea rupestris* Hedw. on a gabbro boulder. According to Nyholm (1981), the moss inhabits siliceous rocks and occurs from the woodland up to the high-alpine belt of the mountains, being common in the north and central part of Fennoscandia.

Live individuals of *B. dzimbowski* sp. n. move forward in the same way as described already for *Milnesioides exsertum* by Claxton (1999: 187), i.e., "... the extended "snout" was observed moving from side to side as if animal was searching for food...". The animals easily retract their proboscis when disturbed, then greatly resembling members of *Milnesium*. The type of diet of the new species is unknown, as in the intestines of examined specimens no plant material, rotifer or nematode remnants could be observed.

REMARKS. – The phylogenetic position of *Bergtrollus dzimbowski* sp. n. within the Milnesiidae has been discussed at the description of new genus.

The pharyngeal organs of *B. dzimbowski* sp. n. represent a chemosensory structural complex discussed already in tardigrades e.g., by Dewel & Clark 1973, Dewel & Eibye-Jacobsen 2006, Walz 1978, Greven 1980, Wiederhöft & Greven 1999. A part of the organ, two lighter, roundish fields within the mouth tube wall (e.g., Fig. 20: *arrowheads*) correspond supposedly to the perforated areas of the tube (comp. Greven 1980: Fig. 17). Such perforation have been already described by the authors (*I.c.*) in *Macrobotus* and *Milnesium* and is discernible only with the electron microscope. Within the Milnesiidae these organs, apart from *Milnesium* and *Bergtrollus* gen. n., occur also in *Milnesioides* (see Figs 44, 45: unpublished) and have been observed as small hardly detectable fields in two of four examined paratypes of *Limmenius porcellus* (unpublished).

The term 'lunula' applied here for the roundish structure at the base (foot) of the basal claw in milnesiids does not indicate a homology with similarly located structures in remote phyletic lineages of Eutardigrada, such as in most macrobiotids or many hypsibiids *s.l.* The origin of lunulae and their phyletic relations in all these taxa is unclear. Supposedly the structures evolved independently as some other structures did within eutardigrades. Among observed genera of the Milnesiidae with a proboscis, the lunulae are relatively the largest in *B. dzimbowski* sp. n.

Key to the genera of the family Milnesiidae

1. Buccal tube short, wide (Fig. 41; the values of the *WT* buccal tube width index *ca.* 40 %), no proboscis (= snout) *Milnesium*
 - Buccal tube long or very long, narrower (Figs 41-43; the *WT* buccal tube width index lower than 20 %), proboscis* present (Figs 15, 50) 2
2. Stylet supports inserted caudally (Fig. 44; the *WTSSA* index *ca.* 80 %), buccal tube relatively wide (the *WT* buccal tube width index *ca.* 20 %) *Milnesioides*
 - Stylet supports inserted more medially (Figs 41-43; *WTSSA ca.* 60%), buccal tube distinctly longer, narrower (the *WT* buccal tube width index lower than 10 %) 3
3. Mouth cavity short, wide (Figs 20, 42; the *MCAVI* index *ca.* 40 %, *n* = 3), buccal tube smooth (no net- /spiral-like strengthening), shorter and more rigid ***Bergtrollus* gen. n.**
 - Mouth cavity much longer, narrower (Fig. 43; *MCAVI ca.* 160 %, *n* = 4), buccal tube with net- /spiral-like strengthening (Fig. 49) ** . . . *Limmenius*

Zusammenfassung

Eine neue Bärtierchengattung und -art, *Bergtrollus dzimbowski* gen. n., sp. n. (Tardigrada) aus Moos der nivalen Zone der Lyngen Alpen in Nordnorwegen wird beschrieben. Charakteristisch für die neue Art ist der außerordentlich verlängerte und herausziehbare Teil der Mundregion (= Proboscis). Bei Eutardigrada wurde ein solches Organ nur in den Gattungen *Milnesioides* Claxton, 1999 und *Limmenius* Horning *et al.*, 1978 festgestellt, die nur selten von Neuseeland und Australien gemeldet wurden. *Bergtrollus dzimbowski* gen. n., sp. n. steht durch die Form und Länge der Mundröhre zwischen den Gattungen *Milnesioides* und *Limmenius*. Durch die Ähnlichkeit der Mundhöhle steht sie nah an der Gattung *Milnesium*. Diagnostische Merkmale von vier bekannten Gattungen der Familie Milnesiidae und der phylogenetische Status innerhalb der Familie werden diskutiert. Ein Bestimmungsschlüssel für diese Gattungen wurde erstellt.

* The milnesiid individuals with strongly retracted proboscis (see e.g. Figs 19, 23) resemble superficially members of *Milnesium* under low (stereo-) microscope magnification.

** The net- /spiral-like strengthening of the mouth tube in *Limmenius* is weakly developed (see Claxton 1999: Fig. 9), often discernible only when its picture is strongly contrasted in an image processing application (Fig. 49).

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Appendix 1. Measurements (μm) of diagnostic characters in the type series of *Bergtrollus dzimbowski* gen. n., sp. n. [the abbreviations (a-y) for particular character are explained in § "Morphometric data", i.e., 'a' = body length, 'b' = proboscis length, etc. The highlighted (**bold**) measurements are those of the holotype].

No. Slide	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s	t	u	v	w	x	y	
1985-J	666.4	91.8	5.4	330.0	123.2	77.0	14.4	4.5	14.4	4.5	14.4	29.7	171.9	103.5	65.7	9.9	22.5	19.8	16.2	13.5	3.6	18.9	18.0	15.3	5.4	
1985-I	512.2				115.2	49.5	13.5	4.5	11.7					67.5	9.0	19.8	17.1	12.6					14.4			
1985-H	736.4	105.3	7.2	292.6	120.6	53.1	14.4	7.2	14.4	7.2	14.4	27.9	162.0	100.8	63.0	9.6	21.6	18.0	15.3	13.5	3.6	22.5	18.9	16.2	14.0	5.0
1985-G	616.0	106.7		277.2	113.4	65.7	14.4	5.4	16.2	28.8	153.0	92.7	63.0	9.9	22.5	18.0	16.2	13.5	3.2	25.2	19.8	16.2	13.5	5.4		
1985-C	492.8			231.0	90.9	48.6	10.8	4.5	11.7						6.8	21.6	18.0	14.4	12.6	2.7						
1982-A	543.2	80.1		6.3										49.5		16.2	13.5	11.7	9.0	2.7		12.6	10.8	4.5		
1982-B	537.6		6.3	7.2		106.2	54.0	12.6	4.5	10.8				65.7	7.2	20.7	16.2	15.3	12.6	3.6	21.6	19.8				
1982-C	608.4				100.8	54.0	13.5	4.1	11.7	24.3					7.2	20.7	18.9	15.3	13.1	3.6	22.5	19.8	16.7	13.5	5.0	
1982-D	621.6		5.4	6.3	260.4	100.8	45.0	12.6	4.1	12.6	24.3			64.8	7.2	21.6	18.0	14.4	12.2	3.6		15.3	12.6	5.4		

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