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Research Paper

Description of *Bryceella perpusilla* n. sp. (Monogononta: Proalidae), a New Rotifer Species from Terrestrial Mosses, with Notes on the Ground Plan of *Bryceella* REMANE, 1929

key words: Rotifera, morphology, taxonomy, trophi, SEM

Abstract

We here describe the new proalid rotifer species *Bryceella perpusilla* n. sp. on the basis of light and electron microscopy. The species, certainly representing one of the smallest rotifer and even metazoan species at all, was obtained in January 2008 from terrestrial mosses of North-west Germany. *Bryceella perpusilla* n. sp. is distinguished from other species of the genus by the very small size, the slender body outline, the short apical styli, the triangular rostrum, the outward curving, blunt and rod-shaped toes, the four-nucleated vitellogermarium, the slender manubria and the caudally directed alulae. With our observations, that can be used for future cladistic analyses of the Proalidae, we are able to define the generic diagnosis of *Bryceella* more precisely and to give an adapted species key.

1. Introduction

The phylum Rotifera is an astonishingly diverse group of aquatic microinvertebrates, rarely exceeding 0.5 mm, that contains more than 2,000 known species worldwide (WALLACE *et al.*, 2006; SEGERS, 2007). The representatives inhabit all kinds of water environments. The monogonont taxon Proalidae is a polyphyletic group (see WILTS *et al.*, 2009a; DE SMET, in press.) of about 50 species that occur free-living, parasitic or epizoic in freshwater, saline water or moist terrestrial habitats. Within Proalidae, one of the smallest genera is *Bryceella* REMANE, 1929 currently containing only two species following DE SMET (1996) and the most recent rotifer checklist published by SEGERS (2007): *Bryceella stylata* (MILNE, 1886) and *Bryceella tenella* (BRYCE, 1897). The species occur in different aquatic and semiaquatic habitats like moors, the psammon of acid waters, mosses and leaf litter. Although new data on the morphology of *Bryceella stylata* have been published recently (WILTS *et al.*, 2009b, WILTS *et al.*, 2010), our knowledge of *B. tenella* remains insufficient. This particularly also

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applies for a third species *Bryceella voigti* sp. inq. RODEWALD, 1934 for which hardly any data exist. The species was initially found in mosses from Romania by RODEWALD (1934), whose description of the species was extremely poor. The minimalistic and rather poor illustrations given by RODEWALD (1934) provide not much more than the general outline of the species and its four trophi elements. One year later, RODEWALD (1935) provides a more detailed description but uses the unmodified figures. Due to its unsatisfactory description the species was queried by KOSTE (1978) and KOSTE and SHIEL (1990).

We found a very small species of *Bryceella*, representing one of the smallest rotiferan and metazoan species at all, in mosses from a forest near Leer, North-west Germany, sharing its habitat with *B. stylata* and several other bdelloid and monogonont rotifer species of *Adineta*, *Philodina*, *Encentrum*, *Dicranophorus* and *Squatinella*. We studied the species on the basis of light and electron microscopy focusing on its anatomy, and revealed several similarities with, but also some differences from, *B. voigti* sp. inq.. Because of these differences and the fragmentary and unreliable description of *B. voigti*, we decided to describe the species we have found as *B. perpusilla* n. sp. We here present a thorough and detailed description of the new species with standardised views of the habitus and the trophi from different angles.

With these results, we are able to improve the existing data for the genus and to define the generic diagnosis more precisely. Moreover, these new morphological data on *Bryceella* are useful for a future cladistic analysis of the Proalidae as suggested by several authors (SØRENSEN, 2005; WILTS *et al.*, 2009a; WILTS *et al.*, 2009b).

2. Materials and Methods

Moist mosses were collected from the Logabirumer Wald, a mixed forest lying marginal above sea level in Leer, North-west Germany (53°15′48.14″ N, 7°31′54.46″ E) in January 2008 and February 2009. Samples were taken from an erratic boulder and a dry ditch, situated in a distance of about 20 meters from each other, returned to the laboratory and subsequently cultured in plastic bags over several weeks at 8 °C. Mosses were washed out at regular intervals and single rotifer specimens were studied by differential interference light microscopy (Leica DMLB) as well as by scanning electron microscopy (SEM) with a Zeiss DSM 940. Light microscopic images were taken with a digital camera (Olympus ColorView) but due to the small size and the very fast, jerky movement of the species it was not easy to obtain images of good quality. Isolated rotifer specimens were narcotized with bupivacaine and fixed with a 4% OsO_4 solution and picric acid formaldehyde at 240 mOsm (after MELONE, 1998). Specimens were dehydrated in a graded ethanol series followed by critical-point drying. Specimens were mounted on stubs and coated with gold. Trophi were prepared under a stereomicroscope (Leica $MZ12_5$) with the procedure of DE SMET (1998) but with SDS/DTT (modified after KLEINOW *et al.*, 1990) as the dissolving agent. Therefore a stock solution was prepared (5.2 g sodium dodecyl sulphate (SDS) + 0.24 g NH_4HCO_3 in 100 ml distilled water). Then 5 ml of the stock solution was mixed with 0.1 g dithiothreitol (DTT) directly before it was applied to a specimen deposited in a droplet of water on a rounded coverslip. After the tissues surrounding the mastax hard parts were completely dissolved, the trophi were carefully washed by degrees with distilled water. Finally, the coverslip carrying the trophi were glued on a SEM stub and coated with platinum. Several attempts were necessary to obtain sucessfull preparations, because the very small and delicate trophi got lost during the preparation several times.

Holotype: A parthenogenetic female in a permanent, glycerine glass slide mount at the Museum für Naturkunde, Germany, Berlin, (ZMB) Generalkatalog freilebende Würmer ZMB Vermes 11368. Paratypes: Deposited paratypes: Three parthenogenetic females in permanent, glycerine glass slide mounts (ZMB Vermes 11369-1, -2 and -3), three parthenogenetic females mounted on a SEM stub (ZMB Vermes 11369-4, -5, -6) and a trophi preparation with three trophi mounted on a SEM stub (ZMB Vermes 11369-7, -8, -9).

Type locality: A moss overgrown boulder in a forest in Leer, Lower Saxony, Germany. January 2008 (53°15′4.42″ N, 7°31′54.56″ E).

Etymology: The species-name is derived from the Latin word *perpusillus*, meaning very small and refers to the very small body size of the species.

3. Results

3.1. Bryceella Remane, *1929 (Proalidae)*

Genus diagnosis: External morphology bilaterally symmetrical; body flattened and fusiform, divided into head with rostrum, neck, trunk and foot with toes; pseudosegmented trunk oval; foot slender, with 2–3 pseudosegments; slender, rounded toes slightly decurved ventrally; eyes absent; corona limited to the ventral head region, with styli and cirri; dorsal antenna covered by an epidermal projection; modified malleate trophi small; inner margins of rami with or without acute or blunt projections anteriorly; ramus foramen subbasalis large; dorsal

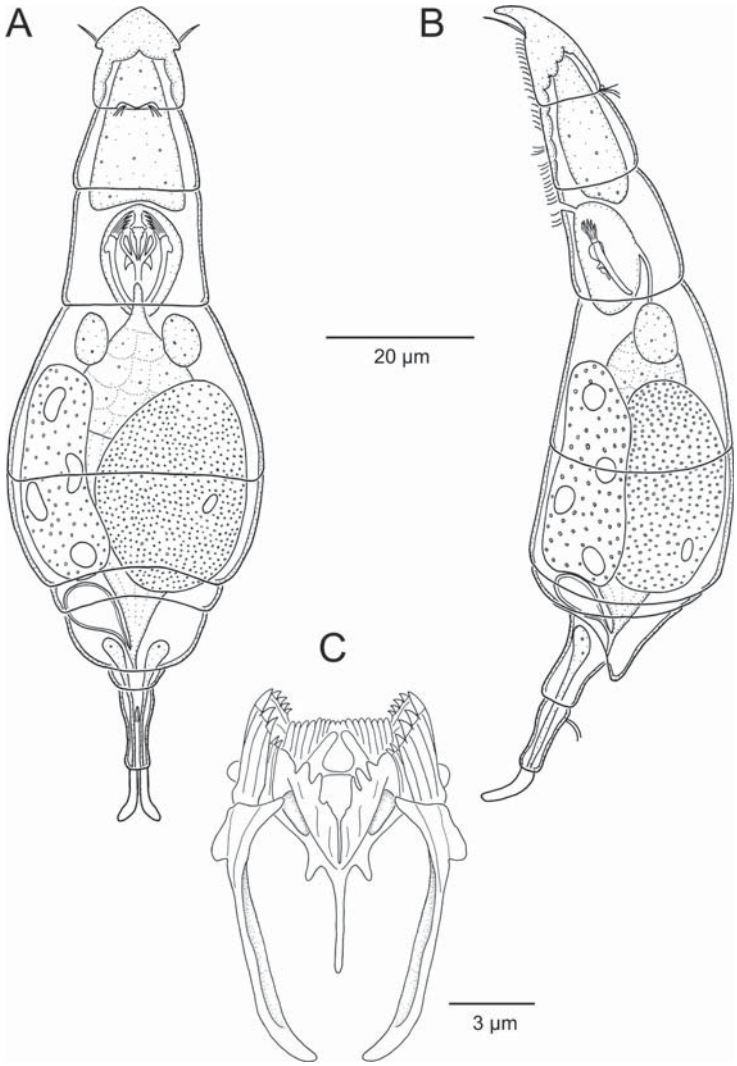

Figure 1. *Bryceella perpusilla* n. sp. A. Habitus in dorsal view. B. Habitus in lateral view. C. Mastax hard parts (trophi) in dorsal view.

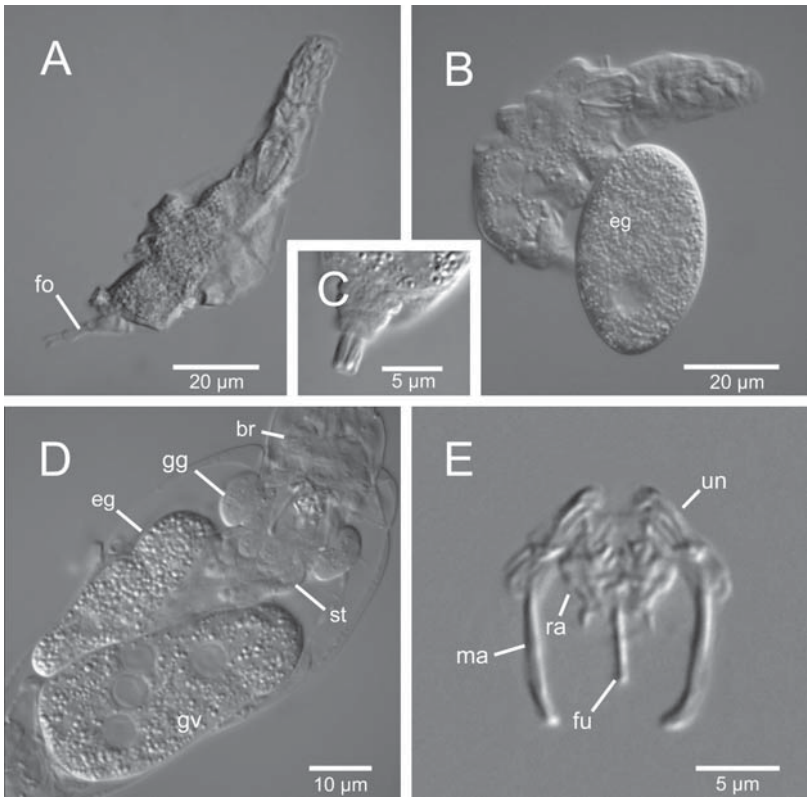

Figure 2. Light microscopic images of *Bryceella perpusilla* n. sp. A. Adult specimen in ventral view. B. Specimen with currently deposited egg. C. Foot with retracted toes. D. Inner organization. E. Mastax hard parts (trophi). **br** brain, **eg** egg, **fo** foot, **fu** fulcrum, **gg** gastric gland, **ma** manubrium, **ra** ramus, **st** stomach, **un** uncus, **gv** germovitellarium.

manubrial chamber drawn out proximally in a thorn-like manner; uncus with 5–7 teeth; distal subuncus with denticulate margin; fulcrum in ventral view rod-shaped, basally with ventral apophysis, caudallly with slanted end; multilayered, digitated hypopharynx.

3.2. Bryceella perpusilla n. sp. (Figs. 1–4)

Species diagnosis: Very small species with slender body outline; corona with two short apical styli; rostrum triangular; foot with two pseudosegments, a caudal antenna and short, blunt, completely retractile toes; vitellarium with four nuclei; inner margins of right ramus with three and left ramus with two cone-shaped projections anteriorly; alulae projecting caudally; right uncus 6-toothed, left uncus 5-toothed; distal subuncus with seven denticles; manubria long and slender; ventral manubrial chamber with shield-like projection; digitated hypopharynx with lobes.

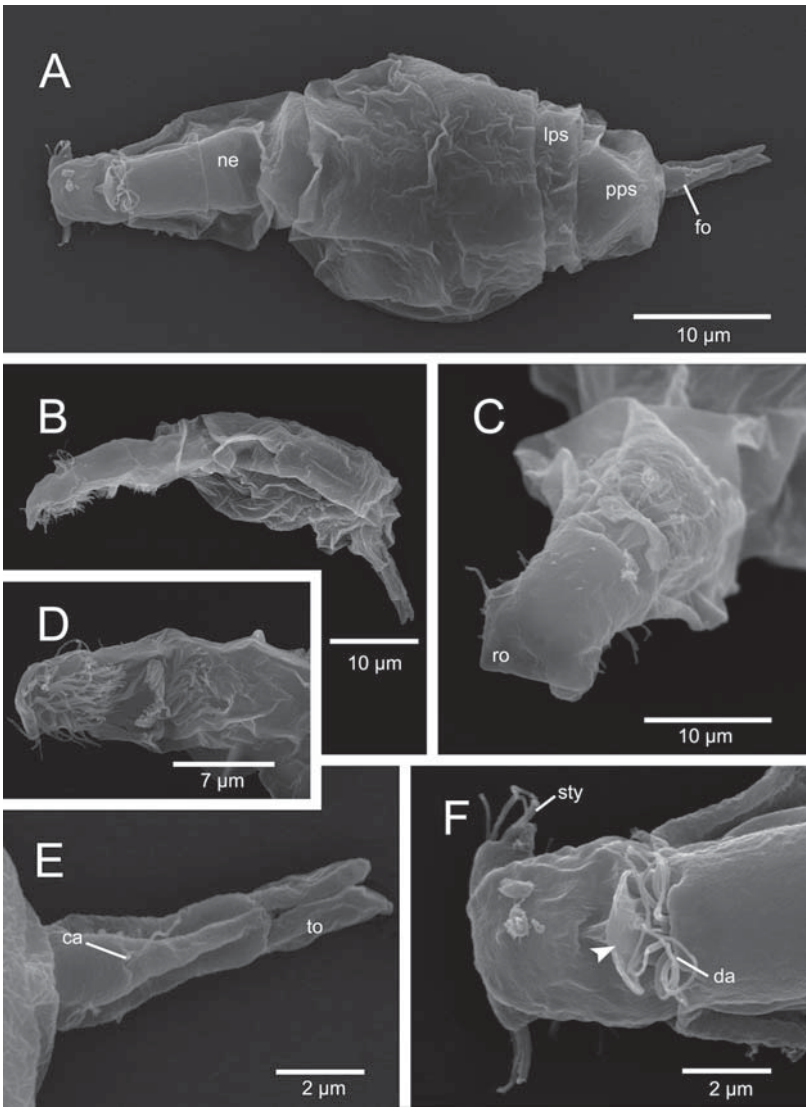

Figure 3. SEM images of the *Bryceella perpusilla* n. sp. A. Specimen in dorsal view. B. Specimen in lateral view. C. Head with rostrum. D. Corona in ventrolateral view. E. Foot in dorsal view. F. Head with dorsal antenna. **ca** caudal antenna, **da** dorsal antenna, **fo** foot, **lps** lumbar pseudosegment, **ne** neck, **pps** preanal pseudosegment, **sty** stylus Arrow head (epidermal projection covering dorsal antenna).

3.2.1. Description of Parthenogenetic Female (Male Unknown)

Habitus: The hyaline, dorsoventrally flattened species has a slender, fusiform outline in dorsal view (Figs. 1A, 2A and 3A) and is divided into three distinct regions: head with neck, trunk and foot with toes (Figs. 1A, B, 3A, B). The epidermis is hardly stiffened and presents a smooth surface (Fig. 3C). The head is only partly contractible into the trunk and consists

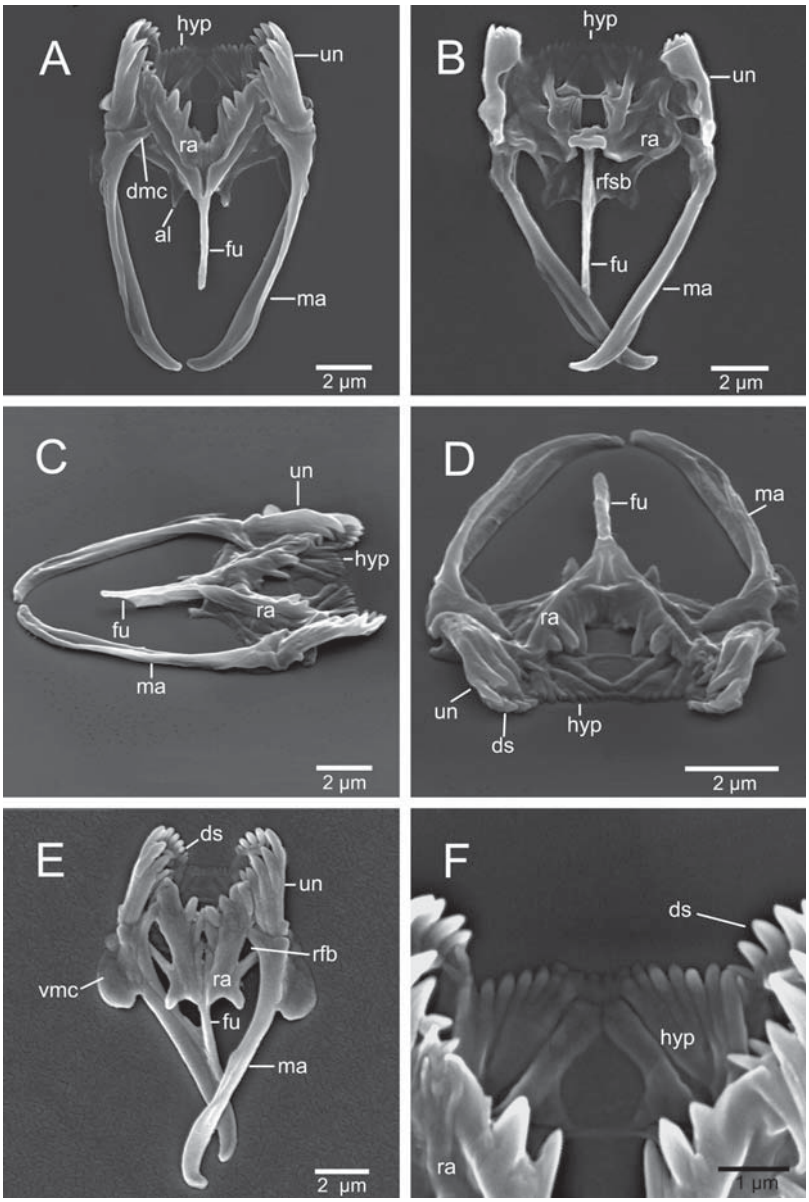

Figure 4. SEM images of the trophi of *Bryceella perpusilla* n. sp. A. Dorsal view. B. Ventral view. C. Dorsolateral view. D. Dorsofrontal view. E. Dorsal view. F. Hypopharynx in dorsal view. **al** alulae, **dmc** dorsal manubrial chamber, **ds** distal subuncus, **fu** fulcrum, **hyp** hypopharynx, **ma** manubrium, **ra** ramus, **rfsb** ramus foramen subbasalis, **rfb** ramus foramen basalis, **un** uncus, **vmc** ventral manubrial chamber.

of three pseudosegments separated from each other and the trunk by distinct transverse folds. The most anterior, rounded pseudosegment carries a triangular, slightly ventrally decurved rostrum (Fig. 3C). At the intersection to the second, subsquare pseudosegment inserts a dorsal antenna. The third head pseudosegment, the so-called neck pseudosegment, is as long as both foregoing pseudosegments and adjoins the trunk. Some individuals show distinct paired light-refracting bodies in the posterior region of the head. The planar corona is limited to the ventral head region (Fig. 3D) and bears two short, diagonal forwards directed styli (compound cilia) that insert anteriorly beneath the rostrum (Figs. 1A, 3F). A small epidermal projection restricts the corona caudally.

The ovoid trunk is wider than the head and is also divided into four pseudosegments that are separated from each other by distinct transverse folds. The two anteriormost pseudosegments are large and are followed by a shorter and narrower lumbar pseudosegment. The fourth, semicircular preanal pseudosegment overlaps the foot partially (Figs. 1B, 3A, B).

The slender foot consists of two equally sized pseudosegments and two blunt, outwardly curving and rod-shaped toes (Figs. 1B and 3E). The toes are completely retractable in the terminal foot pseudosegment (Fig. 2C). A caudal antenna inserts dorsally at the intersection of both foot pseudosegments. Two pedal glands stretch through the foot (Fig. 1A, B).

Digestive system: The digestive tract of *B. perpusilla* consists of the mouth opening, the spherical mastax, the narrow oesophagus, the stomach and the intestine (Fig. 1A). The mouth opening is positioned ventrally at the caudal margin of the corona and leads to the mastax cavity. The mastax resides in the neck pseudosegment and extends only slightly into the trunk (Figs. 1A, 2A, B). Salivary glands are not recognizable. The oesophagus is dorsally attatched to the mastax and leads to the relatively small stomach situated in the first trunk pseudosegment (Figs. 1A, B, 2D). A pair of bulbous gastric glands derives anteriolaterally from the stomach wall (Fig. 2D). The stomach consists of distinctly recognizable stomach cells and is continued by the intestine that is clearly set off from the stomach by a transverse constriction. The intestine leads to the cloaca that opens dorsally below the preanal pseudosegment (Fig. 1A).

Trophi: The dorsoventrally flattened, modified malleate trophi are bilaterally symmetrical, although they show minor asymmetry (Figs. 1C, 2E, 4A).

The unpaired fulcrum usually resides in the longitudinal axis of the body and obliquely attaches to the rami. In dorsal and ventral view it presents a slender, rod-like shape (Fig. 4A, B). Seen from lateral the fulrum exposes an extension and a slanted distal end (Fig. 4C). At its basis the fulcrum presents an oval apophysis (Fig. 4B) ventrally.

The ramus basal and ramus subbasal chambers display distinct openings with the large widened ramus foramen subbasalis directing ventrally (Fig. 4B) and the triangular ramus foramen basalis pointing dorsally (Fig. 4E). The ramus basal chambers are triangular and appear rhombic in combination when seen dorsally. The left ramus features apically two and the right ramus three plump, cone-shaped projections, formed by the ramus subbasal chamber (Figs. 1C and 4A, E). Posteriorly each ramus presents a caudally directed alula (Fig. 4A). Ventral to the rami stretches an unpaired, multilayered and digitated hypopharynx with lobes (Fig. 4A, D, F). The hypopharynx is very fine and only slightly cuticularized.

The paired unci are built on domed plates, carrying the unci teeth decreasing gradually in length from the most dorsal to the most ventral tooth. Both unci carry two weak, lamellar unci teeth followed by three stout teeth on the left and four stout teeth on the right uncus (Fig. 4A, E). Ventral to the largest, bent principal tooth of each uncus is a smaller and angular accessory toothlet located. Ventral to the uncus follows a large and lobate distal subuncus arching under the ramus in the living specimens. It presents about seven denticles that seem to continue the row of the unci teeth (Fig. 4D, E).

The slightly curved manubria are devided into a broad clava and a long, rod-shaped cauda and attach to the unci proximally by fine ligaments. The openings of the three manubrial chambers are not clearly discernable. However, the median chamber forms the elongate

cauda and constitutes therefore the largest part of the manubrium. The ventral manubrial chamber forms a large, shield-like projection expanding ventrolaterally (Figs. 2E, 4A). The dorsal manubrial chamber is drawn out in a thorn-shaped manner (Fig. 4A) and draws into the cauda to a certain degree.

Nervous system and sensory organs: The occipital cerebral ganglion is positioned in the anterior part of the head in front of the mastax (Fig. 2D). At the anterior margin of the second head pseudosegment is a dorsal antenna located that is covered partially by a shield-like projection of the epidermis. The projection arches frontally upwards and backwards over the dorsal antenna caudally (arrow Fig. 3F). The cilia of the dorsal antenna protrude under both sides of the projection. The lateral antennae are apparently absent. At the intersection of the two foot pseudosegments inserts a caudal antenna dorsally, presenting two cilia (Fig. 3E).

Protonephridial system: The protonephridia are paired with distinct terminal organs whose exact number and position were not determined. The collecting tubules open into a contractile bladder that is positioned ventrocaudally in the trunk (Fig. 1A, B). The fluid of the bladder is emptied into the terminal part of the intestine (cloaca).

Reproductive organs: *Bryceella perpusilla* n. sp. is an oviparous species. Parthenogenetic females possess a syncytial germovitellarium situated dorsolaterally in the posterior part of the trunk. The vitellarium contains only four nuclei (Fig. 2D). Most observed amictic females possessed one large, ovoid egg. Germovitellarium and eggs of the investigated specimens show a large amount of refractile lipid droplets inside (Fig. 2B, D).

Measurements: Total length 50–80 µm, maximum dorsoventral dimension 10 µm, maximum width 20 µm, foot length 12 µm, toe length 3 µm, trophi length 13 µm, trophi width 8 µm, ramus length 5 µm, manubria length 10 µm, cauda width 2 µm, fulcrum length 5 µm, egg length 42 µm and egg width 25 µm.

Ecology and Distribution: *Bryceella perpusilla* n. sp. is a perfectly adapted moss inhabitant. The small size and the dorsoventrally flattened body allow the species to penetrate regions of mosses with the finest water film. Specimens glide in a nimble and jerky manner very fast on the moss stalks or graze on detritus particles. In samples they never leave the ground for swimming. We found the species in mosses from one special locality only during cold periods (about 10 °C). However, *Bryceella perpusilla* n. sp. seems to be widely distributed because it was also found among *Sphagnum* in the dystrophic Lake Gorbacz in northeastern Poland by JOLANTA EJSMONT-KARABIN in June 2008 and 2009 (unpublished data).

4. Discussion

4.1. Differential Diagnosis

In the following, we compare *B. perpusilla* n. sp. with *B. stylata*, *B. tenella* and *B. voigti* sp. inq. To this we rely on our own observations and the descriptions given by MILNE (1886), BRYCE (1897), RODEWALD (1934), RODEWALD (1935), KOSTE (1978), DE SMET (1996), KOSTE and TERLUTTER (2001) and WILTS *et al.* (2009b). *Bryceella perpusilla* n. sp. strongly resembles *B. voigti* sp. inq. but as already mentioned, the original description of the latter is not sufficient and reliable enough to identify our species as *B. voigti* sp. inq. Although, both species share the general body outline and the presence of short apical styli, they differ in several morphological aspects: *B. voigti* sp. inq. has only one head pseudosegment in front of the neck, a more rounded rostrum, more acute toes, a smaller mastax and a different, more apical position of the dorsal antenna. Furthermore, *B. voigti* sp. inq. has two pairs of cirrs (one longer pair and one shorter pair) whereas *B. perpusilla* n. sp. has only one short pair of cirrs (so-called styli). *B. voigti* sp. inq. lacks a caudal antenna and has two foot pseudosegments of different length. The toes of *B. voigti* sp. inq. are not retractable whereas in *B. perpusilla* n. sp. they are completely retractable into the terminal foot pseudosegment

(Fig. 2C). The trophi are not illustrated in detail by RODEWALD (1934, 1935) and the author neither stated a subuncus nor a epi- or hypopharynx. After RODEWALD (1935) the uncus of *B. voigti* sp. inq. lacks differentiated uncus teeth. Finally, RODEWALD (1934) reported a body length of 78−130 μm for *B. voigti* sp. inq., whereas *B. perpusilla* n. sp. has only a body length of 50–80 μm.

In comparison with *B. stylata*, *B. perpusilla* n. sp. is notably smaller and has a more slender and a more elongated outline. The latter species lacks lateral styli that are present in *B. stylata* and *B. tenella*. *Bryceella perpusilla* n. sp. also differs from *B. stylata* and *B. tenella* in the lack of lateral antennae and the presence of a caudal antenna. Unlike *B. perpusilla* n. sp., both *B. stylata* and *B. tenella* feature a broad, rounded rostrum. *Bryceella perpusilla* n. sp. and *B. stylata* have a paired epidermal projection restricting the corona caudally, for *B. tenella* the situation is unknown. *Bryceella perpusilla* n. sp. has four trunk pseudosegments whereas *Bryceella stylata* has three and *B. tenella* only two trunk pseudosegments. Dorsal, longitudinal trunk ridges are only present in *B. stylata*. The foot of *B. perpusilla* n. sp. and *B. tenella* presents only two pseudosegments of equal length whereas *B. stylata* possesses three foot pseudosegment of different length. Furthermore, *B. perpusilla* n. sp. has two short, blunt toes without articulating joints that are present in *B. stylata*. The trophi in *B. perpusilla* n. sp. and *B. tenella* have caudally directed alulae unlike the trophi in *B. stylata*. In *B. perpusilla* n. sp., the ramus foramen basalis is triangular and the ramus foramen subbasalis acute-quadrangular. *Bryceella stylata* has a more rounded ramus foramen basalis and a ramus foramen subbasalis of blunt-quadrangular shape. The spine-shaped projections on the inner rami margins of *B. perpusilla* n. sp. are more delicate, less blunt and differently distributed than those in *B. stylata*. *Bryceella tenella* apparently lacks anterior rami projections. Furthermore, *B. stylata* and *B. tenella* possess manubria that are comparatively broader, shorter and more bent than those in *B. perpusilla* n. sp. Each uncus has five teeth in *B. tenella*, six teeth in *B. stylata* and five teeth on the left and six teeth on the right in *B. perpusilla* n. sp. (the small accessory toothlet beyond the principal teeth not included). The fulcrum in *B. perpusilla* n. sp. is proportionately longer and lacks the ventral hook visible in *B. stylata*. The digitated hypopharynx in *B. stylata* has two more or less distinct shovel-like planes contrary to *B. perpusilla* n. sp. whose hypopharnyx has distinct lobes. The vitellarium in *B. perpusilla* n. sp. is four-nucleated whereas in *B. stylata* it presents eight nuclei. For *B. tenella* the number of nuclei is unknown. Finally, after our own observations *B. stylata* is more common and seems to be more widely distributed than *B. perpusilla* n. sp.

Besides, *B. perpusilla* n. sp. corresponds in some respects with *Wierzejskiella vagneri* described by KONIAR (1955) and already KOSTE (1978) expressed the need of verification of *W. vagneri*, due to its similarity with *Bryceella*. It is therefore possible that both species are synonymous. But, similar to the situation of *B. voigti* n. sp., it is not reasonably possible to decide with certainty that our described species is identical with *W. vagneri* due to the insufficient description given by KONIAR (1955) and the differences of the two species, listed in the following. *Bryceella perpusilla* n. sp. and *W. vagneri* share some characters: a dorsoventrally flattened body plan; a spindle-shaped body outline; a triangular, ventrally bent rostrum; a foot with two pseudosegements and rod-shaped, slightly outwards curved memberless toes; absence of lateral antennae; trophi with alulae, jerky movement and appearance in mosses. Furthermore, the body length of *W. vagneri* (100 μm, DE SMET and POURRIOT 1997) is nearly consistent with the size of *B. perpusilla* n. sp. (50–80 μm). Admittedly, *W. vagneri* differs from *B. perpusilla* n. sp. in the following respects: the foot pseudosegments are not equally sized; a caudal antenna is absent; the germovitellarium presents more than four nuclei; a subuncus is absent; a hypopharynx is absent; a large intramalleus is present; the ramus foramen subbasalis are small; the thorn-shaped dorsal manubrial chamber and the shield-like projection of the ventral manubrial chamber are absent.

4.2. Notes on the Ground Plan of Bryceella

The most characteristic feature of *Bryceella* is the presence of a ventrally limited rotatory organ providing compound cilia with a possible sensory function (styli). In comparison with any rotiferan outgroup –, the presence of styli turn out to be an autapomorphic character that has evolved in the stem lineage of *Bryceella*. Further autapomorphic characters of *Bryceella* are the widely opened ramus foramina subbasales and possibly the unpaired, multilayered and digitated hypopharynx. Furthermore, although we do not know *B. tenella* in detail, the following characters can be assumed to be ground pattern features of *Bryceella*: a three-segmented head with neck and rostrum; an epidermal projection covering the dorsal antenna; a digitated distal subuncus, a spur-like, drawn out dorsal manubrial chamber, a fulcrum with a ventral apophysis and a slanted terminal end. Though, without further investigations on the morphology of closely related species, ideally combined with a phylogenetic analysis, it is not possible to decide whether these are plesiomorphic or also autapomorphic characters of *Bryceella*.

4.3. Key to Species

1 Corona with short apical styli; very small, slender body; rostrum triangular; foot with two pseudosegments and caudal antenna; toes short and blunt; vitellarium with 4 nuclei; rami with alulae .....1. *Bryceella perpusilla*
– Corona with long, lateral styli 2
2 Trunk with longitudinal ridges and folds dorsally; foot with three pseudosegments of different length; toes forceps-shaped, slightly curved inwardly, with three articulating joints; fulcrum with ventral directed hook; anterior rami margins with spine-shaped projections; alulae absent; unci with 6 teeth; manubria sickle-shaped .....2. *Bryceella stylata*
– Trunk without longitudinal ridges and folds dorsally; foot with two pseudosegments; toes curved outwardly, without articulating joints; fulcrum without hook; anterior rami margins without projections; alulae present; unci 5-toothed; manubria oval .....3. *Bryceella tenella*

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