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Redescription of *Strombidium coronatum* (Leegaard, 1915) Kahl, 1932 (Ciliophora, Spirotricha) based on live observation, protargol impregnation, and scanning electron microscopy

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Abstract. The oligotrichid ciliate *Strombidium coronatum* (Leegaard, 1915) Kahl, 1932 is redescribed from plankton samples taken in the Irish Sea, using live observation, protargol impregnation, and scanning electron microscopy. The species is characterized by a conspicuous, uniquelly shaped peristome, which is flat and roughly triangular and extends in the sagittal plane. The Irish Sea specimens measure ~ 45 × 25 µm *in vivo* and ~ 40 × 24 µm after protargol impregnation. The girdle kinety is equatorial, ostensibly continuous, and composed of ~ 100 dikinetids. The ventral kinety extends longitudinally on the posterior fifth of the cell and is composed of about five dikinetids. The adoral zone of membranelles is widely open and composed of ~ 18 collar and ~ 12 buccal membranelles; the collar portion is disconnected from the buccal portion. The shape and orientation of the opisthe's adoral zone of membranelles are apparently extraordinary, i.e., the membranelles form an inverted L-shaped stripe extending longitudinally in the elongated posterior cell portion of dividers.

Key words: Marine waters, morphology, Oligotrichida, stomatogenesis, taxonomy.

INTRODUCTION

Oligotrichid spirotrich ciliates are an important component of the microbial loop in the marine pelagial and contribute to the energy flux to the phytoplankton-based food web (Caron *et al.* 2012). Since oligotrichids have species-specific trophic requirements (e.g. bacterivorous, mixotrophic, algivorous; Fenchel and Jonsson 1988, Crawford and Stoecker 1996, Montagnes 1996), proper identification is essential for appreciating their ecological role and for estimating their biodiversity and biogeography. Despite a continuous description of new species and redescription of insufficiently known species (Agatha 2011a), approximately one third of the about 65 *Strombidium* species still require a re-investigation. In the present paper, one of these poorly known species, namely *Strombidium coronatum* (Leegaard, 1915) Kahl, 1932, is thus redescribed based on live observation, protargol-impregnated material, and scanning electron microscopy.

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MATERIALS AND METHODS

Collection: Samples were taken with a 20-µm plankton net from the upper 50 cm of the Irish Sea in front of the Port Erin Marine Laboratory (University of Liverpool, UK) on the Isle of Man in May 2002 at a salinity of ~ 35 psu and a temperature of ~ 12°C. A cultivation of the species for more than two days failed.

Taxonomic studies: Cell movement was studied in a Petri dish (~ 6 cm across; water depth ~ 1.5 cm) under a dissecting microscope (Reichert, Austria) at ~ 20°C. Cell morphology was investigated under a compound microscope equipped with a high-power oil immersion objective as well as bright-field and interference contrast optics (Leitz Diaplan, Leitz Wetzlar GmbH, Germany). Protargol impregnation followed the protocol of Song and Wilbert (1995). For scanning electron microscopy with a Cambridge Stereoscan 250 (Cambridge Instruments Ltd., Cambridge, England), cells were fixed for 30 min in a modified Parducz's solution made of six parts of 2% osmium tetroxide (OsO_4, w/v) in artificial sea water and one part of saturated aqueous mercuric-chloride ($HgCl_2$; Valbonesi and Luporini 1990); further steps followed Foissner (1991). Unfortunately, the sequencing of the small subunit ribosomal RNA gene of six ethanol-fixed cells, following the method of Strüder-Kypke and Lynn (2003), was not successful. Counts and measurements on protargol-impregnated cells were performed at × 1,250 magnification; *in vivo* measurements were made at × 40–1,250 magnification. Drawing of live specimen summarizes the information and is based on mean measurements, while those of protargol-impregnated specimens were made with a drawing device. Terminology follows Agatha and Riedel-Lorjé (2006) and Agatha *et al.* (2005), whereas the classification is according to Agatha (2011b).

Neotype material: Following Foissner (2002), Foissner *et al.* (2002), and Corliss (2003), a neotype is established to provide stability in oligotrichid taxonomy as (i) no type material is available and (ii) the original description lacks many morphologic and morphometric features. The neotype is from the Irish Sea, which belongs to the same cool-temperate biogeographic zone as the original type locality (Skagerrak, North Atlantic; Leegaard 1915, Van der Spoel and Heyman 1983). Slides with protargol-impregnated material, including the neotype, further specimens, and the illustrated divider, are deposited with the relevant cells marked in the Biology Centre of the Museum of Upper Austria (LI) in A-4040 Linz (Austria).

RESULTS

Order Oligotrichida Bütschli, 1887
Family Strombidiidae Fauré-Fremiet, 1970
Genus *Strombidium* Claparède and Lachmann, 1859

Strombidium coronatum (Leegaard, 1915) Kahl, 1932

1915 *Laboea coronata* n. sp. – Leegaard, *Nyt Mag. Naturvid.* **53:** 13.
1932 *Strombidium* (*Laboea*) *coronatum* (Leegaard, 1915) – Kahl, Tierwelt Dtl. **25:** 500 (combining author; revision).
1985 *Strombidium coronatum* (Leegaard, 1915) Kahl, 1932 – Maeda and Carey, *Bull. Ocean Res. Inst., Univ. Tokyo* **19:** 46 (revision).
1988 *Strombidium coronatum* (Leegard, 1915) Kahl, 1932 – Laval-Peuto and Rassoulzadegan, *Hydrobiologia* **159:** 104 (epifluorescence microscopy; incorrect spelling of original author's name).
2005 *Strombidium* sp. – Gismervik, *Aquat. Microb. Ecol.* **40:** 164 (growth and feeding rates).
2008 *Strombidium choronatum* – Claessens, Wickham, Post and Reuter, *Aquat. Microb. Ecol.* **53:** 186 (incorrect subsequent spelling of specific epithet).

Remarks: Since the original description did not provide a diagnosis, the distinguishing features are given here based on the type and neotype populations.

Diagnosis (based on type and neotype populations): Size *in vivo* ~ 45 × 25 µm, after preservation ~ 40–86 × 24–53 µm; obconical, with collar-shaped apical protrusion and peculiarly flattened peristome extending in sagittal plane. Macronucleus and micronucleus usually globular. Girdle kinety equatorial, ostensibly continuous, composed of ~ 100 dikinetids. Ventral kinety extends longitudinally on posterior fifth of cell, composed of about five dikinetids. Adoral zone of membranelles widely open, composed of ~ 18–20 collar and ~ 12 buccal membranelles; collar portion disconnected from buccal portion.

Type locality: The species was discovered in the pelagial of the Skagerrak, North Atlantic, near the village of St. Arendal in Norway (Leegaard 1915). The neotype is from the pelagial of the Irish Sea near the Isle of Man (54°05′06″N, 04°45′50″W), United Kingdom (this study).

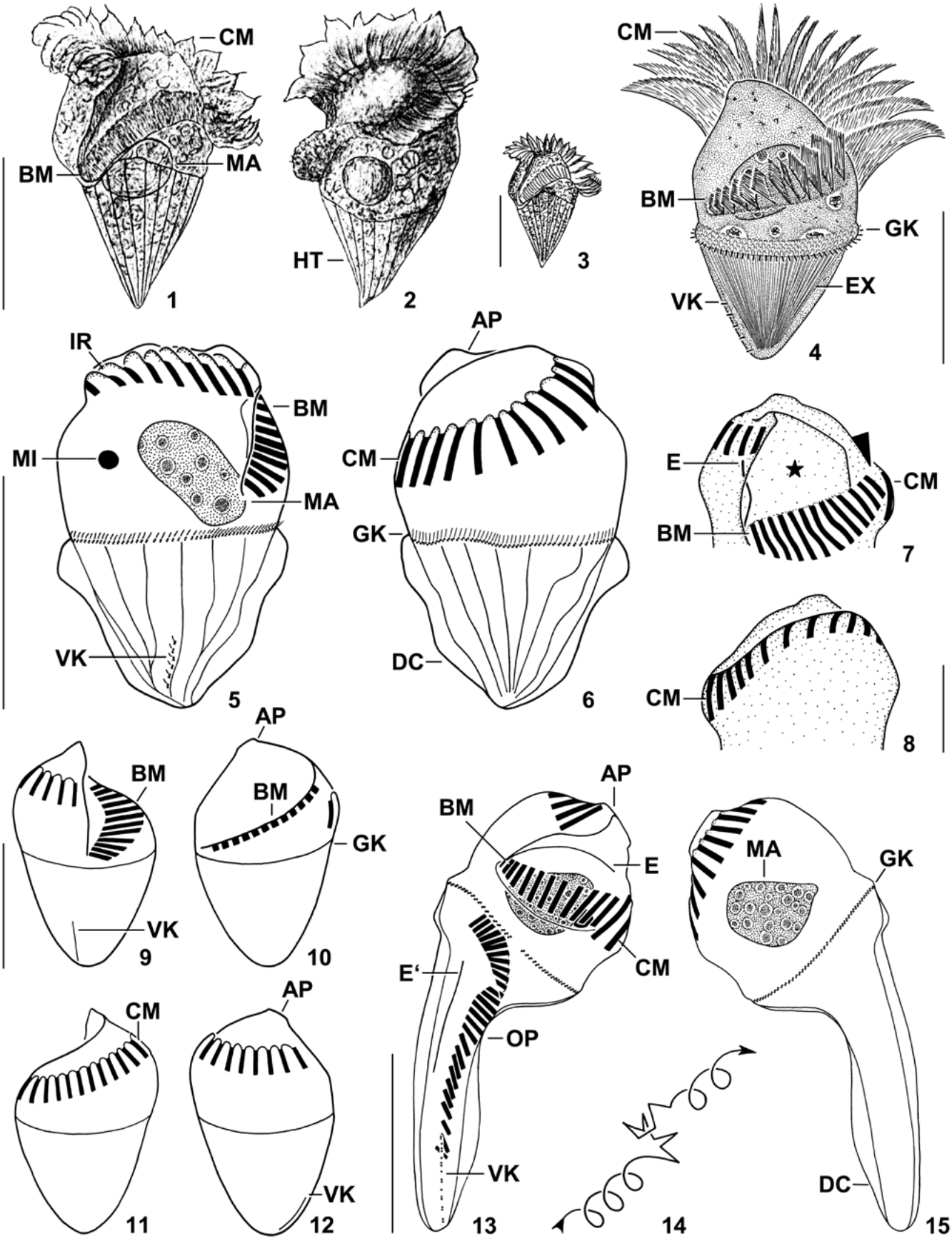
Description of neotype population from the Irish Sea (Figs 4–21; Table 1): Size *in vivo* 35–55 × 20–35 µm (calculated from some measurements of live specimens and values shown in Table 1, assuming a shrinkage of ~ 10% due to the preparation procedure), after protargol impregnation 32–48 × 18–30 µm. Shape roughly obconical, i.e., posterior cell half obconical with rounded end, shape of anterior cell half depends on the side viewed: in right lateral view, roughly triangular with inconspicuous projection at top of buccal lip (Fig. 12); in ventral view, flat peristome separates as sagittal plane vaulted right half from a dorsoventrally inclined left half (Fig. 9); in left lateral view, buccal portion of adoral zone extends on an anti-clockwise inclined shelf more or less perpendicular to the plane, roughly triangular peristome (Figs 4, 10, 17, 19); and in dorsal view, anterior

end slants leftwards (Fig. 11). Apical protrusion up to 4 µm high after protargol impregnation, collar-shaped, increases in height from distal end of collar zone portion to buccal lip, where it often forms a ventrally directed rectangular projection (Figs 5, 6, 9, 11, 12, 17, 21). Macronucleus in anterior cell half, 8–17 × 8–13 µm in size after protargol impregnation, globular to broadly ellipsoidal, with nucleoli ~ 1 µm across (Figs 5, 21). Micronucleus near macronucleus, 1–1.5 µm across after protargol impregnation (Fig. 5). Contractile vacuole and cytopyge not recognizable. Extrusomes insert in a 1.5–2 µm wide stripe directly anteriorly to girdle kinety, form oblique rows with about four attachment sites each, closely spaced, not clustered (Figs 4, 17, 18); individual extrusomes *in vivo* ~ 15–20 × 0.5–0.7 µm in size and acicular (Fig. 4), after protargol impregnation only ~ 7–8 µm long and deformed. Extrusome ejection caused by fixation for scanning electron microscopy (Fig. 17). Cytoplasm colourless, contains food vacuoles with unidentifiable content ~ 3 µm across and occasionally frustules of pennate diatoms ~ 25 × 4 µm in size and centric diatoms ~ 5 µm across. Cell surface posterior to girdle kinety (hemitheca) with several longitudinal ridges in preserved specimens, i.e., distinct ridges extend between girdle kinety and posterior cell end, between each pair about three posteriorly shortened, indistinct ridges (Figs 5, 6, 16–18); polygonal cortical platelets not recognizable. Often, cell surface distinctly distended in protargol-impregnated specimens (Figs 5, 6, 19, 21). Swims in narrow spirals by rotation about main cell axis interrupted by rapid changes in direction (Fig. 14). Somatic cilia ~ 1 µm long *in vivo*. Girdle kinety equatorial, horizontally orientated, ostensibly continuous, and composed of ~ 100 (inferred from their number per 5 µm of circumference) obliquely orientated dikinetids, each has a cilium associated only with the left basal body (Figs 5, 6, 16–18). Ventral kinety extends longitudinally posterior to buccal vertex on rear fifth of cell, composed of 4–6 dikinetids, each has a cilium associated only with the anterior basal body

Table 1. Morphometric data on Strombidium coronatum from the Irish Sea.

Characteristics [a]	x̄	M	SD	SE	CV	Min	Max	n
Cell, length	40.3	40.0	4.5	0.9	11.2	32.0	48.0	23
Cell, width	23.6	23.0	2.6	0.5	11.0	18.0	30.0	23
Cell length:width, ratio	1.7	1.7	0.2	0.0	13.1	1.4	2.1	23
Apical protrusion, height	3.1	3.0	–	–	–	1.0	4.0	10
Anterior cell end to buccal vertex, distance	18.3	19.0	2.3	0.5	12.7	15.0	21.0	23
Anterior cell end to macronucleus, distance	9.3	10.0	2.4	0.5	25.4	5.0	12.0	23
Macronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	24
Macronucleus, length	12.2	12.0	2.1	0.5	17.1	8.0	17.0	21
Macronucleus, width	10.0	10.0	1.2	0.3	12.2	8.0	13.0	21
Micronucleus, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	2
Micronucleus, diameter	1.3	1.3	–	–	–	1.0	1.5	2
Anterior cell end to dorsal portion of girdle kinety, distance	21.9	22.0	2.4	0.5	10.9	18.0	26.0	23
Girdle kinety, number of dikinetids per 5 µm of circumference	7.0	7.0	0.8	0.4	11.7	6.0	8.0	4
Anterior cell end to ventral kinety, distance	32.1	33.0	7.7	2.9	23.9	22.0	44.0	16
Ventral kinety, length	9.0	9.0	2.2	0.8	24.0	5.0	12.0	16
Ventral kinety, number of dikinetids	5.0	5.0	0.7	0.2	14.6	4.0	6.0	16
Adoral zone of membranelles, (outer) diameter	23.6	23.0	2.7	0.6	11.6	21.0	30.0	23
Collar membranelles, number	17.6	18.0	1.1	0.2	6.1	16.0	19.0	21
Buccal membranelles, number	12.1	12.5	1.3	0.3	10.6	9.0	14.0	18

[a] Data based on protargol-impregnated (method of Song and Wilbert 1995) and mounted specimens from field material. Measurements in µm. CV – coefficient of variation in %, M – median, Max – maximum, Min – minimum, n – number of individuals investigated, SD – standard deviation, SE – standard error of arithmetic mean, x̄ – arithmetic mean.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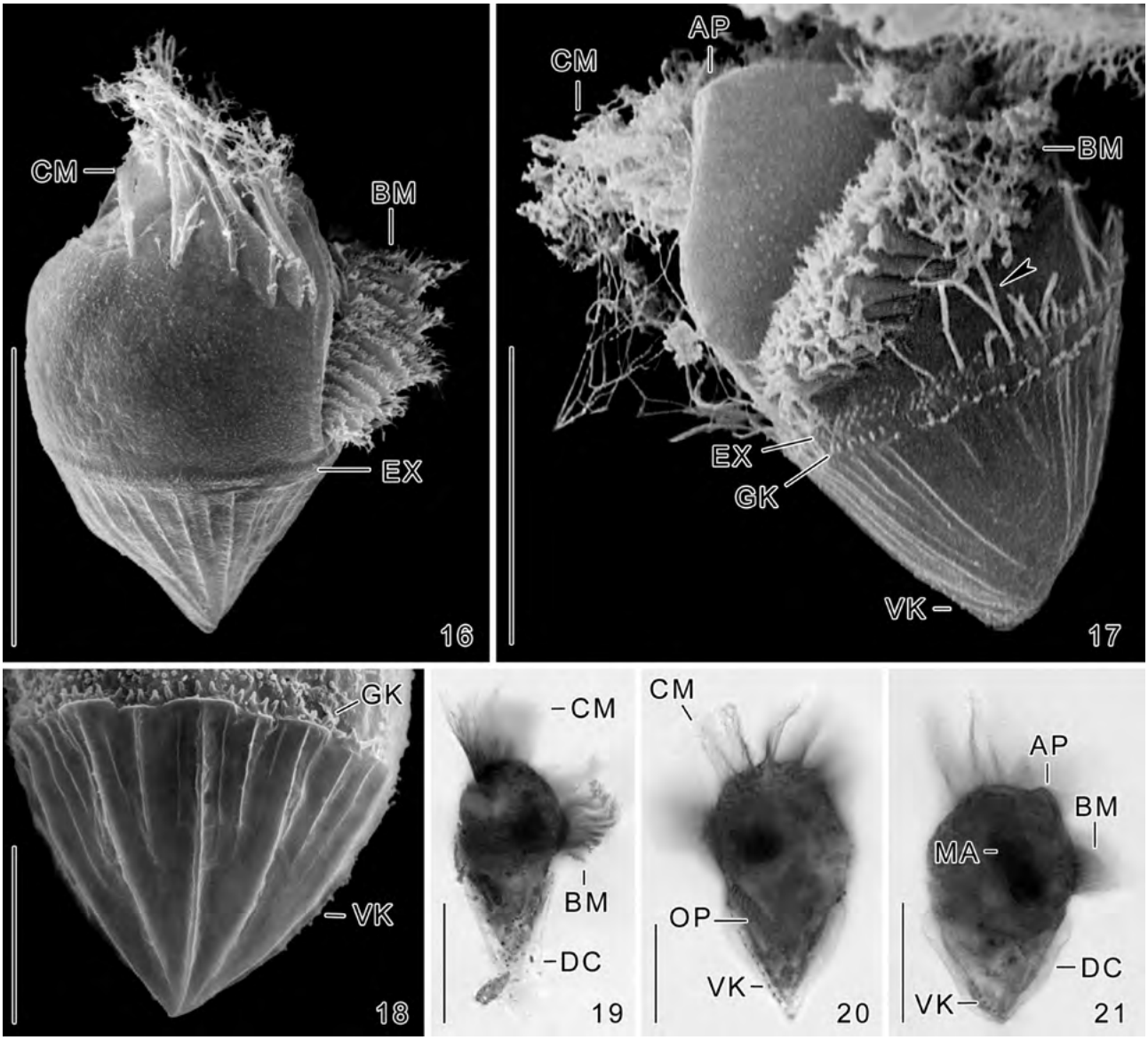

Figs 16–21. *Strombidium coronatum*, Irish Sea specimens (16–18, scanning electron micrographs; 19–21, protargol impregnation, micrographs of several focal planes were stacked, using the computer program CombineZP from Alan Hadley). **16** – ventrolateral view; **17** – left lateral view showing uniquely shaped peristome, which is roughly triangular in outline and almost flat, extending in the sagittal plane. The extrusomes insert in short oblique rows anteriorly to the girdle kinety; note that some of them are just ejected (arrowhead); **18** – posterior cell portion showing the sharp, longitudinal ridges that have already been illustrated in the original description by Leegaard (1915); **19** – left lateral view of an early divider; **20** – dorsolateral view of an early divider; **21** – ventrolateral view. AP – apical protrusion, BM – buccal membranelles, CM – collar membranelles, DC – distended cell surface, EX – extrusome attachment sites, GK – girdle kinety, MA – macronucleus, OP – oral primordium, VK – ventral kinety. Scale bars: 40 µm (16), 20 µm (17, 19–21), and 10 µm (18).

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Figs 1–15. *Strombidium coronatum* (1, 2, after Leegaard 1915; 3, Leegaard's specimen redrawn by Kahl 1932; 4–15, Irish Sea specimens; 1–3, Flemming's fixative; 4, 14, from life; 5–13, 15, protargol impregnation). **1–3** – ventrolateral (1, 3) and left lateral (2) views of same specimen; **4** – left lateral view; **5, 6** – ventrolateral and dorsolateral views of same specimen; **7, 8** – oblique ventral and dorsal views of anterior cell portion in same specimen showing the disconnection of the buccal and collar zone portions (arrowhead) and the flat peristome (asterisk); **9–12** – schematic ventral, left lateral, dorsal, and right lateral views; **13, 15 –** ventrolateral and dorsolateral views of a late early divider; **14** – trajectory. AP – apical protrusion, BM – buccal membranelles, CM – collar membranelles, DC – distended cell surface, E/E' – proter's/opisthe's endoral membrane, EX – extrusomes, GK – girdle kinety, HT – hemitheca, IR – intermembranellar ridges, MA – macronucleus, MI – micronucleus, OP – oral primordium, VK – ventral kinety. Scale bars: 50 µm (1–3), 25 µm (4–6, 9–13, 15), and 10 µm (7, 8).

(Figs 4, 5, 17, 18, 20, 21). Adoral zone of membranelles occupies anterior cell portion, widely open (Figs 4–8, 16, 17). Collar zone portion with "crown-like" appearance (specific epithet derived from Latin noun *corona*), arranged in a semi-circle disconnected from buccal portion, distinctly slanted leftwards on semi-globular right anterior cell portion and especially on dorsal side, composed of 16–19 membranelles. Collar membranelles triangular, up to 15–20 µm long *in vivo*, with cilia decreasing in length from distal to proximal end of membranelles; polykinetids comprise three rows of basal bodies ~ 6 µm long, separated by intermembranellar ridges. Buccal zone portion extends on an oblique shelf more or less perpendicularly to the plane peristome, terminating ~ 45% posteriorly to the apical cell end, composed of 9–14 almost rectangular membranelles with cilia up to 7 µm long *in vivo*; structure of membranelles not recognizable. Endoral membrane not clearly seen in protargol preparations (Figs 5, 7) and not recognizable in scanning electron micrographs as probably covered with perilemma, extends near ventral margin of peristome. Pharyngeal fibres not recognizable.

Data about ontogenesis base on some early dividers and one late early division stage. Oral primordium develops in transient subsurface tube posterior to girdle kinety and left of ventral kinety (Figs 13, 20). Opisthe's adoral zone achieves uncommon shape and orientation in late early divider (Figs 13, 15): it is inversely L-shaped and longitudinally orientated, performing a ~ 180° turn in the unusually elongated posterior cell half. Position of new endoral membrane untypical because distinctly apart from proximal end of opisthe's adoral zone (Fig. 13). Girdle kinety and stripe of extrusome attachment sites with gap in left half of ventral side.

DISCUSSION

Comparison with original description: The short original description by Leegaard (1915) was based on preserved material from a single sampling occasion in the Skagerrak that possibly provided only a single specimen of this species. The Irish Sea specimens match the original description in the uniquely flattened peristome (cp. Figs 4, 10, 17 with Figs 1–3), the arrangement and number of the collar membranelles (16–19 vs. ~ 20 as estimated from Fig. 1), an equatorial upper margin of the hemitheca, and longitudinal ridges on the posterior cell half (cp. Figs 5, 6, 16–18 with Figs 1, 2). The difference in cell size (~ 40 × 25 µm after protargol impregnation vs. ~ 86 × 53 µm after preservation with Flemming's fixative) is attributed to the huge intraspecific variability common in oligotrichid ciliates, and the two populations are regarded as conspecific, especially, as they occur in the same biogeographic region.

Comparison with further populations: Gismervik (2005) collected a *Strombidium* species near the type locality, namely, in the Oslofjord (Norway), and impregnated it with protargol. The specimens were characterized by a cell length of 40 ± 3.4 µm, 18 collar membranelles, 12 buccal membranelles, a ventral kinety with five kinetids, and an equatorial girdle kinety completely surrounding the cell. Like Gismervik (2005), Montagnes *et al.* (2010) observed a detachment of the hemitheca in their Arctic specimens, resulting in a curious elongation of the posterior cell portion not found in the Irish Sea specimens. The morphometric data and micrographs provided by both publications strongly indicate a conspecificity of the Norwegian, Arctic, and Irish Sea specimens. The Mediterranean specimens studied with epifluorescence microscopy match the original description in the cell size (80 × 47 µm vs. 86 × 53 µm; Leegaard 1915, Laval-Peuto and Rassoulzadegan 1988), while the length of ~ 100 µm given by Kahl (1932) and Carey (1992) includes the collar membranelles, which are 15–20 µm long (this study, Leegaard 1915). The North Pacific specimens studied by Sime-Ngando *et al.* (1992) had a length of 65 µm after preservation with mercuric chloride.

Generic affiliation: Agatha (2011b) distinguished three strombidiid genera with a horizontally orientated, ostensibly continuous girdle kinety: *Strombidium* (girdle kinety directly posterior to extrusome attachment sites and anterior to oral primordium), *Opisthostrombidium* (extrusome attachment sites directly anterior to girdle kinety and posterior to oral primordium), and *Foissneridium* (oral primordium between extrusome attachment sites and girdle kinety). Based on the arrangement of the extrusome attachment sites directly anterior to the girdle kinety and the position of the oral primordium posterior to the girdle kinety, the generic affiliation of *Strombidium coronatum* seems to be correct.

Some early dividers and a single late early division stage were found in the protargol slides. While the early dividers of *S. coronatum* match the findings in congeners, the single late early divider shows, however, some conspicuous differences. The shape and orientation of the oral primordium differ from those in

other *Strombidium* species, i.e., the new adoral membranelles form an inversely L-shaped, longitudinally orientated stripe instead of a horizontally orientated C-shaped zone. Concurrent with the growth of the oral primordium, the posterior cell portion shows a unique and conspicuous elongation. Likewise, the position of the endoral membrane is exceptional, because it is apparently distinctly apart from the proximal end of the new adoral zone. Agatha (2003) suspected that the ontogenetic patterns in strombidiids are diverse and might allow a split of the genetically non-monophyletic genus *Strombidium*. However, a new genus for *S. coronatum* should only be established after confirmation of the present anecdotal observation by a detailed study of its cell division.

Comparison with congeners: The shape of the peristome and the elongation of the posterior cell half during stomatogenesis are unique; thus, the species can hardly be confused.

Occurrence and ecology: The species was found in marine and brackish waters. The records from the pelagial of the Arctic Sea (Montagnes *et al.* 2010), the North Atlantic (this study, Leegaard 1915), the Mediterranean Sea (Laval-Peuto and Rassoulzadegan 1988), and the North Pacific (Sime-Ngando *et al.* 1992) as well as from the pelagial of brackish waters in a fjord at the North Atlantic coast (Gismervik 2005) are substantiated by measurements and partially by illustrations. Additionally, there are uncorroborated records from the pelagial of the oligotrophic Gulf of Aqaba, Red Sea (Claessens *et al.* 2008) and the North Atlantic (Nielsen *et al.* 1993, Crespo *et al.* 2008) as well as the brackish waters in the Baltic Sea (Bjørnsen *et al.* 1993) and the Black Sea plus adjacent lagoons (Kurilov 2004, 2006). Likewise, the records from the benthal of the brackish waters in the White Sea are unsubstantiated (Mazei and Burkovsky 2005, Tchesunova *et al.* 2008). The record from a Swedish lake by Xu and Cronberg (2010) is, however, probably a misidentification as the vast majority of marine ciliates do not penetrate into freshwater and freshwater ciliates usually do not tolerate marine waters, which causes a species minimum at 5–7‰ (Ax and Ax 1960).

These records together with own data from the coastal waters off the Island of Sylt (North Sea) and the polder basins of the Beltringharder Koog and the Speicherkoog Dithmarschen (North Sea coast of Northern Germany) indicate that the species tolerates salinities ranging from 35 psu to mesohaline conditions and temperatures from 3–20°C.

In laboratory experiments, Gismervik (2005) cultured *S. coronatum* with the chlorophyte *Nephroselmis pyriformis* as food. The clearance rate of the ciliate was on average 3.3 ± 0.3 µl ind^{-1} h^{-1}, and the species had an ingestion rate of on average 1,456 ± 314 *Nephroselmis* cells per specimen and day. In cultures, the growth rates were 0.61–0.97 d^{-1} at 12.5°C (Gismervik 2005).

In contrast to many of its congeners, *S. coronatum* is apparently not mixotrophic as indicated by its green autofluorescence (Laval-Peuto and Rassoulzadegan 1988). These findings are in congruence with the observations by Gismervik (2005) and the light microscopic investigation on the Irish Sea specimens (this study), which could not reveal sequestered plastids.

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