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Redescription of *Tintinnopsis parvula* Jörgensen, 1912 (Ciliophora: Spirotrichea: Tintinnina), Including a Novel Lorica Matrix

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Summary. *Tintinnopsis parvula* Jörgensen, 1912 has apparently a cosmopolitan distribution in the pelagial of marine and brackish coastal waters. The species is redescribed based on material from the Irish Sea off the Isle of Man, using live observation, protargol impregnation, and scanning electron microscopy. The agglomerated and stiff lorica measures 38–60 × 24–31 µm and is composed of a usually broadly obovate bowl and a slightly narrowed cylindroidal collar with an inner diameter of ~ 20 µm. The somatic ciliary pattern is of the most complex type, viz., it comprises a ventral, dorsal, and posterior kinety as well as a right, left, and lateral ciliary field. The left ciliary field comprises four kineties, the lateral field about ten kineties, and the right field five kineties. The oral primordium develops apparently apokinetally posterior to the lateral ciliary field and generates ~ 15 collar membranelles and one buccal membranelle. Two further populations were studied: one from the North Sea off the Island of Sylt, the other from brackish polder basins at the German North Sea coast; they match the Irish Sea specimens in all main features. The loricae formed in almost particle-free cultures have a thin wall composed of an irregular network of fibres and very few attached or interwoven particles. This matrix type differs from the other three types found in congeners. Hence, the matrix ultrastructure might represent a promising feature for a reliable subdivision of the species-rich genus *Tintinnopsis* Stein, 1867 in the future.

Key words: Biogeography, ciliary pattern, ciliate, lorica ultrastructure, morphology, neotypification, taxonomy, tintinnid.

INTRODUCTION

The current classification of the tintinnid ciliates is exclusively based on lorica features (Kofoid and Campbell 1929, 1939; Laval-Peuto 1994; Lynn 2008), although the polymorphism of this structure due to environmental conditions and the life cycle is known (Biernacka 1965, 1968; Gold and Morales 1974, 1975a; Bakker and Phaff 1976; Laval-Peuto 1977, 1981; Davis 1978, 1981; Bernatzky *et al.* 1981; Laval-Peuto and Brownlee 1986; Boltovskoy *et al.* 1990). A far-reaching revision is thus required, but necessitates cytological investigations and gene sequence analyses in the more than 1,200 tintinnid species. Even though the ~ 160 *Tintinnopsis* species are usually abundant in coastal waters worldwide (Bakker and Phaff 1976, Pierce and Turner 1993), the cell features have been studied in merely four species (Foissner and Wilbert 1979, Agatha and Riedel-Lorjé 2006, Cai *et al.* 2006, Agatha 2008), and seven species have been sequenced (Snoeyenbos-West *et al.* 2002; Strüder-Kypke and Lynn 2003, 2008; Li

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et al. 2009). Accordingly, the present redescription of *Tintinnopsis parvula* Jörgensen, 1912 contributes to the establishment of a natural tintinnid classification, especially, as three populations were investigated and a scanning electron microscopic study of the lorica matrix, a promising taxonomic feature, was performed.

MATERIALS AND METHODS

Collection: The sampling was performed in three different regions and periods.

Irish Sea specimens: The samples were taken with a 20-µm plankton net from the Irish Sea in front of the Port Erin Marine Laboratory (University of Liverpool) on the Isle of Man (54°05′08″N, 04°45′59″W) in May 2002 at a salinity of ~ 35‰ and a water temperature of ~ 12°C. Live observation, protargol impregnation, and scanning electron microscopy were performed.

North Sea specimens: The samples were taken by bucket at high tide in the entrance to the List Harbour on the Island of Sylt (55°01′00″N, 08°26′27″E) between September and December 1995 at a salinity of ~ 31‰ and a water temperature of ~ 9°C. Live observation, protargol impregnation, and scanning electron microscopy were performed.

Polder specimens: The samples were taken between 1991 and 1993 in the basins of two polders, the Beltringharder Koog (54°33′16″N, 08°53′45″E) and the Speicherkoog Dithmarschen (54°05′18″N, 08°58′58″E). These shallow (up to 15 m deep) basins contain brackish waters of changing salinities due to their transient connection with the Wadden Sea by sluice gates and freshwater inflow (rainwater, ground water, streams). Furthermore, they are characterized by reduced tidal currents, high turbidity, and eutrophication due to nutrient loads drained from agricultural areas (Agatha *et al.* 1994, Riedel-Lorjé *et al.* 1998). The collection was performed monthly (December to February), fortnightly (March and November), or weekly (other month) by bucket at the bank of the basins. One subsample was immediately preserved with 1% Lugol's iodine solution and analyzed latest six month after sampling for abundances by J. C. Riedel-Lorjé (Agatha *et al.* 1994), while the other subsample was preserved for protargol impregnation.

Taxonomic studies: Cell movement was studied in a Petri dish (~ 5 cm across; water depth ~ 0.8 cm) under a dissecting microscope 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. Protargol impregnation followed the protocol of Song and Wilbert (1995). For scanning electron microscopy, the cells were fixed for 30 min. in a modified Parducz' solution made of six parts of 2% (w/v) osmium tetroxide in artificial sea water and one part of saturated aqueous mercuric-chloride (Valbonesi and Luporini 1990); further steps followed Foissner (1991).

Counts and measurements on protargol-impregnated cells were performed at a magnification of × 1,000; *in vivo* measurements were conducted at a magnification of × 40–1,200. Since it was usually impossible to count all somatic kineties in a specimen, as the curved and densely spaced ciliary rows could not be discerned in the laterally orientated fields, the kinetal density index established by Snyder and Brownlee (1991) was not calculated.

Specimens from the Irish Sea could be cultured for four days in a plastic Petri dish (~ 5 cm across; water depth ~ 0.8 cm), using water from the sampling site, a temperature of ~ 12°C, a cycle of 12 h light to 12 h dark with an irradiance of ~ 15 µE m^{-2} s^{-1}, and a mixture of the co-occurring flagellates as prey. Live observations were conducted, and the newly formed loricae were studied in the scanning electron microscope.

Unfortunately, the sequencing of the small subunit ribosomal RNA (SSrRNA) gene was not successful.

Illustrations: Drawings of live specimens are based on free-hand sketches and mean measurements and summarize the information, while those of protargol-impregnated specimens were made with a drawing device. The kinetal map depicts the ciliary pattern of a protargol-impregnated morphostatic specimen in two dimensions (Foissner and Wilbert 1979, Choi *et al.* 1992), that is, the cortex is drawn as cut longitudinally along the dorsal kinety; it is also based on mean measurements. Horizontal bars symbolize the collar membranelles, diagonal bars those membranelles that are partially or entirely in the buccal cavity, namely, the elongated collar membranelles and the buccal membranelle. Cell circumference is proportional to the length of the kineties. Kinety curvatures are neglected, except for the ventral and last kinety, whose course might be of taxonomic significance. The somatic cilia are symbolized by perpendicular lines, differences in their length are not considered.

Terminology: The terminology follows Agatha and Riedel-Lorjé (2006) as well as Laval-Peuto *et al.* (1979), who distinguished two types of striae: exterior striae extending longitudinally on the outer portions of the collar membranelles and median striae extending on the middle portions.

Species identification: The diameter of the lorica opening is the least variable dimension and a taxonomically reliable character (Balech 1959; Halme and Lukkarinen 1960; Gold 1969; Gold and Morales 1975a, c, 1976a; Laval-Peuto and Brownlee 1986). Together with the lorica shape, width, and structure, this feature is used for species identification.

Neotype material: Following Foissner (2002), Foissner *et al.* (2002), and Corliss (2003), a neotype is established to provide stability in tintinnid taxonomy as (i) no type material is available, (ii) the original description lacks many morphologic and morphometric features, and (iii) the species has several subjective synonyms. Since the investigations on the Irish Sea specimens were more detailed than those on the two other populations, the species is neotypified from the Irish Sea, which belongs to the same cool-temperate biogeographic zone (Van der Spoel and Heyman 1983) as the original type locality (Kiel Bight, Baltic Sea; Brandt 1906, 1907). 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

Tintinnopsis parvula Jörgensen, 1912

1896 *Tintinnopsis beroidea* Stein – Brandt, *Biblthca zool*. **8:** 57.
1900 *Tintinnopsis beroidea* – Levander, *Acta Soc. Fauna Flora fenn*. **18:** 18.
1906 *Tintinnopsis beroidea* Stein – Brandt, Ergebn. Plankton-Exped. Humboldt-Stiftung 3 La: 16 + Plate 16, Figs 5, 7, 11 (figures and figure explanations).
1907 *Tintinnopsis beroidea* Stein – Brandt, Ergebn. Plankton-Exped. Humboldt-Stiftung 3 La: 138 (species description).
1908 *Tintinnopsis beroidea* Stein – Laackmann, Wiss. Meeresunters., *Abt. Kiel* **10:** 20 (pro parte; Figs 6, 7, 51, 52; conjugation).
1910 *Tintinnopsis fusus* sp. n. – Meunier, Campagne Arctique de 1907: 141 (pro parte; Plate 12, Figs 26–28).
1911 *Tintinnopsis beroidea* – Lohmann, *Int. Revue ges. Hydrobiol. Hydrogr.* **4:** 21.
1912 *Tintinnopsis parvula* n. nom. – Jörgensen, *Sven. Hydrogr. Biol. Komm. Skr.* **4:** 2 (not a new name, but a new species).
1922 *Tintinnopsis beroidea* – Rossolimo, Russk. *Arkh. Protist.* **1:** 24.
1927 *Tintinnopsis parvula* – Jörgensen, *Tierwelt Nord- u. Ostsee* **8 II$_{c1}$:** 7.
1927 *Tintinnopsis beroidea* St. – Rossolimo, *Trudy morsk. nauch. Inst*. **2:** 65 (pro parte; Fig. 1, specimens 1–5).
1937 *Tintinnopsis rapa* Meunier – Hada, *J. Fac. Sci. Hokkaido Univ. (Zool.)* **5:** 171 (pro parte; Fig. 22b–d).
1974 *Tintinnopsis parvula* Jörgensen, 1912 – Burkovsky, Zamyshlyak and Poskryakova, *Zool. Zh*. **53:** 1761 (pro parte; Fig. 5a).
1976 *Tintinnopsis beroidea* Stein – Bakker and Phaff, *Hydrobiologia* **50:** 104 (pro parte; Figs 5, 7).
1976 *Tintinnopsis rapa* Meunier – Gold and Morales, *Biol. Bull. mar. biol. Lab., Woods Hole* **150:** 387 (pro parte; Fig. 3e–g).

Taxonomy and nomenclature: The taxonomy of *Tintinnopsis* species is difficult, as the species limits are often debatable. Therefore, the species are frequently concerned with synonymizations or splits. This is also true for *T. parvula*, which was distinguished from *T. beroidea* Stein, 1867 by Jörgensen (1912). The original description of *T. beroidea* is very short and lacks measurements and illustrations (Stein 1867). The first redescription by Entz (1884) remedied these deficiencies and was thus regarded as authoritative (Jörgensen 1912, Kofoid and Campbell 1929). Brandt (1896; Fig. 1) identified loricae found in Vanhöffen's material from the Arctic Sea and samples taken in the Baltic Sea (Brandt 1906, 1907; Figs 2–5) with *T. beroidea*. However, they differ from those studied by Entz (1884) in a narrowed collar (present vs. absent) and a smaller size (bowl width 25–35 µm vs. 50–60 µm; opening diameter 20–24 µm vs. 50–60 µm). Thus, Jörgensen (1912) established for Brandt's (1906, 1907) specimens from the Baltic Sea a distinct species, namely, *Tintinnopsis parvula*.

Meunier (1910) described four loricae in *Tintinnopsis fusus*: the typical form (~ 80 × 40 µm in size; opening ~ 26 µm across; collar with spiralled structures) as well as three shape and size variants (Figs 33–35; ~ 40–55 × 20–30 µm in size; opening ~ 15–20 µm across; collar without spiralled structures). Kofoid and Campbell (1929) synonymized all of them with *T. parvula*. At the present state of knowledge, however, only the variants match the type and neotype in the lorica size and the absence of a spiralled collar, justifying a synonymization with *T. parvula*. Van Breemen (1905) described a *Tintinnopsis* spec. from the North Sea plankton, which was also synonymized with *T. parvula* by Kofoid and Campbell (1929), although the acute (27°) posterior end of the lorica (54–66 µm long; opening 24–28 µm across) indicates a conspecificity with *Tintinnopsis rapa* (see 'Comparison with similar congeners'). In the Kara Sea, Rossolimo (1927) found a series of twenty loricae (52–75 × 31–38 µm in size; opening 22–38 µm across) varying in the presence of a narrowed collar and the shape of the posterior end (obconical with an angle of 45° to broadly rounded). Although they did not agree with the authoritative redescription by Entz (1884) in the opening diameter (22–38 µm vs. 50–60 µm across), Rossolimo (1927) identified the specimens with *T. beroidea*. Hence, I agree with Kofoid and Campbell (1929) in affiliating at least the five loricae with narrowed collars (Figs 28–32) to *T. parvula*; the conspecificity of the remaining loricae of Rossolimo's (1927) series is unlikely, but verification is required.

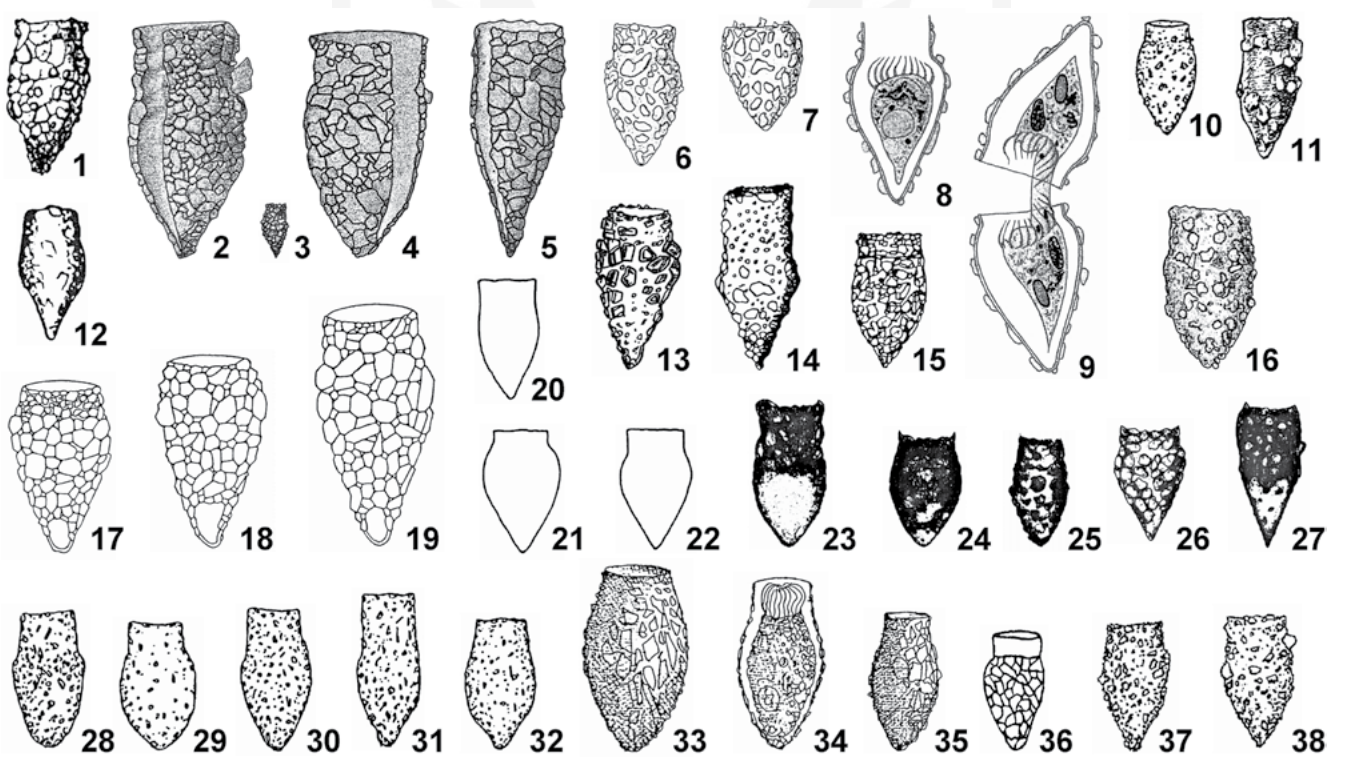
Improved diagnosis (based on type and neotype populations): Lorica on average 50–60 µm long and 28–30 µm wide, densely agglomerated, stiff, composed of a usually broadly obovate bowl with a posterior angle of ~ 50–60° and a ~ 10–17 µm long cylindroidal collar with an inner diameter of ~ 20–22 µm. Extended cell *in vivo* ~ 55–65 × 18–20 µm, elongate obconical, and highly contractile. Two macronuclear nodules and two micronuclei. Ventral kinety usually commences anterior to second kinety of right ciliary field. Invariably five kineties in right ciliary field and four in left ciliary field, all composed of monokinetids and one anterior dikinetid, except for second kinety with on average three anterior dikinetids. Lateral ciliary field with about ten monokinetidal kineties. On average 16 dikinetids in

dorsal kinety and six in posterior kinety, with a cilium only at each posterior basal body. About 15 collar membranelles, of which four extend into buccal cavity; one buccal membranelle.

Type locality: Jörgensen (1912) established the species for specimens collected by Brandt (1906, 1907) from the pelagial of the Kiel Bight (~ 54°26′N, 10°12′E), Baltic Sea. The neotype material is from the pelagial of the Irish Sea near the village of Port Erin, Isle of Man (54°05′08″N, 04°45′59″W).

Description of neotype population from the Irish Sea (Figs 39–73; Table 1): Lorica 38–60 µm long and 24–31 µm wide after protargol impregnation, composed of a bowl and a collar (Figs 39, 42, 47–60; Table 1). Bowl occupies ~ 80% of lorica length, usually broadly obovate and bluntly pointed with an angle of ~ 60°, without posterior process. Collar cylindroidal, narrower than bowl, with an inner diameter of 18–23 µm and a highly variable length of up to 19 µm. Wall of loricae from field material densely agglomerated, stiff, and ~ 2 µm thick, without spiralled or annulated structures. Agglomerated particles of abiotic and, rarely, biotic (e.g. diatom frustules and their fragments) origin, larger in bowl (up to 11 × 6 µm) than in collar, mask lorica matrix and live cell. Wall of loricae formed in almost particle-free cultures transparent, weak, and often deformed as composed of an only ~ 1 µm thick, sparsely agglomerated matrix comprising an irregular network of fibres ~ 0.04–0.3 µm thick and some attached or interwoven particles (fluffy material probably debris, bacteria, silt grains, rarely diatom frustules and crystals; Figs 64–73).

Fully extended cell *in vivo* 40–65 × 16–20 µm; elongate obconical, i.e. cell proper gradually merges ven-



Figs 1–38. *Tintinnopsis parvula* and its synonyms from the literature. Lateral views (1–7, 10–19, 23–33, 35–38), optical sections (8, 9, 34), and outlines (20–22) of loricae, including those of a post-conjugant (8) and a conjugating pair (9). **1** – from Brandt (1896), length 55 µm; **2–5** – specimens from the type population according to Brandt (1906), length 59 µm, ? µm, 57 µm, 59 µm; **6–9** – from Laackmann (1908), length 60 µm, 46 µm, 50 µm, 50 µm; **10** – from Rossolimo (1922), length 45 µm; **11** – from Biernacka (1956), length ? µm; **12** – from Biernacka (1948), length ? µm; **13** – from Burkovsky *et al.* (1974), length 58 µm; **14** – from Osorio-Tafall (1941), length 47 µm; **15** – from Paulmier (1995), length ? µm; **16** – from Cordeiro and Sassi (1997), length 48 µm; **17–19** – from Hada (1937), length 37 µm, 41 µm, 53 µm; **20–22** – from Gold and Morales (1976a), length 46 µm, 46 µm, 46 µm; **23–27** – from Bakker and Phaff (1976), length 60 µm, 48 µm, 45 µm, 48 µm, 64 µm; **28–32** – from Rossolimo (1927), length ? µm; **33–35** – from Meunier (1910), length 56 µm, 54 µm, 42 µm; **36** – from Lohmann (1911), length ? µm; **37**, **38** – from Levander (1900), length 57 µm, 60 µm.

Table 1. Morphometric data on *Tintinnopsis parvula* from the Irish Sea (IS), the North Sea (NS), and the polder basins (PB).

Characteristics [a]	Pop	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Lorica, length	IS	50.9	50.0	4.3	0.5	8.4	38.0	60.0	62
	NS	47.5	46.0	5.0	1.1	10.5	40.0	56.0	21
	PB [d]	46.3	45.0	4.6	0.6	10.0	37.0	60.0	61
Lorica, bowl length	IS	40.5	40.0	3.7	0.5	9.2	31.0	55.0	62
Lorica, bowl width	IS	27.7	28.0	1.5	0.2	5.3	24.0	31.0	62
	NS	26.3	25.0	3.0	0.7	11.4	23.0	33.0	21
Lorica, length of acute portion	IS	24.8	25.0	3.7	0.5	15.0	19.0	38.0	62
Lorica, angle of acute portion [b]	IS	58.9	58.5	7.6	1.0	12.9	36.4	74.7	62
	NS [c]	44.8	45.0	3.9	1.3	8.7	38.0	49.0	9
	PB [d]	55.1	54.0	8.1	3.1	14.7	45.0	70.0	7
Lorica, collar length	IS	10.7	10.0	3.6	0.5	33.6	0.0	19.0	60
	PB [d]	8.8	8.0	2.6	0.3	29.3	4.0	16.0	56
Lorica, inner collar diameter	IS	19.8	20.0	1.0	0.1	5.1	18.0	23.0	62
	NS	17.5	18.0	2.2	0.5	12.8	14.0	23.0	21
	PB [d]	17.2	16.5	1.8	0.2	10.7	14.0	24.0	59
Lorica, length:width ratio	IS	1.8	1.8	0.2	0.0	11.1	1.5	2.4	62
	NS	1.8	1.8	0.3	0.1	14.4	1.4	2.3	21
Lorica, bowl width:inner collar diameter	IS	1.4	1.4	0.1	0.0	5.5	1.1	1.6	62
ratio	NS	1.5	1.6	0.1	0.0	7.5	1.3	1.7	21
Cell proper, length	IS	28.1	28.0	4.0	0.6	14.3	20.0	36.0	44
	NS	31.3	32.0	4.1	0.8	13.1	22.0	41.0	26
	PB	35.3	37.0	4.4	1.4	12.6	28.0	40.0	10
Cell proper, width	IS	14.7	15.0	2.0	0.3	13.7	10.0	19.0	44
	NS	17.2	17.0	2.0	0.4	11.7	12.0	20.0	30
	PB	23.0	22.0	3.5	1.1	15.1	19.0	29.0	10
Cell, stalk length	IS	11.2	10.0	5.8	1.0	51.6	0.0	21.0	37
Cell, total length	IS	39.4	39.0	6.1	1.0	15.5	25.0	52.0	37
Apical cell end to buccal vertex, distance	IS	9.1	9.0	0.8	0.1	8.7	8.0	10.0	42
Anterior macronuclear nodule, length	IS	8.7	9.0	1.3	0.2	14.7	6.0	12.0	43
	NS	8.5	8.0	1.3	0.3	15.6	6.0	11.0	22
	PB	10.8	11.0	1.9	0.6	17.3	8.0	14.0	10
Anterior macronuclear nodule, width	IS	4.6	4.0	0.6	0.1	13.8	4.0	6.0	43
	NS	4.2	4.0	1.4	0.3	33.5	3.0	7.0	24
	PB	6.4	6.0	1.3	0.4	21.1	4.0	9.0	10
Macronuclear nodules, number	IS	2.0	2.0	–	–	–	1.0	2.0	50
	NS	2.0	2.0	0.0	0.0	0.0	2.0	2.0	28
	PB	2.0	2.0	0.0	0.0	0.0	2.0	2.0	10
Apical cell end to anterior macronuclear nodule, distance	IS	7.3	7.5	1.8	0.3	24.2	4.0	11.0	42
Micronuclei, diameter	IS	1.5	1.5	–	–	–	1.0	2.0	33
Micronuclei, number	IS	2.0	2.0	0.0	0.0	0.0	2.0	2.0	31
	NS	2.0	2.0	0.0	0.0	0.0	2.0	2.0	5
	PB	2.0	2.0	–	–	–	2.0	2.0	2

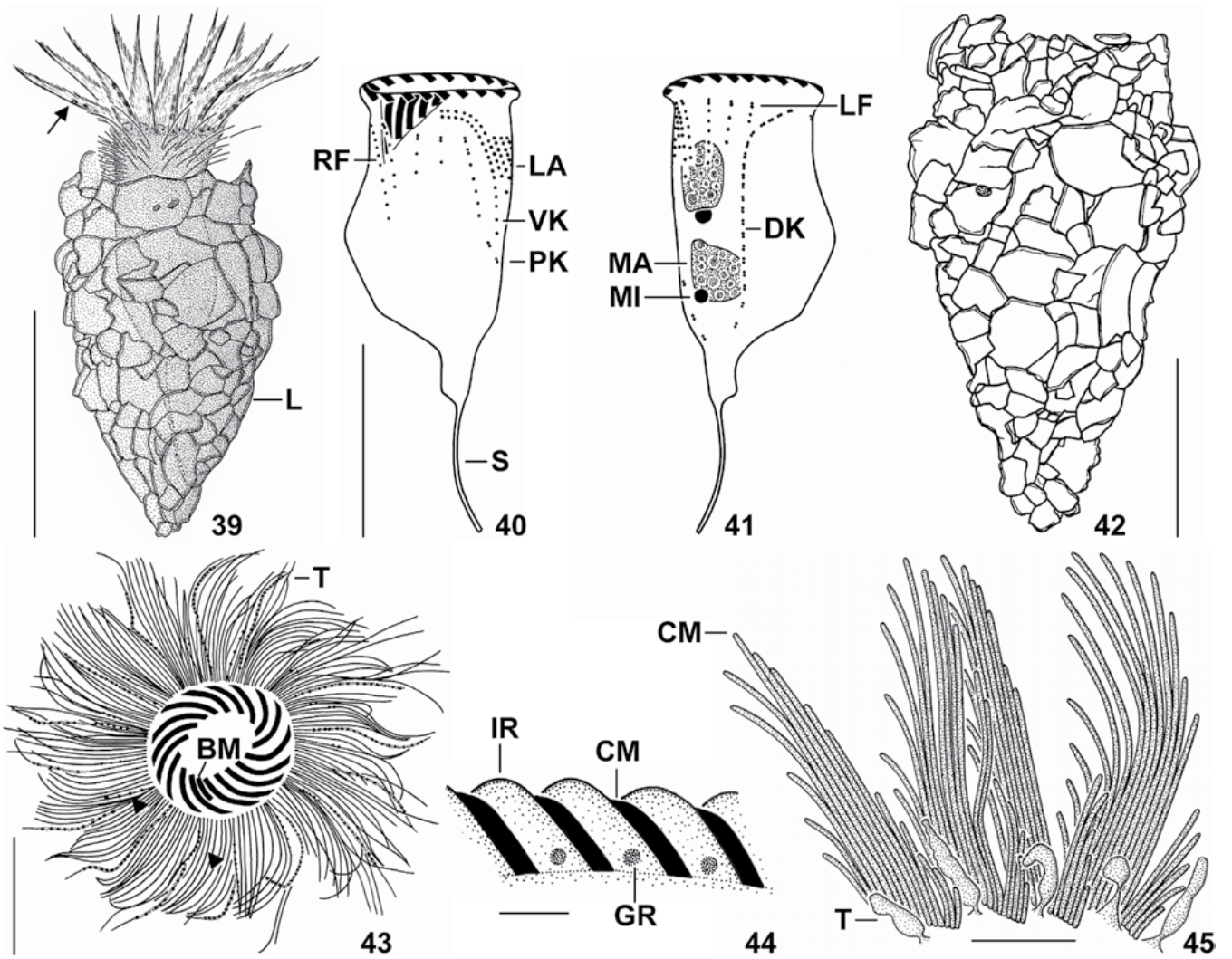
Characteristics [a]	Pop	$\bar{x}$	M	SD	SE	CV	Min	Max	n
Ventral kinety, length	IS	11.0	11.0	1.2	0.6	10.5	10.0	12.0	4
Dorsal kinety, length	IS	23.5	23.0	3.3	0.6	13.8	19.0	30.0	26
Dorsal kinety, number of dikinetids	IS	15.8	15.5	3.0	0.6	18.8	11.0	24.0	26
	NS	9.5	9.0	1.8	0.8	18.9	8.0	12.0	5
Posterior kinety, length	IS	11.0	12.0	2.7	0.8	24.2	6.0	14.0	10
Posterior kinety, number of dikinetids	IS	6.4	6.0	0.7	0.2	10.9	6.0	8.0	10
	NS	6.2	7.0	1.2	0.5	21.6	4.0	7.0	6
Apical cell end to posterior kinety, distance	IS	14.6	14.0	3.2	1.0	21.7	11.0	21.0	10
Lateral ciliary field, number of kineties	IS	10.3	10.0	0.8	0.2	7.3	9.0	11.0	13
	NS	10.3	10.0	–	–	–	10.0	11.0	3
Lateral ciliary field, length	IS	7.8	8.0	1.7	0.5	21.4	5.0	10.0	12
Left ciliary field, number of kineties	IS	4.0	4.0	0.0	0.0	0.0	4.0	4.0	15
	NS	3.3	3.0	–	–	–	3.0	4.0	6
Kinety 1 in left ciliary field, length	IS	3.2	3.0	0.7	0.2	20.5	2.0	5.0	17
Kinety 1 in left ciliary field, number of kinetids	IS	2.8	3.0	0.6	0.1	20.3	2.0	4.0	17
Kinety 2 in left ciliary field, length	IS	6.4	6.0	1.7	0.4	26.5	4.0	10.0	17
Kinety 2 in left ciliary field, number of kinetids	IS	5.5	5.0	1.3	0.3	24.0	4.0	8.0	17
Kinety 3 in left ciliary field, length	IS	7.8	6.0	2.5	0.6	31.7	5.0	12.0	17
Kinety 3 in left ciliary field, number of kinetids	IS	6.5	6.0	1.6	0.4	25.1	5.0	10.0	17
Kinety 4 in left ciliary field, length	IS	7.8	8.0	2.1	0.5	27.0	5.0	13.0	18
Kinety 4 in left ciliary field, number of kinetids	IS	7.2	7.0	1.3	0.3	17.5	5.0	10.0	18
Right ciliary field, number of kineties	IS	5.0	5.0	0.0	0.0	0.0	5.0	5.0	14
	NS	7.0	7.0	1.0	0.6	14.3	6.0	8.0	3
Kinety 1 of right ciliary field, length	IS	9.3	9.0	1.5	0.6	16.1	8.0	12.0	6
Kinety 1 of right ciliary field, number of kinetids	IS	8.0	8.0	1.1	0.4	13.7	7.0	9.0	6
Kinety 2 of right ciliary field, length	IS	3.8	4.0	1.3	0.4	35.0	3.0	8.0	13
Kinety 2 of right ciliary field, number of kinetids	IS	3.1	3.0	1.3	0.3	40.8	2.0	7.0	13
Kinety 3 of right ciliary field, length	IS	4.3	4.0	1.6	0.5	37.3	3.0	8.0	12
Kinety 3 of right ciliary field, number of kinetids	IS	3.4	3.5	1.1	0.3	31.7	2.0	5.0	12
Kinety 4 of right ciliary field, length	IS	8.0	8.0	1.9	0.6	23.8	6.0	11.0	12
Kinety 4 of right ciliary field, number of kinetids	IS	6.4	6.0	1.2	0.3	18.1	5.0	8.0	12
Kinety 5 of right ciliary field, length	IS	12.0	11.0	1.8	0.5	15.1	10.0	15.0	12
Kinety 5 of right ciliary field, number of kinetids	IS	8.7	9.0	0.9	0.3	10.2	7.0	10.0	12
Adoral zone of membranelles, diameter	IS	16.2	16.0	1.2	0.2	7.5	14.0	18.0	57
	NS	13.4	14.0	1.1	0.2	8.2	10.0	16.0	30
Collar membranelles, number	IS	15.4	15.0	0.6	0.2	4.2	15.0	17.0	14
	NS	18.9	18.0	2.1	0.6	11.0	17.0	23.0	11
Buccal membranelle, number	IS	1.0	1.0	0.0	0.0	0.0	1.0	1.0	24
	NS	1.0	1.0	0.0	0.0	0.0	1.0	1.0	16

[a] Data are based – if not stated otherwise – on protargol-impregnated, mounted, and randomly selected specimens from field material. Measurements in µm. CV – coefficient of variation in %; M – median; Max – maximum; Min – minimum; n – number of individuals investigated; Pop – population; SD – standard deviation; SE – standard error of arithmetic mean; $\bar{x}$ – arithmetic mean.

[b] In degrees.

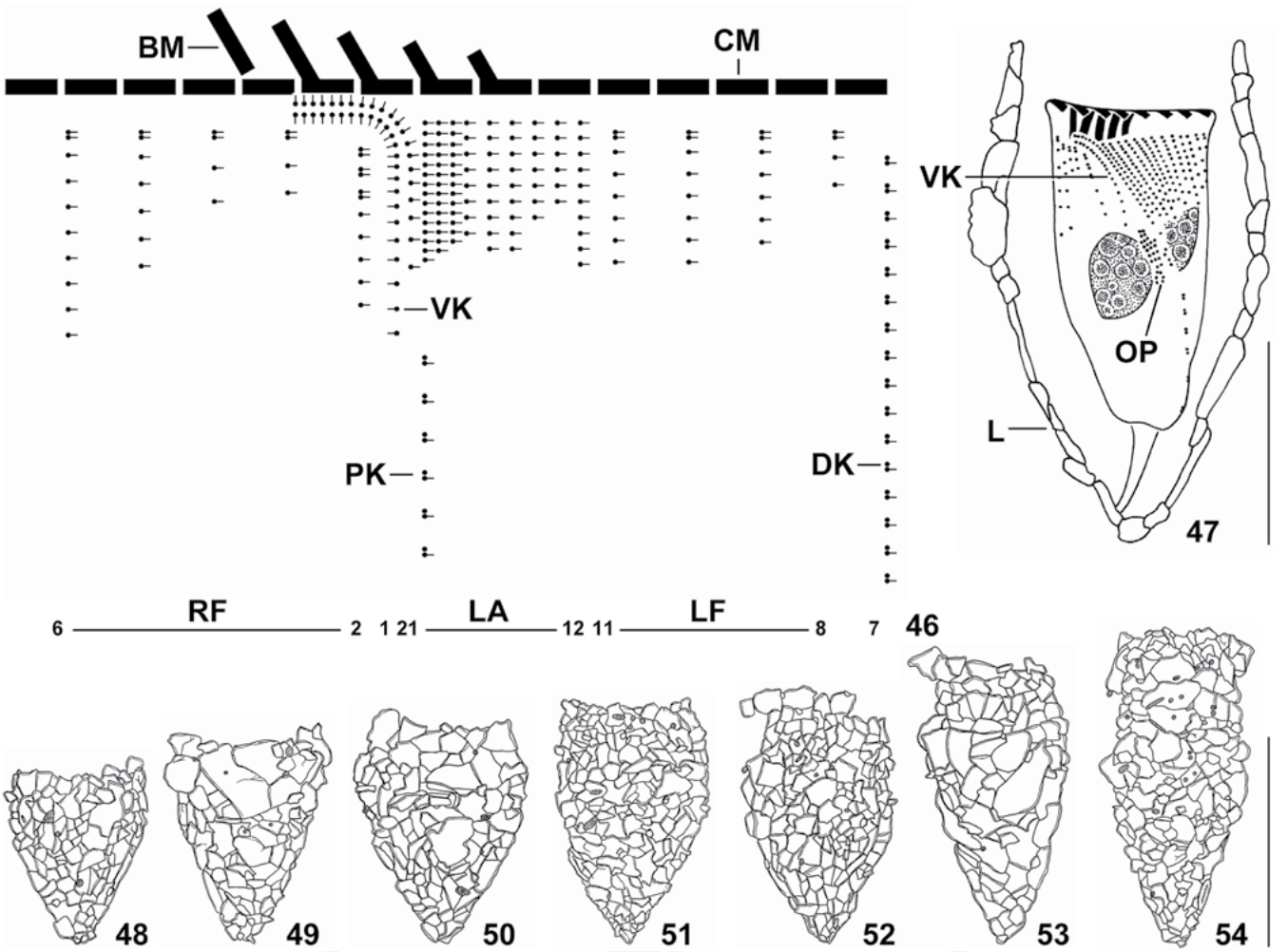
[c] From scanning electron micrographs.

[d] From Lugol-fixed material.



Figs 39–45. *Tintinnopsis parvula*, Irish Sea specimens from life (39, 44), after protargol impregnation (40–43), and from the scanning electron microscope (45). **39** – lateral view of an extended specimen. Exterior striae (arrow) extend longitudinally on the collar membranelles; **40**, **41** – ventral and dorsal views of same specimen showing the ciliary pattern and the nuclear apparatus; **42** – lorica of the specimen shown in Figures 40 and 41; **43** – top view showing two strands of argyrophilic granules, probably the capsules enclosed in the tentaculoids and the exterior striae (arrowheads). The elongated portions of the proximalmost four collar membranelles are not recognizable as they plunge perpendicularly into the buccal cavity. The endoral membrane is not impregnated; **44**, **45** – details of the peristomial rim. Instead of tentaculoids (45), live specimens often show refractive granules ~ 0.5 µm across in the outer portions of the intermembranellar ridges (44). BM – buccal membranelle, CM – collar membranelles, DK – dorsal kinety, GR – refractive granules, IR – intermembranellar ridges, L – lorica, LA – lateral ciliary field, LF – left ciliary field, MA – macronuclear nodules, MI – micronucleus, PK – posterior kinety, RF – right ciliary field, S – stalk, T – tentaculoids, VK – ventral kinety. Scale bars: 40 µm (39), 20 µm (40–43), 5 µm (45), and 2 µm (44).

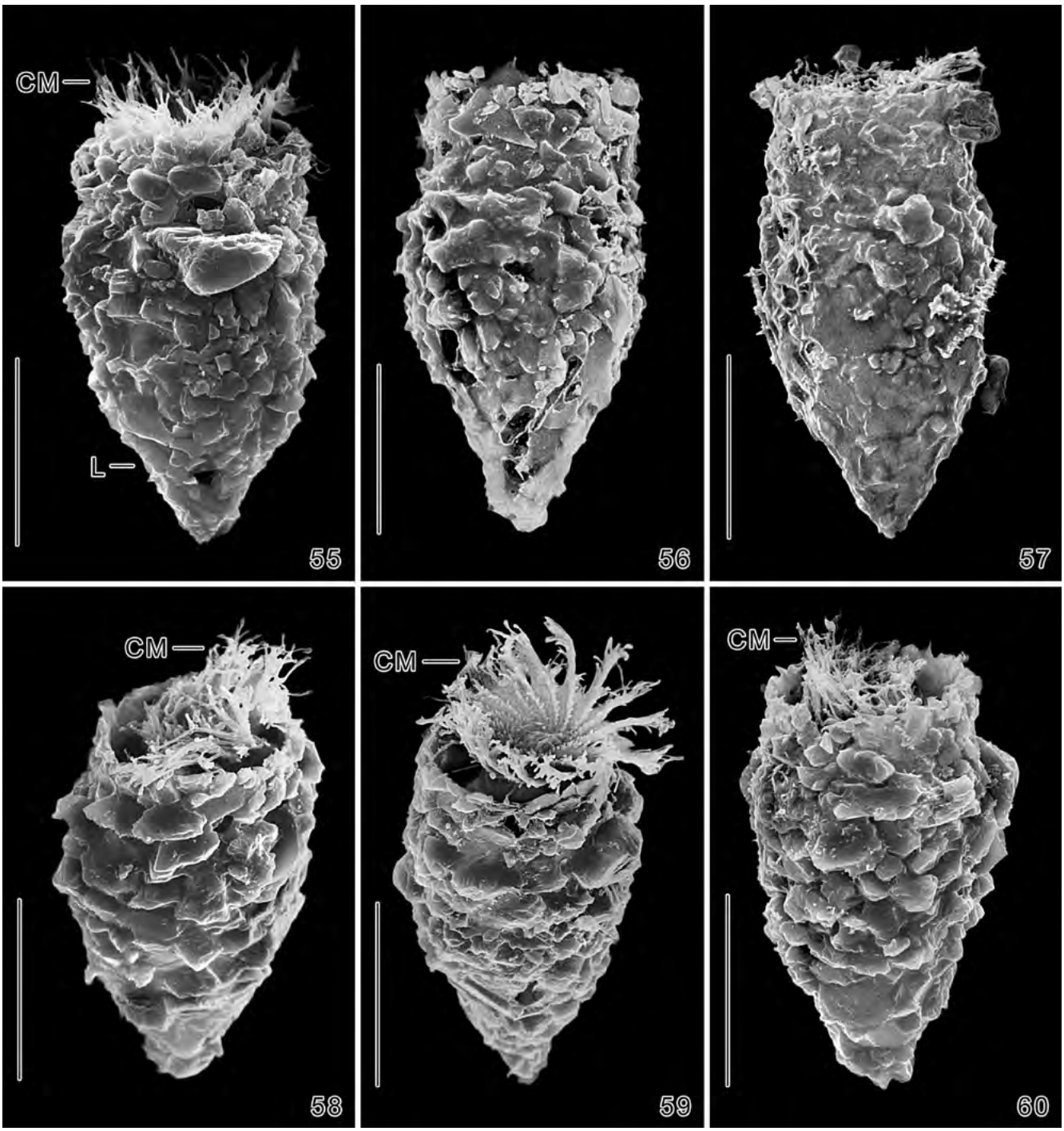
trolaterally into the slender, wrinkled, and highly contractile stalk up to 25 µm long, attached to bottom of lorica (Fig. 39). Disturbed or preserved cells contracted by ~ 25%, with ellipsoidal cell proper (Figs 40, 41, 47; Table 1); right cell half sigmoidal due to an indentation in the anterior portion and a bulge in the posterior, left cell half straight. Macronuclear nodules usually in posterior two thirds of cell proper, ellipsoidal or ovoidal, with nucleoli 0.5–1 µm across (Fig. 41). Micronuclei adjacent to macronuclear nodules, i.e. one close to posterior end of anterior nodule, the other usually near anterior end of posterior nodule, globular, difficult to recognize as usually faintly impregnated. Contractile vacuole and cytopyge neither recognizable in specimens from field with densely agglomerated loricae nor in cultured specimens with transparent loricae.



Figs 46–54. *Tintinnopsis parvula*, Irish Sea specimens after protargol impregnation. **46** – kinetal map of a morphostatic specimen. The numbering of the somatic kineties commences with the ventral kinety and continues in clockwise direction (top view); **47** – ventral view of an early divider showing the oral primordium posterior to the lateral ciliary field; **48–54** – variability of the lorica shape and size. BM – buccal membranelle, CM – collar membranelles, DK – dorsal kinety, L – lorica, LA – lateral ciliary field, LF – left ciliary field, OP – oral primordium, PK – posterior kinety, RF – right ciliary field, VK – ventral kinety. Scale bars: 40 µm (48–54), and 20 µm (47).

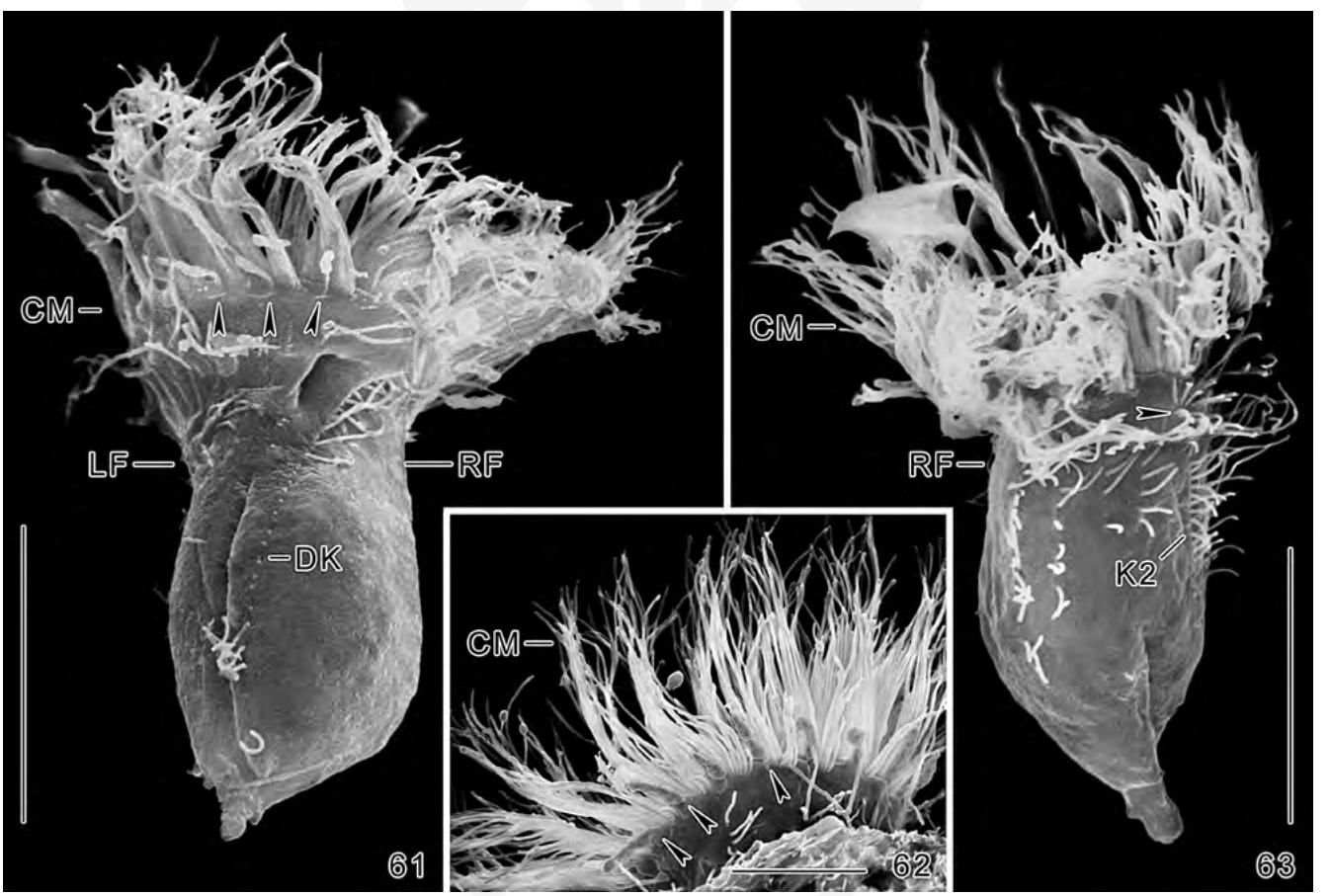
Myonemes not impregnated. Capsules in tentaculoids and exterior striae, argyrophilic, and ~ 1 × 0.5 µm in size. Tentaculoids originate from the outer portions of the shallow intermembranellar ridges, consist of a conical base, a stalk ~ 0.8 × 0.4 µm in size, and an inflated distal portion 3–9 × 0.6–1 µm in size, rarely seen (Figs 43, 45, 61, 62); specimens without tentaculoids have refractive granules ~ 0.5 µm across in the outer portions of the intermembranellar ridges (Fig. 44). Striae extend longitudinally on the outer portions of the collar membranelles, occasionally absent (Figs 39, 43). Cytoplasm colourless, contains food vacuoles up to 8 µm across with flagellates; cultured specimens filled with lipid droplets and food vacuoles ~ 5 µm across enclosing yellowish to brownish granules 1–2 µm across. Swims by rotation about main cell axis, twitches back on obstacles. Disturbed specimens retract quickly (< 1 s) into lorica, with motionless membranelles bent to centre of peristomial field; lorica abandonment never observed. When disturbance stops, specimens slowly (> 30 s) extend, spread the collar membranelles almost perpendicularly to the main cell axis, and restart swimming (Fig. 39).

Somatic ciliary pattern of most complex type (Agatha and Strüder-Kypke 2007), i.e. it comprises a ventral, dorsal, and posterior kinety as well as a right, left, and lateral ciliary field (Figs 40, 41, 46, 47, 61,



Figs 55–60. *Tintinnopsis parvula*, Irish Sea specimens in the scanning electron microscope. **55–57** – lateral views of loricae. The loricae are composed of a usually broadly obovate bowl and a cylindroidal collar. Their agglomeration is dense and mainly consists of mineral particles; **58**, **60** – oblique top views of slightly contracted specimens; **59** – oblique top view of an extended specimen showing the frayed collar membranelles. CM – collar membranelles, L – lorica. Scale bars: 20 µm.

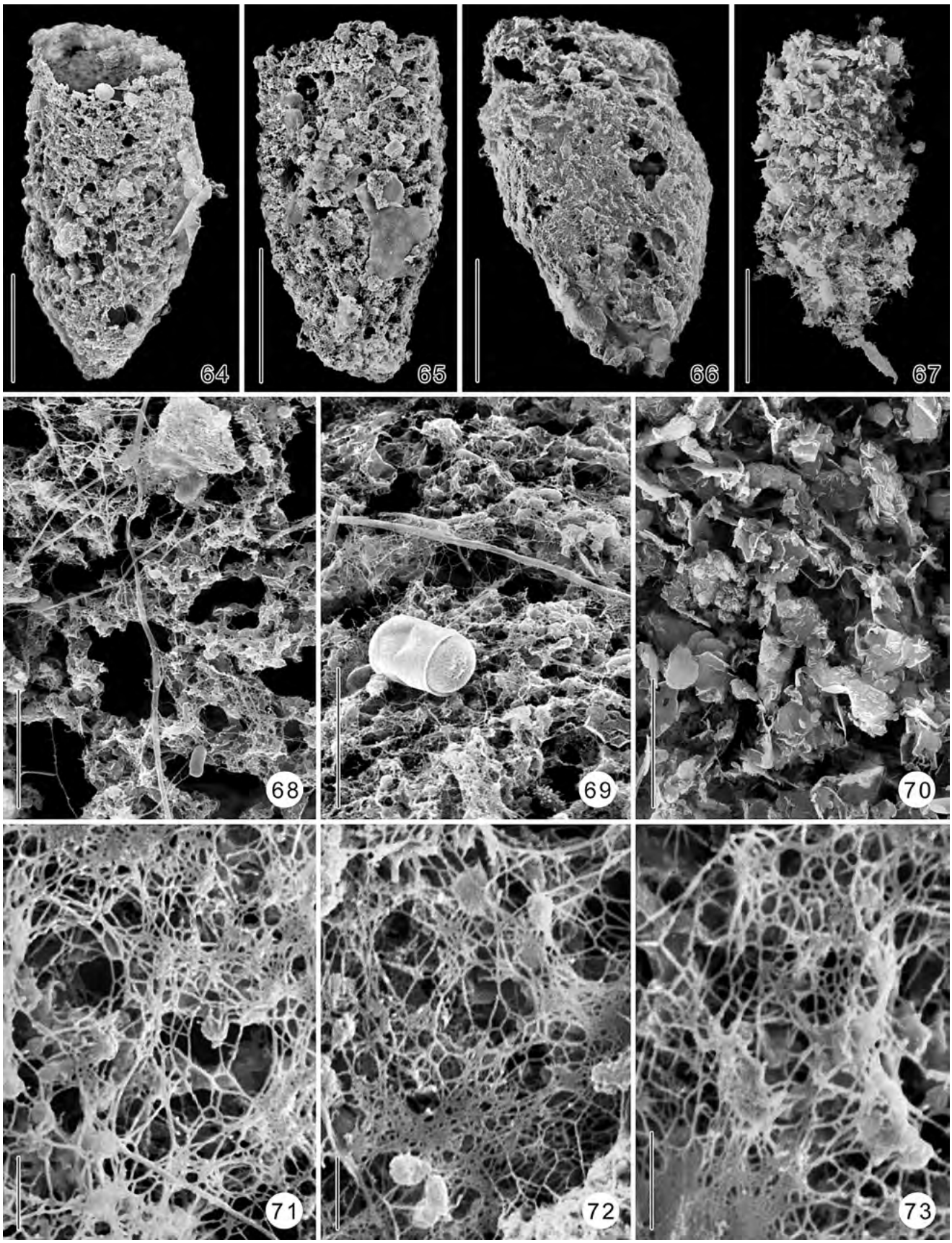
63). Length of kineties and number of kinetids usually highly variable possibly due to a basal body proliferation or resorption in late dividers and/or postdividers. Ventral kinety commences ~ 1 μm posterior to collar membranelles and usually anterior to second kinety of right ciliary field, curves leftwards and extends more or less parallel to kineties of lateral ciliary field, but terminates somewhat posteriorly; composed of monokinetids densely spaced in anterior portion, but more widely spaced in posterior, with cilia ~ 7 μm long after protargol impregnation (Figs 40, 46, 47, 63). Kineties of right ciliary field commence ~ 2 μm posterior to collar membranelles, i.e. ~ 3 μm posterior to apical cell end, increase in length in clockwise direction (top view), composed of monokinetids and one anterior dikinetid, except for first kinety starting with 2–6, usually 3 (n = 6) dikinetids ~ 1 μm posterior to remaining kineties and terminating ~ 12 μm posterior to collar mem-



Figs 61–63. *Tintinnopsis parvula*, Irish Sea specimens in the scanning electron microscope. **61** – dorsal view of a specimen that abandoned its lorica. Arrowheads denote tentaculoids, viz., finger-shaped cytoplasmic extensions containing capsules. The deciliated posterior portion of the dorsal kinety probably represents an artifact as it is ciliated in the protargol-impregnated specimens; **62** – anterior cell portion showing tentaculoids (arrowheads) at the outer portions of the intermembranellar ridges; **63** – ventrolateral view of a specimen that abandoned its lorica. Arrowhead marks the beginning of the ventral and last kinety, which extend anteriorly to the right ciliary field. CM – collar membranelles, DK – dorsal kinety, K2 – second kinety (first kinety of right ciliary field), LF – left ciliary field, RF – right ciliary field. Scale bars: 20 μm (61, 63), and 10 μm (62).

▶▶

Figs 64–73. *Tintinnopsis parvula*, scanning electron micrographs of loricae formed in almost particle-free cultures by the Irish Sea specimens. **64–67** – lateral views of loricae that are sparsely agglomerated due to the scarcity of particles in the cultures; **68–73** – details of lorica walls showing the matrix which consists of an irregular network of fibres ~ 0.04–0.3 μm thick and some attached or interwoven particles (fluffy material, bacteria, diatom frustules, and crystals). Scale bars: 20 μm (64–67), 5 μm (68–70), and 1 μm (71–73).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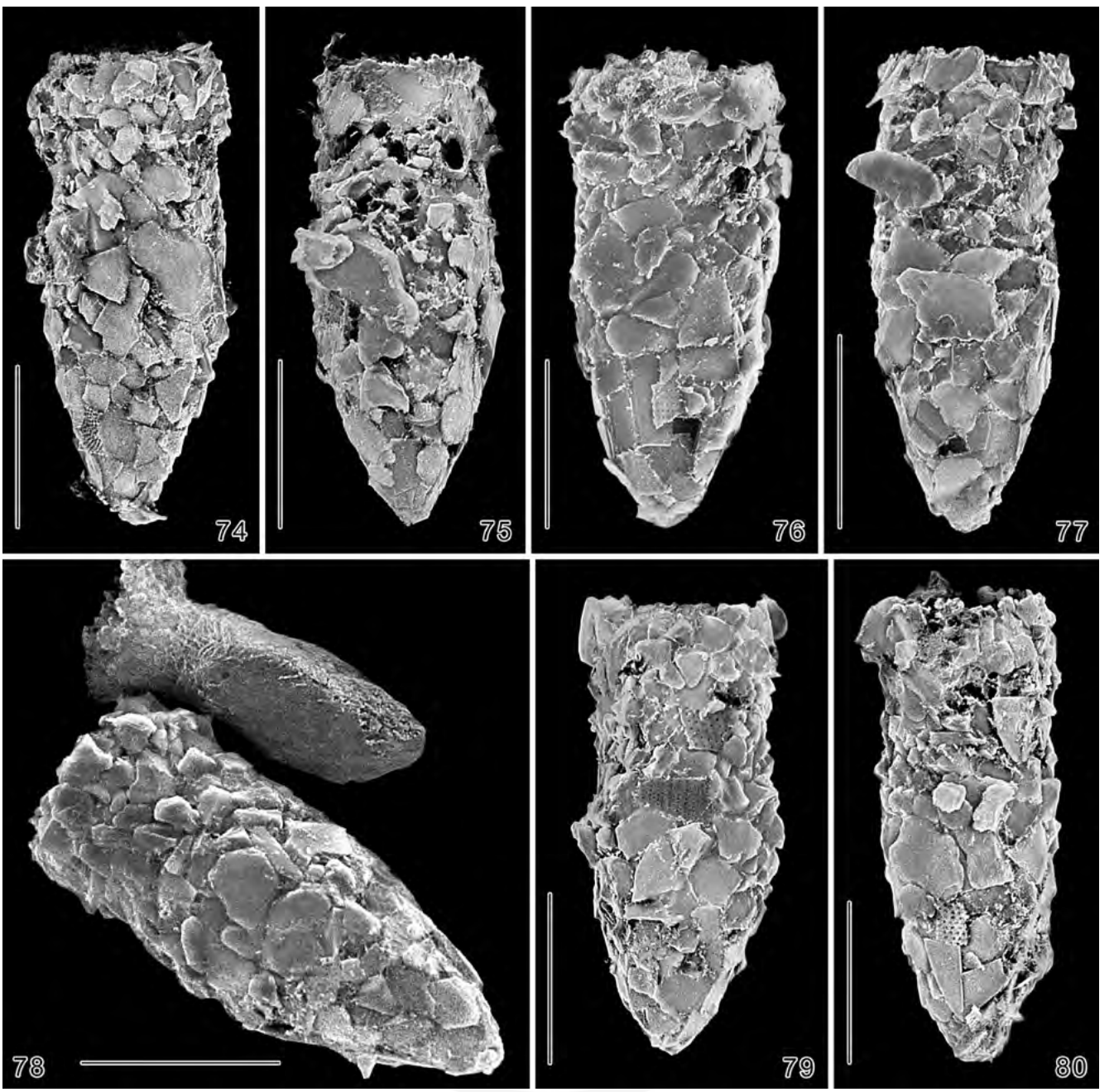
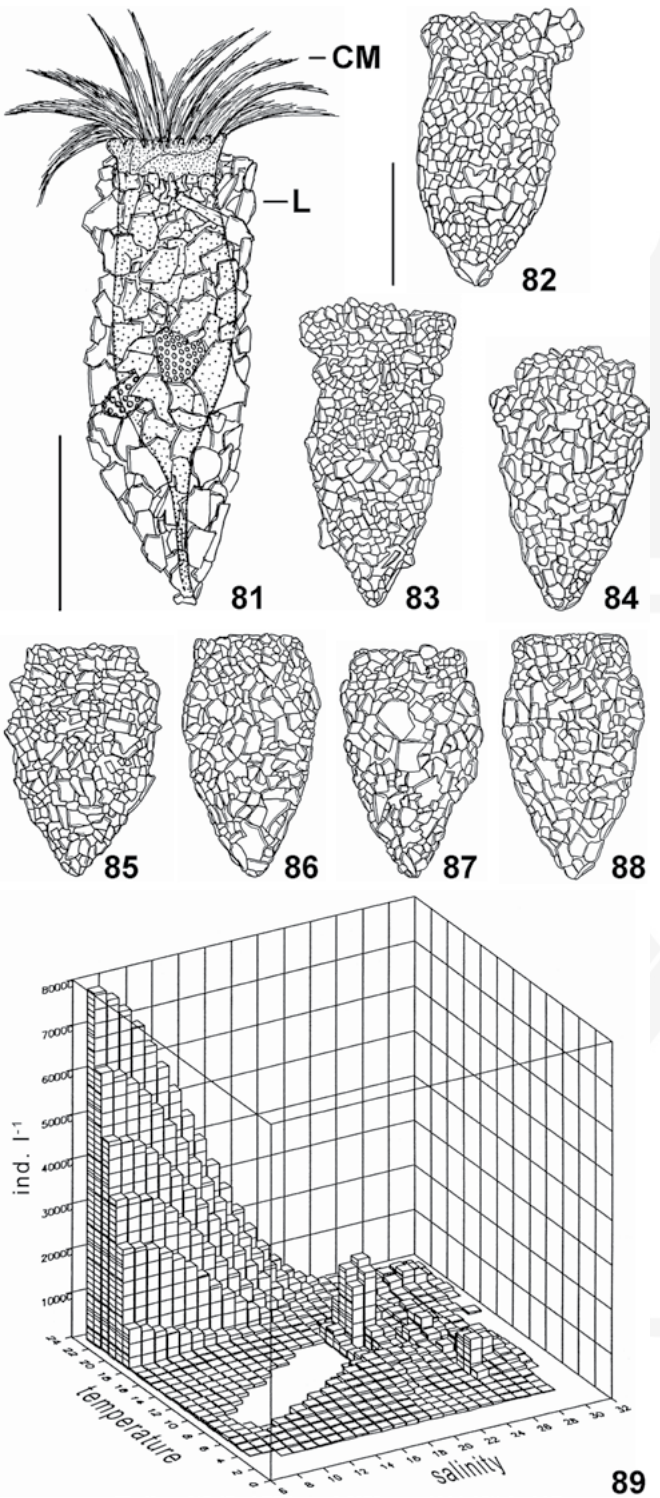


Figs 74–80. *Tintinnopsis parvula*, North Sea specimens in the scanning electron microscope. **74–77**, **79**, **80** – lateral views of loricae with a dense agglomeration of mineral particles and some fragments of diatom frustules. The posterior ends of the loricae are more acute than those of the neotype population (cf. Figs 39, 42, 48–60); **78** – lateral views of a tintinnid cell that abandoned its house and a lorica; possibly, they are conspecific. Scale bars: 20 µm.

branelles (Figs 40, 46, 63). Cilia of right ciliary field 2–4 µm long after protargol impregnation, except for anterior cilia of dikinetids (soies; Fauré-Fremiet 1924) measuring ~ 8 µm. Dikinetidal dorsal kinety commences 2–4 µm and 3–5 µm apart from the left and right ciliary fields, respectively, and 3–4 µm posterior to the collar membranelles, extends in a leftwards curvature to posterior end of cell proper and posterior kinety, occasionally accompanied by argyrophilic granules (Figs 41, 46, 61). Dikinetids of dorsal kinety connected by



Figs 81–89. *Tintinnopsis parvula*, specimens from the North Sea *in vivo* (81) and from the polder basins after Lugol-fixation (82–89). **81** – lateral view of a swimming specimen; **82–88** – variability of the lorica shape and size; **89** – abundances [ind. l^{-1}] at different salinities [‰] and temperatures [°C] in the polder basins (after Agatha 1995). CM – collar membranelles, L – lorica. Scale bars: 20 µm.

an argyrophilic structure of probably fibrillar nature, with cilia 6–8 µm long after protargol impregnation at each posterior basal body. Kineties of left ciliary field commence ~ 2 µm posterior to collar membranelles, increase in length in clockwise direction (top view), composed of monokinetids and one anterior dikinetid (Figs 41, 46, 61). Cilia of left ciliary field 4–5 µm long after protargol impregnation, except for anterior cilia of dikinetids (soies; Fauré-Fremiet 1924) measuring ~ 8 µm. Kineties of lateral ciliary field commence ~ 1.5 µm posterior to collar membranelles, except for the last kinety that usually commences anterior to second kinety of right ciliary field and performs a leftwards curvature parallel to the ventral kinety; clockwise inclined, composed of densely spaced monokinetids, ~ 8 µm long, the first six kineties more widely spaced than the remaining ones, with cilia ~ 3 µm long after protargol impregnation (Figs 40, 41, 46). Dikinetidal posterior kinety commences close to posterior end of ventral kinety and curves leftwards to posterior end of cell proper and dorsal kinety, occasionally accompanied by argyrophilic granules (Figs 40, 41, 46, 47); cilia only at each posterior dikinetidal basal body, 6–8 µm long after protargol impregnation.

Oral apparatus occupies anterior cell portion. Adoral zone of membranelles closed, perpendicular to main cell axis (Figs 39–41, 59, 61, 63). Collar membranelles triangular: cilia increase in length from ~ 0.7 µm at the inner ends of the membranelles to 15–20 µm in the outer quarters, and then abruptly decrease to ~ 1.5–2.5 µm at the outer ends in scanning electron micrographs; distal membranellar portions frayed, producing a comb-like appearance, inflated cilia ends probably represent preparation artifacts. Bases (polykinetids) of collar membranelles extend obliquely across peristomial rim, separated by shallow ridges, comprise three rows of basal bodies; bases of proximalmost four collar membranelles successively elongated, terminating 1.5–5 µm posterior to apical cell end in buccal cavity (Figs 40, 46, 47). Single buccal membranelle, with base ~ 6 µm long, structure not recognizable (Figs 43, 46). Fibrillar associates of adoral zone of membranelles as well as endoral membrane and pharyngeal fibres not recognizable.

Enantiotropic division with hypoapokinetal formation of the oral primordium in a subsurface pouch posterior to the lateral ciliary field, i.e. between the posterior end of the ventral kinety and the anterior end of the posterior kinety (Fig. 47). Adoral membranelles immediately commence to differentiate in the cuneate field of basal bodies. One replication band each traverses the

macronuclear nodules, which then fuse to form an elongate ellipsoidal mass. Eventually, the opisthe's dorsal side faces the proter's ventral side. Lorica formation neither observed in live nor in preserved specimens.

Observations on North Sea specimens (Figs 74–81; Table 1): The North Sea specimens are identical to the Irish Sea population in all main features, for instance, the size of the loricae and impregnated specimens, the number of kineties in the lateral and left ciliary fields, and the occurrence of tentaculoids originating from the outer portions of the intermembranellar ridges. There are only a few minor differences: the angle of the posterior lorica end (on average 45° vs. 59°), the number of dikinetids in the dorsal kinety (on average 10 vs. 16), the number of kineties in the right ciliary field (on average 7 vs. 5), and the number of collar membranelles (on average 19 vs. 15). At least in the former two features, the differences might be due to the distinctly lower number of North Sea specimens investigated. The cilia of the ventral kinety decrease in length from ~ 6 µm at the anterior end to ~ 3 µm at the posterior. The cilia of the posterior kinety are 3–4 µm long after protargol impregnation. The pharyngeal fibres are ~ 14 µm long. The endoral membrane extends on the right wall of the buccal cavity and comprises a single row of basal bodies with a probably monostichomonad structure.

Observations on polder specimens (Figs 82–88; Table 1): The data from specimens preserved with Lugol's solution (lorica size) or impregnated with protargol (size of the cell and the macronuclear nodules, number of the macronuclear nodules and micronuclei; this study, Agatha 1995) agree with the findings from the Irish Sea population.

DISCUSSION

Comparison with original description: The Baltic Sea specimens studied by Brandt (1906, 1907) have loricae 40–75 × 25–35 µm in size with a posterior angle of 36–62° and a nuclear apparatus comprising two macronuclear nodules and two micronuclei. The collar is 13–20 µm long and has an inner diameter of 20–24 µm, as estimated from the illustrations provided, using the data on the lorica size. The neotype population is identical to the type population in these measurements (Table 1), the lorica shape (cf. Figs 39, 42, 47–60 with Figs 2–5), and the cell features. Accordingly, the specimens from the Irish Sea are identified with *Tintinnopsis parvula* Jörgensen, 1912 (see 'Taxonomy and nomenclature').

Comparison with further populations: The loricae of the neotype population fall into the size range of most other populations with a lorica length of 34–75 µm, a bowl width of 20–38 µm, a collar diameter of 18–26 µm, and a posterior lorica angle of 45–65° (Figs 1, 6–38; Brandt 1896; Levander 1900; Laackmann 1908; Meunier 1910; Rossolimo 1922, 1927; Hada 1937; Dolgopolskaia 1940; Osorio-Tafall 1941; Biernacka 1948; Schulz 1964; Marshall 1969; Travers and Travers 1971; Cosper 1972; Burkovsky *et al.* 1974; Bakker and Phaff 1976; Gold and Morales 1976a; Burns 1983; Van der Spoel 1987; Cordeiro and Sassi 1997; Tempelman and Agatha 1997). In the North Pacific, Hada (1937) observed a seasonal variability in the lorica length with small specimens (40–45 µm long) in the summer and large ones (50–60 µm long) in the winter. However, the conspecificity is questionable in specimens with much larger and/or differently shaped loricae (Laackmann 1908; Hofker 1931; Wailes 1943; Balech 1945, 1948, 1959; Marshall 1969; Souto 1970; Blackbourn 1974; Hedin 1974; Rampi and Zattera 1982; Verity 1987; Fernandes 2004; Kogan 2005). Cell features were only rarely investigated. According to Laackmann (1908), the nuclear apparatus comprises two micronuclei ~ 1 µm across and two globular or ellipsoidal macronuclear nodules often with a replication band. The conjugation stage he also studied (Fig. 9) indicates differences to the conjugation in the morphologically related *Halteria grandinella* concerning the interlocking arrangement (absent vs. present), the reduction of the adoral membranelles (indistinct vs. distinct), and the formation of a common membranellar zone (absent vs. present; Laackmann 1908, Agatha and Foissner 2009).

Comparison with similar congeners: The intraspecific variability of the loricae is unknown and cytological and molecular data are only available for a few *Tintinnopsis* species (see 'Introduction'). This results in shoals of questionable splits and synonymizations (e.g. Kofoid and Campbell 1929, 1939) and deviating species diagnoses. To avoid a further and still premature discussion of the species' limits, the following comparison exclusively considers the original descriptions.

The following species were occasionally regarded as synonyms of *Tintinnopsis parvula* (lorica ~ 50–60 × 28–30 µm in size; posterior angle of the broadly obovate bowl ~ 50–60°; collar cylindroidal with an in-

ner diameter of ~ 20–22 µm): *T. acuminata* (lorica cylindroidal and ~ 75 × 48 µm in size; Daday 1887), *T. baltica* Brandt, 1896 (lorica collar flaring and spiralled; Möbius 1887), *T. beroidea* Stein, 1867 (for distinguishing features see 'Taxonomy and nomenclature'), *T. fistularis* (lorica cylindroidal with a broadly rounded end; Meunier 1919), *T. minuta* (lorica cylindroidal with a broadly rounded end; Wailes 1925), *T. nana* (lorica opening ~ 9 µm across; Lohmann 1908), *T. nucula* (lorica bowl globular; Fol 1884), *T. tocantinensis* (lorica ~ 85 µm long and with a conspicuous collar; angle of posterior end ~ 35°; Brandt 1906, 1907), and *T. vasculum* (lorica opening ~ 40 µm across; Meunier 1919). In typical specimens of *T. rapa*, the posterior lorica end is more acute than in *T. parvula* (~ 25° vs. ~ 50–60°; Plate 12, Figs 29–35 in Meunier 1910); however, further features are required to verify this separation. The deviating matrix ultrastructures of loricae formed in particle-free cultures indicate that *T. parva* established by Merkle (1909) does not represent an immature lorica of *T. parvula* (see 'Comparison of lorica ultrastructures'; Laval-Peuto *et al.* 1979).

Phylogeny and taxonomy: Sequence analyses of the small subunit ribosomal RNA (SSrRNA) gene indicate a paraphyly of the genus *Tintinnopsis* (Strüder-Kypke and Lynn 2003, 2008; Gao *et al.* 2009; Li *et al.* 2009). However, all *Tintinnopsis* species cytologically studied show with inconspicuous deviations the most complex somatic ciliary pattern (inferred from illustrations in Small and Lynn 1985: *T. baltica*, *T. subacuta*; Agatha and Riedel-Lorjé 2006: *T. cylindrica*; Agatha and Strüder-Kypke 2007: *T. campanula*, *T. tubulosoides*; Agatha 2008: *T. fimbriata*; this study: *T. parvula*), except for *T. brasiliensis* and *T. cylindrata*. The former species lacks a posterior kinety (Cai *et al.* 2006), while *T. cylindrata* resembles *Tintinnidium* species in the presence of ventral organelles and the absence of a dorsal kinety, a posterior kinety, and a lateral ciliary field (Foissner and Wilbert 1979, Agatha and Strüder-Kypke 2007). Possibly, the different branches of the genus *Tintinnopsis* found in the SSrRNA gene trees correspond to the observed deviations in the somatic ciliary patterns and certain types of lorica matrices (see 'Comparison of lorica ultrastructures'). Since these features have not been studied in the type species *T. beroidea*, any revision of the species-rich genus *Tintinnopsis* is premature.

The most complex somatic ciliary pattern is quite common, also occurring in *Climacocylis scalaroides* (inferred from illustrations in Small and Lynn 1985), *Codonella cratera* (Foissner and Wilbert 1979; due to the lack of a closing apparatus and a lorica sac, the species is not any longer representative for the genus; Agatha 2010), *Codonellopsis glacialis*, *Cymatocylis calyciformis* (Petz *et al.* 1995), the *Cymatocylis affinis/convallaria*-group (Wasik and Mikołajczyk 1994, Petz *et al.* 1995), *Protorhabdonella simplex* (inferred from illustrations in Small and Lynn 1985), *Stenosemella lacustris* (Foissner and O'Donoghue 1990; an incorrect generic affiliation due to the lack of a hyaline collar; Agatha and Tsai 2008), *S. pacifica* (Agatha and Tsai 2008), and *S. steini* (inferred from illustrations in Small and Lynn 1985). This feature thus demonstrates the low significance of the general lorica wall structure for higher taxonomic ranks: agglomerated loricae occur in *Tintinnopsis*, hyaline collars and agglomerated bowls in *Codonellopsis* and *Stenosemella*, and hyaline loricae in *Cymatocylis* and *Protorhabdonella*.

Comparison of lorica ultrastructures: The sparsely agglomerated loricae formed by *Tintinnopsis parvula* in almost particle-free cultures exhibited the matrix ultrastructure. Although the outlines and sizes of these loricae were similar to those found in the field material, it cannot be excluded that the matrices produced *in vitro* were strongly influenced by the cultivation conditions. Culture-dependent artifacts were, for instance, observed in *Helicostomella subulata*, which revealed an uncommon globular wall texture due to a faster hardening or reduced viscosity of the substances *in vitro* (Gold 1980).

Apparently, four types of matrices occur in the genus *Tintinnopsis*: (i) A trilaminar matrix with solid inner and outer layers enclosing an alveolar layer (*T. lobiancoi*; Wasik *et al.* 1997, Wasik 1998). (ii) A matrix with a variable number of discontinuous alveolar layers (*T. parva* grown in particle-free cultures; Laval-Peuto *et al.* 1979). (iii) A compact monolaminar matrix (*Tintinnopsis* spec.; Laval-Peuto 1980). (iv) A fibrous matrix (*T. parvula* grown in almost particle-free cultures; this study); Gold and Morales (1975b, 1976b) mentioned a similar matrix in *T. tubulosoides*, but neither provided data nor illustrations. The matrix ultrastructure might thus represent a promising feature for a reliable subdivision of the species-rich genus *Tintinnopsis* Stein, 1867 in the future.

The ultrastructure of entirely or partially agglomerated loricae was studied in several further genera. In *Tintinnidium fluviatile*, the matrix is weak and jelly-like and appears structure-less in the scanning electron microscope (Foissner and Wilbert 1979, Bernatzky *et al.* 1981). It resembles that of the freshwater species

Tintinnopsis cylindrata (Bernatzky *et al.* 1981), whose close relationship to the genus *Tintinnidium* is also inferred from its somatic ciliary pattern (see 'Phylogeny and taxonomy'). In loricae of a marine *Tintinnidium* spec. formed in almost particle-free cultures, a thin film covers several layers of fibrous globules held together by anastomosing fibres (Gold and Morales 1976c). The particle-free lorica portions in *Acanthostomella*, *Dictyocysta fenestrata*, and *D. reticulata* have a smooth surface (Burns 1983, Young and Geisen 2002) and are obviously not composed of fibres. The data concerning the genus *Codonellopsis* are contradictory: the matrix is alveolar in *C. gaussi* (Wasik *et al.* 1997), while a possibly continuous organic matrix overlaid with fibrous material becomes visible in *C. americana* after the dissolution of the agglomerated particles (Gold and Morales 1977a, b). These covering fibres resemble those composing the *in vitro*-formed loricae of *T. parvula* (this study), in which, however, an inner organic layer was not found.

The hyaline loricae of *Cyttarocylis*, *Proplectella*, *Undella* (Laval-Peuto 1980, 1994), *Favella* (own data, Hedin 1975b, Laval-Peuto 1994), *Helicostomella subulata*, *Laackmanniella naviculaefera* (Wasik *et al.* 1997, Wasik 1998), *Parafavella denticulata* (Sokolova and Gerassimova 1984), and *P. gigantea* (Hedin 1975b) have trilaminar walls, viz., solid inner and outer layers enclose an alveolar layer, while the middle layer is tubular in *Petalotricha ampulla* (Laval 1972, Laval-Peuto 1994). Two matrix types occur in the genus *Cymatocylis*: in *C. drygalskii* and *C. vanhöffeni*, the wall is again trilaminar with solid inner and outer layers and an alveolar middle layer (Wasik *et al.* 1997, Wasik 1998); in *C. convallaria*, however, the inner and outer layers are alveolar and the middle layer consists of tubular structures similar to those found in *Petalotricha ampulla*. Furthermore, the wall ultrastructure changes towards the anterior lorica end in *C. convallaria* due to a reduction of the middle layer and its final disappearance in the collar (Wasik and Mikołajczyk 1992). In some species, the alveolar pattern becomes more complex by a branching of the alveoli septa (*Cymatocylis drygalskii*, *C. vanhöffeni*, *Helicostomella subulata*; Wasik *et al.* 1997, Wasik 1998) or the formation of triangles with minute alveoli at their corners (*Parafavella denticulata*, *P. gigantea*; Hedin 1975b, Sokolova and Gerassimova 1984, Wasik *et al.* 1997). In contrast to the particle-free lorica regions in *Dictyocysta fenestrata* and *D. reticulata* (see above), the hyaline lorica of the congener *D. mitra* reveals a tubular wall organization in transmission (Laval-Peuto 1994) and scanning electron micrographs (Agatha 2010); inner and outer layers are not recognizable. According to Laval-Peuto (1980, 1994), the lorica wall of *Eutintinnus* consists of a single compact layer. However, micrographs of longitudinal and transversal lorica sections (kindly provided by W. Coats, Smithsonian Environmental Research Center, Edgewater, Maryland, USA) reveal distinct constrictions in the wall, indicating that it consists of perpendicularly striated platelets stuck together with their narrowed margins. The lorica wall of *Dadayiella ganymedes* comprises a complex pattern of longitudinal and dextrally spiralled lines. The outer lorica surface exhibits irregularly arranged globules of different sizes and ridges formed by whorls overlapping the posterior portion of the next whorl (Lecal 1967).

Ontogenetic comparison: Ontogenesis was at least partially studied after protargol-impregnation in five species with a similar somatic ciliary pattern: *Codonella cratera* (Petz and Foissner 1993), *Cymatocylis convallaria* (Petz *et al.* 1995), *Stenosemella pacifica* (Agatha and Tsai 2008), *Tintinnopsis cylindrica* (Agatha and Riedel-Lorjé 2006), and *T. fimbriata* (Agatha 2008). These species agree with *Tintinnopsis parvula* in the position of the oral primordium posterior to the lateral ciliary field.

Occurrence and ecology: The following compilation merely comprises records of *Tintinnopsis parvula* and the synonyms mentioned above. Due to the problematic taxonomy, however, the species might possess further synonyms and hence a much larger distribution. On the other hand, misidentifications cannot be excluded, especially, among the unsubstantiated records.

The records from the pelagial of the Barents Sea (Meunier 1910), Davis Strait (Brandt 1896; Brandt 1906, 1907), Kara Sea (Rossolimo 1927), White Sea (Burkovsky *et al.* 1974), temperate North Atlantic (this study; Brandt 1906, 1907; Bakker and Phaff 1976; Gold and Morales 1976a; Van der Spoel 1987; Paulmier 1995; Cordeiro and Sassi 1997; Tempelman and Agatha 1997), subtropical North Atlantic (Cosper 1972), tropical South Atlantic (Brandt 1906, 1907), Mediterranean Sea (Travers and Travers 1971), temperate North Pacific (Hada 1937), subtropical North Pacific (Osorio-Tafall 1941), and temperate South Pacific (Burns 1983) are accompanied by measurements and/or illustrations. Additionally, there are uncorroborated records from the Arctic Sea (Bursa 1963, Nielsen and Hansen 1995, Ikävalko 2003), Kara Sea (Burkovsky 1976a), White Sea (Burkovsky 1976b, Kolosova and Ilyash

2009), temperate North Atlantic (Hansen-Ostenfeld 1916, Gaarder 1946, El Maghraby and Perkins 1956, Johansen 1977, Middlebrook *et al.* 1987, Paranjape 1987, Cordeiro *et al.* 1997), subtropical North Atlantic (Gaarder 1946), tropical South Atlantic (Porto Neto 2003, Oliveira Areas *et al.* 2006), temperate South Atlantic (Barría de Cao 1986, 1992; Barría de Cao *et al.* 2003, 2005; Biancalana *et al.* 2007; Diodato and Hoffmeyer 2008), Mediterranean Sea (Travers and Travers 1975, Moscatello *et al.* 2004, Hannachi *et al.* 2008, Kchaou *et al.* 2009), temperate North Pacific (Chester 1978, Kim and Lee 2003, Lee and Kim 2010), Arabian Gulf (Skryabin and Al-Yamani 2007), tropical Indian Ocean (Damodara Naidu and Krishnamurthy 1985, Krishnamurthy *et al.* 1987, Modigh *et al.* 2003), and the Antarctic region of the Atlantic Ocean (Fonda Umani and Monti 1991). Occasionally, the species was found in the pelagial of brackish waters. Substantiated records exist for the Black Sea (Rossolimo 1922, Dolgopolskaia 1940), estuaries (Schulz 1964, Bakker and Phaff 1976) and polder basins (this study, Agatha 1995) at the North Sea coast as well as for the Baltic Sea and adjacent waters (Levander 1900; Brandt 1906, 1907; Laackmann 1908; Lohmann 1911; Biernacka 1948, 1956). Further records are not substantiated, namely, those from the Baltic Sea (Hansen-Ostenfeld 1916, Halme 1958, Halme and Lukkarinen 1960, Schwarz 1961, Biernacka 1968, Hedin 1975a, Kivi 1986, Leppänen and Bruun 1986, Fenchel *et al.* 1990, Nielsen and Kiørboe 1994, Telesh *et al.* 2008, Mironova *et al.* 2009), the Black Sea (Kurilov 2000, Gavrilova and Dolan 2007), a fjord (Jonsson 1989), polder basins (Agatha and Riedel-Lorjé 1997), and estuaries at the temperate North Atlantic coast (Paulmier 1971, Hargraves 1981), an estuary at the temperate South Atlantic coast (Hoffmeyer and Barría de Cao 2007), and an estuary at the coast of the tropical Indian Ocean (Ashok Prabu *et al.* 2005). Only once the species was found in the epibenthic community, viz., at the North Atlantic coast of Spain (Fernandez-Leborans *et al.* 1999); however, this record was not substantiated by measurements or illustrations.

According to Halme's (1958) uncorroborated records from the Baltic Sea, *T. parvula* is a stenotherm, stenohaline, and β-mesohaline cold water tintinnid. However, the species apparently occurs from Arctic to tropic sites and at temperatures ranging from –1.5°C (Brandt 1896) to 29°C (Krishnamurthy *et al.* 1987). Likewise, it apparently tolerates a broad range of salinities, viz., the species was found at 2‰ (Biernacka 1956, Leppänen and Bruun 1986) to 35‰ (this study, Krishnamurthy *et al.* 1987, Nielsen and Hansen 1995). In the polder basins, *T. parvula* was most abundant at salinities of 6–18‰ and temperature above 18°C (Fig. 89; Agatha 1995). Furthermore, the occurrence of *T. parvula* is apparently not restricted to a certain season: in the North Atlantic, it was recorded from winter to spring (Hansen-Ostenfeld 1916), in spring (this study, Hargraves 1981, Cordeiro and Sassi 1997), from spring to late summer (this study, Agatha 1995), and in autumn (this study, Middlebrook *et al.* 1987). Halme (1958) observed a maximum abundance of ~ 130 individuals per litre in the Baltic Sea at the end of May and in Autumn, while the densities were much higher in the polder basins with up to 39,000 individuals per litre at a mixo-mesohaline to mixo-polyhaline sampling site at the end of May (this study, Agatha 1995). In the North Sea, *T. parvula* achieved a maximum biomass of ~ 5.4 mg C m^{-2} at a temperature of 10°C and a salinity of 32‰ in spring (Cordeiro *et al.* 1997). The species accumulates near the water surface (this study, Jonsson 1989), while osmium tetroxide-fixed cells sink at an average rate of 72 ± 9 µm s^{-1} (Jonsson 1989). In feeding experiments, Spittler (1973) observed a maximum filtration rate of 1.7 µl ind^{-1} h^{-1} at temperatures of 8.6–10°C. The ammonia and urea excretion rates of *T. parvula* are one or two orders higher than those reported for copepods and macrozooplankton organisms (Johansen 1977).

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REFERENCES

Agatha S. (1995) Taxonomie und Ökologie ausgewählter planktischer und tychopelagischer Ciliaten (Protozoa, Ciliophora) des Speicherkoogs Dithmarschen und des Beltringharder

Koogs. PhD Thesis, Univ. Hamburg, Germany, 1–211 + Figures 1.1–1.19, 2.1–2.35

Agatha S. (2008) Redescription of the tintinnid ciliate *Tintinnopsis fimbriata* Meunier, 1919 (Spirotricha, Choreotrichida) from coastal waters of Northern Germany. *Denisia* **23:** 261–272

Agatha S. (2010) A light and scanning electron microscopic study of the closing apparatus in tintinnid ciliates (Ciliophora, Spirotricha, Tintinnina): a forgotten synapomorphy. *J. Eukaryot. Microbiol*. **57:** (in press)

Agatha S., Foissner W. (2009) Conjugation in the spirotrich ciliate *Halteria grandinella* (Müller, 1773) Dujardin, 1841 (Protozoa, Ciliophora) and its phylogenetic implications. *Eur. J. Protistol.* **45:** 51–63

Agatha S., Riedel-Lorjé J. C. (1997) Taxonomy and ecology of some Oligotrichea from brackish water basins at the west coast of Schleswig-Holstein (Northern Germany). *J. Eukaryot. Microbiol*. **44:** 27A

Agatha S., Riedel-Lorjé J. C. (2006) Redescription of *Tintinnopsis cylindrica* Daday, 1887 (Ciliophora: Spirotricha) and unification of tintinnid terminology. *Acta Protozool.* **45:** 137–151

Agatha S., Strüder-Kypke M. C. (2007) Phylogeny of the order Choreotrichida (Ciliophora, Spirotricha, Oligotrichea) as inferred from morphology, ultrastructure, ontogenesis, and SSrRNA gene sequences. *Eur. J. Protistol.* **43:** 37–63

Agatha S., Tsai S.-F. (2008) Redescription of the tintinnid *Stenosemella pacifica* Kofoid and Campbell, 1929 (Ciliophora, Spirotricha) based on live observation, protargol impregnation, and scanning electron microscopy. *J. Eukaryot. Microbiol.* **55:** 75–85

Agatha S., Hesse K. J., Nehring S., Riedel-Lorjé J. C. (1994) Plankton und Nährstoffe in Brackwasserbecken am Rande des Schleswig-Holsteinischen Wattenmeeres unter besonderer Berücksichtigung der Ciliaten und Dinoflagellaten-Dauerstadien sowie blütenbildender und toxischer Formen. *Forschungsbericht des Umweltbundesamtes* **10802085/01:** 1–242

Ashok Prabu V., Perumal P., Rajkumar M. (2005) Diversity of microzooplankton in Parangipettai coastal waters, southeast coast of India. *J. mar. biol. Ass. India* **47:** 14–19

Bakker C., Phaff W. J. (1976) Tintinnida from coastal waters of the S.W.-Netherlands I. The genus *Tintinnopsis* Stein. *Hydrobiologia* **50:** 101–111

Balech E. (1945) Tintinnoinea de Quequén. *Physis, B. Aires* **20:** 1–15

Balech E. (1948) Tintinnoinea de Atlantida (R. O. del Uruguay) (Protozoa Ciliata Oligotr.). *Com. Mus. argent. Cienc. nat. "Bernardino Rivadavia" (Zool.)* **7:** 1–23 + Plates 1–8

Balech E. (1959) Tintinnoinea del Mediterraneo. *Trab. Inst. esp. Oceanogr.* **28:** 1–88 + Plates 1–22

Barría de Cao M. S. (1986) Contribución al conocimiento de Tintinnina (Protozoa, Ciliophora) de la zona de Bahía Blanca, II (Argentina). *Bol. Inst. Esp. Oceanogr.* **3:** 143–150

Barría de Cao M. S. (1992) Abundance and species composition of Tintinnina (Ciliophora) in Bahía Blanca estuary, Argentina. *Estuar. Coastal Shelf Sci.* **34:** 295–303

Barría de Cao M. S., Pettigrosso R., Parodi E., Freije R. (2003) Abundance and species composition of planktonic Ciliophora from the wastewater discharge zone in the Bahía Blanca estuary, Argentina. *Iheringia, Sér. Zool.* **93:** 229–236

Barría de Cao M. S., Beigt D., Piccolo C. (2005) Temporal variability of diversity and biomass of tintinnids (Ciliophora) in a southwestern Atlantic temperate estuary. *J. Plankton Res.* **27:** 1103–1111

Bernatzky G., Foissner W., Schubert G. (1981) Rasterelektronenmikroskopische und biometrische Untersuchungen über die Variabilität der Form, Struktur und Größe des Gehäuses einiger limnischer Tintinnina (Protozoa, Ciliophora). *Zool. Scr.* **10:** 81–90 (with English summary)

Biancalana F., Barría de Cao M. S., Hoffmeyer M. S. (2007) Micro and mesozooplankton composition during winter in Ushuaia and Golondrina Bays (Beagle Channel, Argentina). *Braz. J. Oceanogr.* **55:** 83–95 (with Portuguese summary)

Biernacka I. (1948) Tintinnoinea w Zatoce Gdańskiej i wodach przyległych (Tintinnoinea in the Gulf of Gdańsk and adjoining waters). *Biul. morsk. Lab. ryb. w Gdyni* **4:** 73–91 + Table (with English summary)

Biernacka I. (1956) Przyczynek do znajomości pierwotniaków Zalewu Wiślanego (Contribution to the knowledge of the Vistula Lagoon protozoans). *Polskie Archwm Hydrobiol.* **3:** 43–68 (with Russian and English summaries)

Biernacka I. (1965) Ausscheidung gehäusebildender Substanzen durch reife Formen gewisser Arten der Gattung *Tintinnopsis* Stein. *Acta Protozool.* **3:** 265–268 (with Polish summary)

Biernacka I. (1968) Influence de la salinité et de la thermique sur les protistes de la mer Baltique et de la Lagune de la Vistule. *Ekol. pol. Ser. A* **16:** 261–278 (with Polish summary)

Blackbourn D. J. (1974) The feeding biology of tintinnid protozoa and some other inshore microzooplankton. PhD Thesis, Univ. British Columbia, Canada, i–xi + 1–186 + Appendices 1–11

Boltovskoy D., Dinofrio E. O., Alder V. A. (1990) Intraspecific variability in Antarctic tintinnids: the *Cymatocylis affinis*/*convallaria* species group. *J. Plankton Res.* **12:** 403–413

Brandt K. (1896) Die Tintinnen. *Biblthca zool.* **8:** 45–72 + Plate 3

Brandt K. (1906) Die Tintinnodeen der Plankton-Expedition. Tafelerklärungen nebst kurzer Diagnose der neuen Arten. *Ergebn. Plankton-Exped. Humboldt-Stiftung* **3 La:** 1–33 + Plates 1–70

Brandt K. (1907) Die Tintinnodeen der Plankton-Expedition. Systematischer Teil. *Ergebn. Plankton-Exped. Humboldt-Stiftung* **3 La:** 1–488

Burkovsky I. V. (1976a) New data on Tintinnida (Ciliata) of Arctic and revision of fauna. *Zool. Zh.* **55:** 325–336 (in Russian with English summary)

Burkovsky I. V. (1976b) Ecology of Tintinnida (Ciliata) of the White Sea. *Zool. Zh.* **55:** 497–507 (in Russian with English summary)

Burkovsky I. V., Zamyshlyak E. A., Poskryakova N. P. (1974) Tintinnidae (Ciliata) of the White Sea. Revision of the fauna. *Zool. Zh.* **53:** 1757–1766 (in Russian with English summary)

Burns D. A. (1983) The distribution and morphology of tintinnids (ciliate protozoans) from the coastal waters around New Zealand. *N. Z. J. mar. Freshwat. Res.* **17:** 387–406

Bursa A. (1963) Phytoplankton in coastal waters of the Arctic Ocean at Point Barrow, Alaska. *Arctic* **16:** 239–262

Cai S., Song W., Xu D., Chiang K. (2006) Morphological studies on the infraciliature of a planktonic ciliate, *Tintinnopsis brasiliensis* (Ciliophora: Tintinina). *J. Ocean Univ. China* **5:** 55–57

Chester A. J. (1978) Microzooplankton in the surface waters of the Strait of Juan de Fuca. *NOAA Tech. Rep.* **ERL 403-PMEL 30:** 1–26

Choi J. K., Coats D. W., Brownlee D. C., Small E. B. (1992) Morphology and infraciliature of three species of *Eutintinnus* (Ciliophora; Tintinnina) with guidelines for interpreting protargol-stained tintinnine ciliates. *J. Protozool.* **39:** 80–92

Cordeiro T. A., Sassi R. (1997) Tintinnina (Ciliophora, Protista) of the North Sea during the spring of 1986. *Helgoländer Meeresunters.* **51:** 155–172

Cordeiro T. A., Brandini F. P., Martens P. (1997) Spatial distribution of the Tintinnina (Ciliophora, Protista) in the North Sea, spring of 1986. *J. Plankton Res.* **19:** 1371–1383

Corliss J. O. (2003) Comments on the neotypification of protists, especially ciliates (Protozoa, Ciliophora). *Bull. zool. Nom.* **60:** 48

Cosper T. C. (1972) The identification of tintinnids (Protozoa: Ciliata: Tintinnida) of the St. Andrew Bay system, Florida. *Bull. Mar. Sci.* **22:** 391–418

Daday E. von (1887) Monographie der Familie der Tintinnodeen. *Mitt. zool. Stn Neapel* **7:** 473–591 + Plates 18–21

Damodara Naidu W., Krishnamurthy K. (1985) Biogeographical distribution of tintinnids (Protozoa: Ciliata) from Porto Novo waters. *Mahasagar – Bull. Natl. Inst. Oceanogr.* **18:** 417–423

Davis C. C. (1978) Variations of the lorica in the genus *Parafavella* (Protozoa: Tintinnida) in northern Norway waters. *Can. J. Zool.* **56:** 1822–1827 (with French summary)

Davis C. C. (1981) Variations of lorica shape in the genus *Ptychocylis* (Protozoa: Tintinnina) in relation to species identification. *J. Plankton Res.* **3:** 433–443

Diodato S. L., Hoffmeyer M. S. (2008) Contribution of planktonic and detritic fractions to the natural diet of mesozooplankton in Bahía Blanca Estuary. *Hydrobiologia* **614:** 83–90

Dolgopolskaia M. A. (1940) Das Zooplankton des Schwarzen Meeres in der Nähe von Karadag. *Trav. Sta. biol. Karadagh* **6:** 57–111 + Table (in Russian with German summary and table explanation)

El Maghraby A. M., Perkins E. J. (1956) Additions to the marine fauna of Whitstable. *Ann. Mag. nat. Hist., Ser. (12)* **9:** 481–496

Entz G. (1884) Über Infusorien des Golfes von Neapel. *Mitt. zool. Stn Neapel* **5:** 289–444 + Plates 20–25

Fauré-Fremiet E. (1924) Contribution a la connaissance des infusoires planktoniques. *Bull. biol. Fr. Belg. Suppl.* **6:** 1–171

Fenchel T., Kristensen L. D., Rasmussen L. (1990) Water column anoxia: vertical zonation of planktonic protozoa. *Mar. Ecol. Prog. Ser.* **62:** 1–10

Fernandes L. F. (2004) Tintininos (Ciliophora, Tintinnina) de águas subtropicais na região Sueste-Sul do Brasil. I. Famílias Codonellidae, Codonellopsidae, Coxliellidae, Cyttarocylidae, Epiplocylidae, Petalotrichidae, Ptychocylidae, Tintinnididae e Undellidae. *Rev. Bras. Zool.* **21:** 551–576 (with English summary)

Fernandez-Leborans G., Valgañon B., Castro de Zaldumbide M. (1999) Characterization of a marine sublittoral area facing the open sea, using epibenthic protists. *Bull. Mar. Sci.* **65:** 725–743

Foissner W. (1991) Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. *Eur. J. Protistol.* **27:** 313–330

Foissner W. (2002) Neotypification of protists, especially ciliates (Protozoa, Ciliophora). *Bull. zool. Nom.* **59:** 165–169

Foissner W., O'Donoghue P. J. (1990) Morphology and infraciliature of some freshwater ciliates (Protozoa: Ciliophora) from Western and South Australia. *Invertebr. Taxon.* **3:** 661–696

Foissner W., Wilbert N. (1979) Morphologie, Infraciliatur und Ökologie der limnischen Tintinnina: *Tintinnidium fluviatile* Stein, *Tintinnidium pusillum* Entz, *Tintinnopsis cylindrata* Daday und *Codonella cratera* (Leidy) (Ciliophora, Polyhymenophora). *J. Protozool.* **26:** 90–103 (with English summary)

Foissner W., Agatha S., Berger H. (2002) Soil ciliates (Protozoa, Ciliophora) from Namibia (Southwest Africa), with emphasis on two contrasting environments, the Etosha region and the Namib Desert. Part I: Text and line drawings. Part II: Photographs. *Denisia* **5:** 1–1459

Fol H. (1884) Sur la famille des Tintinnodea. *Rec. zool. suisse* **1:** 27–64 + Plates 4, 5

Fonda Umani S., Monti M. (1991) Microzooplankton populations in the Strait of Magellan. *Boll. Oceanol. Teor. Applic.* **9:** 151–162 (with Italian summary)

Gaarder K. R. (1946) Tintinnoinea from the "Michael Sars" North Atlantic deep-sea expedition 1910. *Rep. Sci. Res. "Michael Sars" North Atlant. deep-sea exped. 1910* **2:** 1–35

Gao S., Gong J., Lynn D., Lin X., Song W. (2009) An updated phylogeny of oligotrich and choreotrich ciliates (Protozoa, Ciliophora, Spirotrichea) with representative taxa collected from Chinese coastal waters. *System. Biodiv.* **7:** 235–242

Gavrilova N., Dolan J. R. (2007) A note on species lists and ecosystem shifts: Black Sea tintinnids, ciliates of the microzooplankton. *Acta Protozool.* **46:** 279–288

Gold K. (1969) Tintinnida: feeding experiments and lorica development. *J. Protozool.* **16:** 507–509

Gold K. (1980) SEM studies on the lorica of various Tintinnina. *Scanning Electron Microscopy* **3:** 537–541

Gold K., Morales E. A. (1974) Effects of temperature on 2 strains of *Tintinnopsis tubulosa*. *J. Protozool.* **21:** 442

Gold K., Morales E. A. (1975a) Tintinnida of the New York Bight: loricae of *Parafavella gigantea*, *P. parumdentata*, and *Ptychocylis obtusa*. *Trans. Am. microsc. Soc.* **94:** 142–145

Gold K., Morales E. A. (1975b) A new hypothesis to account for lorica building by certain Tintinnida. *J. Protozool.* **22:** 38A

Gold K., Morales E. A. (1975c) Seasonal changes in lorica sizes and the species of Tintinnida in the New York Bight. *J. Protozool.* **22:** 520–528

Gold K., Morales E. A. (1976a) Studies on the sizes, shapes, and the development of the lorica of agglutinated Tintinnida. *Biol. Bull. mar. biol. Lab., Woods Hole* **150:** 377–392

Gold K., Morales E. A. (1976b) Observations on the nature and significance of the particles used by Tintinnida during lorica-building. *Trans. Am. microsc. Soc.* **95:** 69–72

Gold K., Morales E. A. (1976c) Studies on Tintinnida using scanning electron microscopy. *Trans. Am. microsc. Soc.* **95:** 707–711

Gold K., Morales E. A. (1977a) The role of protozoa in cycling minerals in the sea: studies on the structure of the lorica of some agglutinated Tintinnida. *Prog. Protozool.*, *V. Int. Congr. Protozool., USA,* **1977:** Abstract 41

Gold K., Morales E. A. (1977b) Studies on the Tintinnida of Enewetak Atoll. *J. Protozool.* **24:** 580–587

Hada Y. (1937) The fauna of Akkeshi Bay IV. The pelagic Ciliata. *J. Fac. Sci. Hokkaido Univ. (Zool.)* **5:** 143–216

Halme E. (1958) Planktologische Untersuchungen in der Pojo-Bucht und angrenzenden Gewässern. IV Zooplankton. *Suomal. eläin-ja kasvit. Seur. van. eläin. Julk.* **19:** 1–62 (with Finnish summary)

Halme E., Lukkarinen T. (1960) Planktologische Untersuchungen in der Pojo-Bucht und angrenzenden Gewässern. V Die Ziliaten *Tintinnopsis tubulosa* Levander und *T. brandti* (Nordqv.) Levander. *Suomal. eläin-ja kasvit. Seur. van. eläin. Julk.* **22:** 1–24 (with Finnish summary)

Hannachi I., Drira Z., Belhassen M., Hamza A., Ayadi H., Bouain A., Aleya L. (2008) Abundance and biomass of the ciliate community during a spring cruise in the Gulf of Gabes (Eastern Mediterranean Sea, Tunisia). *Acta Protozool.* **47:** 293–305

Hansen-Ostenfeld C. (1916) De danske Farvandes Plankton i Aarene 1898–1901. Phytoplankton og Protozoer. 2. Protozoer; Organismer med usikker Stilling; Parasiter i Phytoplanktonter. *K. danske Vidensk. Selsk. Skr. (ser. 8)* **2:** 365–451 (with French translation)

Hargraves P. E. (1981) Seasonal variations of tintinnids (Ciliophora: Oligotrichida) in Narragansett Bay, Rhode Island, U.S.A. *J. Plankton Res.* **3:** 81–91

Hedin H. (1974) Tintinnids on the Swedish west coast. *Zoon* **2:** 123–133

Hedin H. (1975a) On the ecology of tintinnids on the Swedish west coast. *Zoon* **3:** 125–140

Hedin H. (1975b) On the ultrastructure of *Favella ehrenbergii* (Claparède & Lachmann) and *Parafavella gigantea* (Brandt), Protozoa, Ciliata, Tintinnida. *Zoon* **3:** 11–18

Hoffmeyer M. S., Barría de Cao M. S. (2007) Zooplankton assemblages from a tidal channel in the Bahía Blanca Estuary, Argentina. *Braz. J. Oceanogr.* **55:** 97–107 (with Portuguese summary)

Hofker J. (1931) Studien über Tintinnoidea. *Arch. Protistenk.* **75:** 315–402

Ikävalko J. (2003) D4.2.3.1: Report on Sea Ice Communities. *Finnish Inst. Mar. Res., Growth Project* **GRD2-2000-30112 "ARCOP":** 1–42

Johansen P. L. (1977) The role of marine protozoa in nitrogen regeneration. *Prog. Protozool.*, *V. Int. Congr. Protozool., USA,* **1977:** Abstract 363

Jonsson P. R. (1989) Vertical distribution of planktonic ciliates – an experimental analysis of swimming behaviour. *Mar. Ecol. Prog. Ser.* **52:** 39–53

Jörgensen E. (1912) Bericht über die von der schwedischen Hydrographisch-Biologischen Kommission in den schwedischen Gewässern in den Jahren 1909–1910 eingesammelten Planktonproben. *Sven. Hydrogr. Biol. Komm. Skr.* **4:** 1–20

Jörgensen E. (1927) Ciliata. Tintinnidae. In: Die Tierwelt der Nord- und Ostsee 8 II_{c1}, (Eds. G. Grimpe, E. Wagler). Akademische Verlagsgesellschaft, Leipzig, 1–26

Kchaou N., Elloumi J., Drira Z., Hamza A., Ayadi H., Bouain A., Aleya L. (2009) Distribution of ciliates in relation to environmental factors along the coastline of the Gulf of Gabes, Tunisia. *Estuar. Coastal Shelf Sci.* **83:** 414–424

Kim Y.-H., Lee J.-B. (2003) Seasonal variations and species composition of planktonic ciliates in the southern coastal waters of Jeju Island, Korea. *J. Korean Soc. Oceanogr.* **8:** 59–69

Kivi K. (1986) Annual succession of pelagic protozoans and rotifers in the Tvärminne Storfjärden, SW coast of Finland. *Ophelia Suppl.* **4:** 101–110

Kofoid C. A., Campbell A. S. (1929) A conspectus of the marine and fresh-water Ciliata belonging to the suborder Tintinnoinea, with descriptions of new species principally from the Agassiz Expedition to the eastern tropical Pacific 1904–1905. *Univ. Calif. Publs Zool.* **34:** 1–403

Kofoid C. A., Campbell A. S. (1939) Reports on the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross," from October, 1904, to March, 1905, Lieut.-Commander L. M. Garrett, U. S. N. Commanding. XXXVII. The Ciliata: The Tintinnoinea. *Bull. Mus. comp. zool., Harv.* **84:** 1–473 + Plates 1–36

Kogan M. (2005) Estudio de la composición específica, abundancia y distribución espacial del microzooplancton (protozoos y micrometazoos) en el estuario del Río de la Plata (Argentina-Uruguay). PhD Thesis, Univ. Buenos Aires, Argentina, 1–174 (with English summary)

Kolosova E. G., Ilyash L. V. (2009) Cryo-fauna of the Velikaya Salma Strait of the Kandalaksha Bay in the White Sea. In: Biological Resources of the White Sea and Inland Waters of European North. Proc. XXVIII. Int. Conf. 2009. Russian Academy of Sciences, Petrozavodsk, 285–289

Krishnamurthy K., Damodara Naidu W., Sultan Ali M. A. (1987) Community structure and organization of tintinnids (Protozoa: Ciliata). In: Indian Ocean – Biology of Benthic Marine Organisms – Techniques and Methods as applied to the Indian Ocean, (Eds. M.-F. Thompson, R. Sarojini, R. Nagabhushanam). A. A. Balkema, Rotterdam, 307–313

Kurilov A. V. (2000) Ciliates of coastal habitats of Odessa Bay. *Ekol. Morya* **52:** 9–11 (in Russian with English summary)

Laackmann H. (1908) Ungeschlechtliche und geschlechtliche Fortpflanzung der Tintinnen. *Wiss. Meeresunters., Abt. Kiel* **10:** 13–38 + Plates 1–3

Laval M. (1972) Ultrastructure de *Petalotricha ampulla* (Fol). Comparaison avec d'autres Tintinnides et avec les autres ordres de ciliés. *Protistologica* **8:** 369–386 (with English summary)

Laval-Peuto M. (1977) Reconstruction d'une lorica de forme *Coxliella* par le trophonte nu de *Favella ehrenbergii* (Ciliata, Tintinnina). *C. r. hebd. Séanc. Acad. Sci. Paris, Ser.* **D 284:** 547–550

Laval-Peuto M. (1980) Ultrastructure of the lorica-wall of Tintinnina (Ciliata, Spirotricha). *J. Protozool.* **27:** 83A

Laval-Peuto M. (1981) Construction of the lorica in Ciliata Tintinnina. *In vivo* study of *Favella ehrenbergii*: variability of the phenotypes during the cycle, biology, statistics, biometry. *Protistologica* **17:** 249–272 (with French summary)

Laval-Peuto M. (1994) Classe des Oligotrichea Bütschli, 1887. Ordre des Tintinnida Kofoid et Campbell, 1929. In: Traité de Zoologie. Anatomie, Systématique, Biologie. II. Infusoires Ciliés. 2. Systématique, (Ed. P. de Puytorac). Masson, Paris, Milano, Barcelona, 181–219

Laval-Peuto M., Brownlee D. C. (1986) Identification and systematics of the Tintinnina (Ciliophora): evaluation and suggestions for improvement. *Annls Inst. océanogr., Paris* **62:** 69–84 (with French summary)

Laval-Peuto M., Gold K., Storm E. R. (1979) The ultrastructure of *Tintinnopsis parva*. *Trans. Am. microsc. Soc.* **98:** 204–212

Lecal J. (1967) Le nannoplancton des côtes d'Israël. *Hydrobiologia* **29:** 305–387 (with Russian summary)

Lee J.-B., Kim Y.-H. (2010) Distribution of tintinnids (loricate ciliates) in East Asian waters in summer. In: Coastal Environmental and Ecosystem Issues of the East China Sea, (Eds. A. Ishimatsu, H. J. Lie). Terrapub and Nagasaki University, 173–180

Leppänen J.-M., Bruun J.-E. (1986) The role of pelagic ciliates including the autotrophic *Mesodinium rubrum* during the spring bloom of 1982 in the open northern Baltic proper. *Ophelia Suppl.* **4:** 147–157

Levander K. M. (1900) Über das Herbst- und Winter-Plankton im finnischen Meerbusen und in der Ålands-See 1898. *Acta Soc. Fauna Flora fenn.* **18:** 1–25

Li Z., Yi Z., Yang J., Gong J., Clamp J. C., Al-Rasheid K. A. S., Al-Arifi S., Al-Khedhairy A. A., Song W. (2009) Phylogenetic investigation on five genera of tintinnid ciliates (Ciliophora, Choreotrichia), based on the small subunit ribosomal RNA gene sequences. *Prog. nat. Sci.* **19:** 1097–1101

Lohmann H. (1908) Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. *Wiss. Meeresunters., Abt. Kiel* **10:** 129–370 + Plates 9–17

Lohmann H. (1911) Über das Nannoplankton und die Zentrifugierung kleinster Wasserproben zur Gewinnung desselben in lebendem Zustande. *Int. Revue ges. Hydrobiol. Hydrogr.* **4:** 1–38 (with English summary)

Lynn D. H. (2008) The Ciliated Protozoa. Characterization, Classification, and Guide to the Literature. 3rd ed. Springer, i–xxxiii + 1–605

Marshall S. M. (1969) Protozoa, Order: Tintinnida, Family: Tintinnidiidae, Genus: *Tintinnidium*, Family: Codonellidae, Genus: *Tintinnopsis*. In: Fiches d'identification du zooplankton, (Eds. J. H. Fraser, V. K. Hansen). Conseil Permanent International pour l'Exploration de la Mer, Charlottenlund slot – Denmark: Sheet **117**

Merkle H. (1909) Untersuchungen an Tintinnodeen der Ost- und Nordsee. *Wiss. Meeresunters., Abt. Kiel* **11:** 139–186 + Plates 2, 3

Meunier A. (1910) Microplankton des Mers de Barents et de Kara. Campagne Arctique de 1907. C. Bulens, Bruxelles, i–xviii + 1–355 + Plates 1–37

Meunier A. (1919) Microplankton de la mer Flamande. Les Tintinnides et caetera. *Mém. Mus. r. Hist. nat. Belg.* **8:** 1–59 + Plates 22, 23

Middlebrook K., Emerson C. W., Roff J. C., Lynn D. H. (1987) Distribution and abundance of tintinnids in the Quoddy Region of the Bay of Fundy. *Can. J. Zool.* **65:** 594–601 (with French summary)

Mironova E. I., Telesh I. V., Skarlato S. O. (2009) Planktonic ciliates of the Baltic Sea (a review). *Inland Wat. Biol.* **2:** 13–24

Möbius K. (1887) Systematische Darstellung der Thiere des Plankton gewonnen in der westlichen Ostsee und auf einer Fahrt von Kiel in den Atlantischen Ocean bis jenseit der Hebriden. *Ber. Komm. wiss. Unters. Deutsch. Meere, Kiel* **5:** 108–126 + Plates 7, 8

Modigh M., Castaldo S., Saggiomo M., Santarpia I. (2003) Distribution of tintinnid species from 42° N to 43° S through the Indian Ocean. *Hydrobiologia* **503:** 251–262

Moscatello S., Rubino F., Saracino O. D., Fanelli G., Belmonte G., Boero F. (2004) Plankton biodiversity around the Salento Peninsula (South East Italy): an integrated water/sediment approach. *Sci. Mar.* **68, Suppl. 1:** 85–102 (with Spanish summary)

Nielsen T. G., Hansen B. (1995) Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. *Mar. Ecol. Prog. Ser.* **125:** 239–257

Nielsen T. G., Kiørboe T. (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 2. Ciliates. *Limnol. Oceanogr.* **39:** 508–519

Oliveira Areas M. de, Tenenbaum D. R., Gomes E. A. T. (2006) Microvariações temporais do protozooplâncton na Baía de Guanabara (RJ): composição específica e densidade durante o verão de 2004. *Univ. Unigranrio, Saúde & Ambiente em Revista* **1:** 14–22

Osorio-Tafall B. F. (1941) Tintinnidos nuevos o poco conocidos del plancton neritico de Mexico. *Revta Soc. mex. Hist. nat.* **2:** 147–173 + Plates 5–9

Paranjape M. A. (1987) The seasonal cycles and vertical distribution of tintinnines in Bedford Basin, Nova Scotia, Canada. *Can. J. Zool.* **65:** 41–48 (with French summary)

Paulmier G. (1971) Cycle des matières organiques dissoutes, du plancton et du micro-phytoplancton dans l'estuaire du Belon leur importance dans l'alimentation des huitres. *Rev. Trav. Inst. Pêches marit.* **35:** 157–200

Paulmier G. (1995) Les tintinnides (Ciliophora, Oligotrichida, Tintinnina) des côtes françaises de la Manche et de l'Atlantique. *Annls Soc. Sci. nat. Charente-Maritimeg.* **8:** 453–487

Petz W., Foissner W. (1993) Morphogenesis in some freshwater tintinnids (Ciliophora, Oligotrichida). *Eur. J. Protistol.* **29:** 106–120

Petz W., Song W., Wilbert N. (1995) Taxonomy and ecology of the ciliate fauna (Protozoa, Ciliophora) in the endopagial and pelagial of the Weddell Sea, Antarctica. *Stapfia* **40:** 1–223

Pierce R. W., Turner J. T. (1993) Global biogeography of marine tintinnids. *Mar. Ecol. Prog. Ser.* **94:** 11–26

Porto Neto F. F. (2003) Zooplankton as bioindicator of environmental quality in the Tamandaré reef system (Pernambuco-Brazil): anthropogenic influence and interaction with mangroves. PhD Thesis, Univ. Bremen, Germany, i–vi + 1–99 + appendix with tables (with German and Portuguese summaries)

Rampi L., Zattera A. (1982) Chiave per la determinazione dei Tintinnidi mediterranei. *Comitato nazionale per la ricerca e per lo sviluppo dell'energia nucleare e delle energie alternative* **ENEA-RT/BIO(82)28:** 1–104

Riedel-Lorjé J. C., Hesse K.-J., Agatha S., Nehring S. (1998) Sind die Speicherkoogbecken Brutstätten für Planktonblüten? In: Umweltatlas Wattenmeer Band I Nordfriesisches und Dithmarscher Wattenmeer, (Eds. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Umweltbundesamt). Ulmer, Stuttgart, 80–81

Rossolimo L. (1922) Die Tintinnodea des Schwarzen Meeres. *Russk. Arkh. Protist.* **1:** 22–34 + Plate 2 (in Russian with German summary)

Rossolimo L. L. (1927) Planktische Infusorien des Karischen Meeres. *Trudy morsk. nauch. Inst.* **2:** 63–77 (in Russian with German summary)

Schulz H. (1964) Die Tintinnoinea des Elbe-Aestuars. *Arch. Fisch-Wiss.* **15:** 216–225 (with English summary)

Schwarz S. (1961) Produktionsbiologische Untersuchungen am Zooplankton der Rügenschen, Hiddenseer und Darßer Boddengewässer (1953 bis 1955). *Z. Fisch. N.F.* **10:** 401–428 (with English and Russian summaries)

Skryabin V., Al-Yamani F. (2007) Composition, distribution and seasonal changes of tintinnids in the northwestern Arabian Gulf around the Bubiyan Island. *Int. J. Oceans Oceanogr.* **2:** 99–106

Small E. B., Lynn D. H. (1985) Phylum Ciliophora Doflein, 1901. In: An Illustrated Guide to the Protozoa, (Eds. J. J. Lee, S. H. Hutner, E. C. Bovee). Society of Protozoologists, Allen Press, Lawrence, Kansas, 393–575

Snoeyenbos-West O. L. O., Salcedo T., McManus G. B., Katz L. A. (2002) Insights into the diversity of choreotrich and oligotrich ciliates (Class: Spirotrichea) based on genealogical analyses of multiple loci. *Int. J. Syst. Evol. Microbiol.* **52:** 1901–1913

Snyder R. A., Brownlee D. C. (1991) *Nolaclusilis bicornis* n. g., n. sp. (Tintinnina: Tintinnidiidae): a tintinnine ciliate with novel lorica and cell morphology from the Chesapeake Bay estuary. *J. Protozool.* **38:** 583–589

Sokolova Y. Y., Gerassimova Z. P. (1984) The ultrastructure of the ciliates *Parafavella denticulata* Ehrenberg, 1840. *Tsitologiya* **26:** 1237–1245 + Plates 1–4 (in Russian with English summary)

Song W., Wilbert N. (1995) Benthische Ciliaten des Süßwassers. In: Praktikum der Protozoologie, (Ed. R. Röttger). Gustav Fischer Verlag, Stuttgart, 156–168

Souto S. (1970) Tintinnidos de la costa atlantica entre los 31° y 35° de latitud sur (Uruguay y sur de Brasil) (Protozoa Ciliata). *Physis*, *B. Aires* **30:** 187–208 (with English summary)

Spittler P. (1973) Feeding experiments with tintinnids. *Oikos Suppl.* **15:** 128–132 (with English and Russian summaries)

Stein F. (1867) Der Organismus der Infusionsthiere nach eigenen Forschungen in systematischer Reihenfolge bearbeitet II. Abtheilung. 1) Darstellung der neuesten Forschungsergebnisse über Bau, Fortpflanzung und Entwickelung der Infusionsthiere.

2) Naturgeschichte der heterotrichen Infusorien. W. Engelmann, Leipzig, i–viii + 1–355 + Plates 1–16

Strüder-Kypke M. C., Lynn D. H. (2003) Sequence analyses of the small subunit rRNA gene confirm the paraphyly of oligotrich ciliates sensu lato and support the monophyly of the subclasses Oligotrichia and Choreotrichia (Ciliophora, Spirotrichea). *J. Zool. (Lond.)* **260:** 87–97

Strüder-Kypke M. C., Lynn D. H. (2008) Morphological versus molecular data – phylogeny of tintinnid ciliates (Ciliophora, Choreotrichia) inferred from small subunit rRNA gene sequences. *Denisia* **23:** 417–424

Telesh I., Postel L., Heerkloss R., Mironova E., Skarlato S. (2008) Zooplankton of the Open Baltic Sea. *BMB Publications 20. Meereswiss. Ber., Warnemünde* **73:** 1–251

Tempelman D., Agatha S. (1997) Biomonitoring van microzoöplankton in de Nederlandse zoute wateren 1996. *TRIPOS for Rijkswaterstaat, Rijksinstituut voor Kust en Zee* **97.T0017-1b:** i–ii + 1–77

Travers A., Travers M. (1971) Catalogue des Tintinnides (cilies oligotriches) récoltés dans le Golfe de Marseille de 1962 a 1964. *Tethys* **2:** 639–645

Travers A., Travers M. (1975) Catalogue du microplancton du Golfe de Marseille. *Int. Revue ges. Hydrobiol. Hydrogr.* **60:** 251–276

Valbonesi A., Luporini P. (1990) A new marine species of *Euplotes* (Ciliophora, Hypotrichida) from Antarctica. *Bull. Br. Mus. (Nat. Hist.) Zool.* **56:** 57–61

Van Breemen P. J. (1905) Plankton van Noordzee en Zuiderzee. PhD Thesis, Univ. Amsterdam, Netherlands, 1–180 + Plates 1, 2

Van der Spoel S. (1987) Annotated species list of the Mollusca, Tintinnida, Amphisolenia (Dinoflagellata) and Radiolaria collected in pump samples by the Amsterdam Mid North Atlantic Plankton Expeditions, 1980–1983 (PROJ.101A). *Inst. Tax. Zool., Amsterdam, Verslagen en Tech. Gegevens* **48:** 1–99

Van der Spoel S., Heyman R. P. (1983) A Comparative Atlas of Zooplankton. Biological Patterns in the Oceans. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo, 1–186

Verity P. G. (1987) Abundance, community composition, size distribution, and production rates of tintinnids in Narragansett Bay, Rhode Island. *Estuar. Coastal Shelf Sci.* **24:** 671–690

Wailes G. H. (1925) Tintinnidae from the Strait of Georgia, B.C. *Contr. Can. Biol. Fish., Ottawa, N.S.* **2:** 533–539 + Plates 1, 2

Wailes G. H. (1943) 1. Protozoa. 1f. Ciliata. 1g. Suctoria. *Canadian Pacific Fauna* **1:** 1–46

Wasik A. (1998) Antarctic tintinnids: their ecology, morphology, ultrastructure and polymorphism. *Acta Protozool.* **37:** 5–15

Wasik A., Mikołajczyk E. (1992) The morphology and ultrastructure of the Antarctic ciliate, *Cymatocylis convallaria* (Tintinnina). *Acta Protozool.* **31:** 233–239

Wasik A., Mikołajczyk E. (1994) Infraciliature of *Cymatocylis affinis*/*convallaria* (Tintinnina). *Acta Protozool.* **33:** 79–85

Wasik A., Mikołajczyk E., Gołębiowska M. (1997) Morphology and microstructure of selected Tintinnina loricae. *Acta Protozool.* **36:** 31–38

Young J. R., Geisen M. (2002) Xenospheres – associations of coccoliths resembling coccospheres. *J. Nannoplankton Res.* **24:** 27–34

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