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Redescription of *Tintinnopsis cylindrica* Daday, 1887 (Ciliophora: Spirotricha) and Unification of Tintinnid Terminology

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Summary

Although *Tintinnopsis cylindrica* Daday, 1887 is apparently widely distributed in the plankton of marine and brackish coastal waters, its ciliary pattern remained unknown. Without detailed knowledge of the cell morphology, however, the proposed synonymies cannot be proved. Hence, the cell and lorica features of *T. cylindrica* are redescribed from live and protargol-impregnated specimens collected in mixo-polyhaline basins at the German North Sea coast. An improved species diagnosis and a comprehensive unified terminology are provided. The somatic ciliary pattern of *T. cylindrica* is complex, comprising a ventral, dorsal, and posterior kinety as well as a right, left, and lateral ciliary field. Accordingly, the species differs from its congener *T. cylindrata* that has merely a right and left ciliary field and ventral organelles. On the other hand, the genera *Codonella*, *Codonellopsis*, *Cymatocylis*, *Helicostomella*, *Leprotintinnus*, and *Stenosemella* share this pattern. The oral primordium of *T. cylindrica* develops hypoapokinetally posterior to the lateral ciliary field as in *Codonella cratera* and *Cymatocylis convallaria*.

Keywords

biogeography; ciliary pattern; ecology; morphology; ontogenesis; taxonomy; Tintinnina

INTRODUCTION

Entz (1884, 1909b), Bütschli (1887-1889), Daday (1887), Brandt (1907), Schweyer (1909), and Hofker (1931) emphasized the significance of cytological features for a natural tintinnid taxonomy. Nevertheless, the majority of the ~ 1,200 tintinnid species was described in the following years, using merely lorica features (e.g., Kofoid and Campbell 1929, 1939). It was only in the eighties and nineties of the last century, that the investigation of the cell morphology experienced a renaissance by the redescription of 16 tintinnid species (Foissner and Wilbert 1979, Song and Wilbert 1989, Blatterer and Foissner 1990, Foissner and O'Donoghue 1990, Sniezek *et al*. 1991, Snyder and Brownlee 1991, Choi *et al*. 1992, Song 1993, Wasik and Mikołajczyk 1994, Petz *et al*. 1995). The number of reinvestigated species is, however, still too low for a revision of the classification and a comparison with the gene trees (Snoeyenbos-West *et al*. 2002, Strüder-Kypke and Lynn 2003). Hence, a further tintinnid species, *viz*., *Tintinnopsis cylindrica*, is redescribed in the present paper, including both, features of the lorica and the cell.

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MATERIALS AND METHODS

Collection

The samples were collected between 1991 and 1993 in the basins of two polders, *viz.*, the Beltringharder Koog and the Speicherkoog Dithmarschen, at the North Sea coast of Schleswig-Holstein, northern Germany. These shallow (up to 15 m deep) basins contain brackish water of changing salinities as they are temporarily connected with the Wadden Sea by sluice gates and have freshwater inflow by rainwater, ground water, and streams. Likewise, they are characterized by reduced tidal currents, high turbidity, and eutrophication due to nutrient loads drained from agricultural areas. The abiotic factors that prevailed during the investigation period were described in detail by Agatha *et al.* (1994) and Riedel-Lorjé *et al.* (1998). Samples were taken monthly by bucket from December to February, fortnightly in March and November, and weekly during all other months 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 (Agatha *et al.* 1994), while an unpreserved subsample was used for taxonomical investigations.

Taxonomic studies

All observations are from field material as culture trials failed, using a temperature of ~ 12°C, a 12 h light to 12 h dark cycle with an irradiance of ~ 15 $\mu E\ m^{-2}\ s^{-1}$, and a mixture of flagellates from the sampling sites as prey. Cell movement was studied in a Petri dish (~ 6 cm across; water depth ~ 2.5 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, cells were fixed for 30 min in a modified Parducz’ solution made of 6 parts of 2% OsO_4 (w/v) in sea water and one part of saturated aqueous $HgCl_2$ (Valbonesi and Luporini 1990); further steps followed Foissner (1991).

Counts and measurements on protargol-impregnated cells were performed at ×1,000; *in vivo* measurements were made at ×40-1,200.

The kinetal density index is the ratio of kinety number to cell circumference posterior to the membranellar zone [kineties/μm] in protargol-impregnated cells (Snyder and Brownlee 1991). Usually, it was 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; hence, the kinetal index was not calculated.

Illustrations

Drawings of live specimens summarize information and are based on mean measurements, while those of protargol-impregnated specimens were made with a camera lucida. The kinetal map depicts the morphostatic ciliary pattern of a protargol-impregnated 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 membranelles. The ratio of cell circumference to length of kineties is 1:1. Kinetids are equidistantly arranged in the ciliary rows and the kinety curvature is neglected, except for the ventral and last kinety whose course might be of taxonomic significance. The somatic cilia are symbolized by oblique lines, differences in their length are not considered.

Neotype material

A slide with protargol-impregnated neotype specimens is deposited with the relevant cells marked in the Biology Centre of the Museum of Upper Austria (LI) in A-4040 Linz (Austria). The reasons for and the problems with neotypification are discussed by Foissner (2002), Foissner *et al.* (2002), and Corliss (2003).

RESULTS

Terminology

Since more than thirty years, the orders Halteriida and Oligotrichida have been separated from the order Choreotrichida by the shape of the adoral zone of membranelles (C-shaped *vs.* ring-shaped; Fauré-Fremiet 1970). However, Kim *et al.* (2005) discovered a new member of the family Strombidinopsidae (order Choreotrichida) with a slightly open membranellar zone, representing a transitional stage. Hence, a different terminology for the large and small membranelles/polykinetids in the Halteriida and Oligotrichida (anterior and ventral membranelles) on the one hand and the Choreotrichida (external and internal membranelles) on the other hand seems not any longer justified. Accordingly, a unifying and neutral terminology concerning the oral ciliature is introduced here. Additionally, the confusing terminology of the somatic ciliary components and some further features in the suborder Tintinnina is unscrambled here.

Adoral zone of membranelles

The adoral zone of membranelles is an orderly arrangement of membranelles around the peristomial field, terminating in the buccal cavity. The term was probably introduced by Bütschli (1887-1889) and is favoured, as the younger term “oral polykinetids” (Sniezek *et al.* 1991, Snyder and Brownlee 1991, Choi *et al.* 1992, Wasik and Mikołajczyk 1994) is restricted to the basal bodies of the membranelles and their associated fibres; both are only recognizable after silver impregnation. Furthermore, the expression “adoral zone of membranelles” is also used in the related class Hypotrichea (hypotrichs and stichotrichs).

Collar membranelles

The collar membranelles form a closed zone on the peristomial rim and constitute the anterior portion of the oral primordium in early dividers. They have larger polykinetids and longer cilia than the buccal membranelles. Some collar membranelles are elongated into the eccentric buccal cavity (praeorale Membranellen, Foissner and Wilbert 1979; Buccalmembranellen, Blatterer and Foissner 1990; somatic adoral membranelles, Foissner and O’Donoghue 1990). Although there are several other names for these membranelles (adorale Pectinellen, Entz 1909b; Membranulae, Entz 1929; Peristomal-Pektinellen, Entz 1937; adoral membranelles, Foissner and Wilbert 1979, Foissner and O’Donoghue 1990, Petz and Foissner 1993; external membranelles, Petz *et al.* 1995), the term “collar membranelles” is chosen, as it clearly explains the position of the membranelles and can also be used for the large membranelles in the Halteriida and Oligotrichida.

Buccal membranelles

The buccal membranelles are entirely situated in the buccal cavity and constitute the posterior portion of the oral primordium in early dividers. Note that some authors do not differentiate between elongated collar membranelles and buccal membranelles, but lump them to infundibular membranelles/polykinetids (e.g., Wasik and Mikołajczyk 1994). The term “buccal membranelles” is preferred instead of “internal membranelles” (Petz *et al.* 1995), as it clearly describes the position of the membranelles in the buccal cavity and is also applicable for the small membranelles in the Halteriida and Oligotrichida.

Endoral membrane

The endoral membrane extends across the peristomial field into the buccal cavity. It is usually named paroral membrane; however, due to its monostichomonad structure and probable homology to the endoral membrane of the stichotrichs, halteriids, oligotrichids, and most hypotrichs, this undulating membrane should likewise be called endoral membrane (Agatha 2004a, b).

Numbering of somatic kineties

The numbering commences with the ventral kinety or, when this ciliary row is absent, with the leftmost kinety of the right ciliary field and continues in clockwise direction when the cell is viewed from anterior (Chatton *et al.* 1931). Despite the fact that this numbering opposes that in the closely related suborder Strobilidiina (order Choreotrichida; Deroux 1974), it is maintained here to avoid confusion.

Ventral kinety

The ventral kinety is on the left side of the right ciliary field and on the right side of the oral primordium. It is the longest entirely monokinetidal ciliary row on the ventral side (Figs 1b, f). Although older expressions existed (frange bordante, frange ondulante, Fauré-Fremiet 1924; ciliary membrane, Campbell 1926, Kofoid and Campbell 1939, Tappan and Loeblich 1968), the term “ventral kinety” was introduced by Snyder and Brownlee (1991) to indicate the position of the ciliary row.

Right ciliary field

The right ciliary field is on the right side of the ventral kinety, the ventral organelles, or a blank stripe. The name for this ciliary field on the right cell side was introduced by Snyder and Brownlee (1991).

Dorsal kinety

The dorsal kinety is separate from the right and left ciliary field between which it is situated dorsally. It is the longest kinety, usually extending from the membranellar zone to the base of the stalk. The term was introduced by Choi *et al.* (1992). Foissner and Wilbert (1979), Foissner and O’Donoghue (1990), and Petz *et al.* (1995) named it “ventral kinety”, although this ciliary row is on the cell side almost opposite to the eccentric buccal cavity.

Left ciliary field

The left ciliary field is on the left side of the dorsal kinety. Its ciliary rows are more closely spaced than those of the right ciliary field. The name for this ciliary field on the left cell side was introduced by Snyder and Brownlee (1991).

Lateral ciliary field

The lateral ciliary field is between the ventral kinety and the left ciliary field, with which it is occasionally lumped (Laval-Peuto 1994, Wasik and Mikołajczyk 1994). The term was introduced by Fauré-Fremiet (1924), and there are two similar expressions: Lateralfeld (Foissner and Wilbert 1979) and lateral field of kineties (Petz *et al.* 1995).

Posterior kinety

The posterior kinety is posterior to the lateral ciliary field. The term was introduced by Choi *et al.* (1992) and is favoured, as the names “Ventro-Lateralkinete” (Foissner and Wilbert 1979, Foissner and O’Donoghue 1990, Petz and Foissner 1993) and “dorsolateral kinety” (Petz *et al.* 1995) do not emphasize its unique position in the posterior cell portion.

Ventral organelles

The ventral organelles comprise a transverse (V1) and an oblique (V2) organelle, i.e., two short dikinetidal kineties posterior to the ventral collar membranelles. The term was introduced by Foissner and Wilbert (1979).

Capsules

Capsules are probably extrusive organelles that are attached to the cell membrane of cytoplasmic extensions, such as, accessory combs, striae, and tentaculoids. They are subspherical, 200-600 nm in size, and often form clusters; three morphotypes are known (Laval-Peuto and Barria de Cao 1987). Laval (1971 cited in Laval 1972) introduced the term "capsules torquées", but in the English literature only "capsules" is used (Hedin 1975, Gold 1979, Laval-Peuto *et al.* 1979, Capriulo *et al.* 1986, Wasik and Mikołajczyk 1992); the older expressions "Bacterioidkörperchen" (Entz 1909b) and "trichocysts" (Campbell 1926) are less specific and are thus rejected.

Accessory combs

Accessory combs are conspicuous intermembranellar ridges. The term was introduced by Campbell (1926); the alternative names "Begleitkämme" (Entz 1909b) and "crêtes adorales" (Laval-Peuto 1994) were rarely used in the literature.

Striaes

Striae are beaded, longitudinal cytoplasmic strands that are enclosed together with an collar membranelle by the perilemma (Laval 1972, Laval-Peuto 1994). The term was introduced by Entz (1929) and more often used than the expressions "lames de revêtement" (Laval-Peuto *et al.* 1979) and "Deckplättchen" (Entz 1909b).

Tentaculoids

Tentaculoids are small, finger-like, and possibly contractile cytoplasmic extensions between the collar membranelles (Corliss 1979, Laval-Peuto and Brownlee 1986). The term was introduced by Haeckel (1873).

Lorica

A lorica is a house, fitting the cell loosely, with an anterior (oral) and occasionally posterior (aboral) opening. It is carried about by free-swimming species or fixed to the substratum by sessile ones (Corliss 1979). A lorica should not be confused with the distended and often reticulate posterior cell surface of the related Oligotrichida.

Protolorica

A protolorica is built by the proter just after cell division (Laval-Peuto and Brownlee 1986).

Paralorica

A paralorica is a replacement lorica formed by a morphostatic cell (Laval-Peuto and Brownlee 1986).

Epilorica

An epilorica is a spiralled or annulated portion frequently added to the anterior end of a protoor paralorica (Laval-Peuto and Brownlee 1986).

***Tintinnopsis cylindrica* Daday, 1887 (Figs 1-3, Table 1)—**1887 *Tintinnopsis Davidoffii* var. *cylindrica* - Daday, Mitt. zool. Stn Neapel 7: 553.

1907 *Tintinnopsis cylindrica* - Wright, Ann. Rep. Dept. of Marine and Fisheries, Fisheries Branch, Ottawa 39: 11 (raise to species rank).

1913 *Tintinnopsis radix* forma *cylindrica* - Laackmann, Akad. Wiss. Wien, Math. nat. Kl. 122: 145.

1929 *Tintinnopsis davidoffi* var. *cylindrica* Daday, 1887 - Kofoid and Campbell, Univ. Calif. Publs Zool. 34: 33 (first revisers).

1929 *Tintinnopsis cylindrica* Daday - Kofoid and Campbell, Univ. Calif. Publs Zool. 34: 33 (first revisers).

1932 *Tintinnopsis kofoidi* sp. nov. - Hada, Zool. Inst., Fac. Sci. Hokkaido Imp. Univ., Sapporo 30: 210 (new subjective synonym).

1981 *Tintinnopsis kofoidii* - Hargraves, J. Plankton Res. 3: 85.

1983 *Tintinnopsis kofoidi* - Stoecker *et al.*, Mar. Biol. 75: 293 (growth experiments).

1986 *Tintinnopsis kofoidi* - Verity, Mar. Ecol. Prog. Ser. 29: 117 (growth rates).

1990 *Tintinnopsis kofoidi* - Kamiyama and Aizawa, Bull. Plankton Soc. Jap. 36: 137 (excystment).

1997 *Tintinnopsis kofoidi* - Kamiyama, J. Oceanogr. 53: 299 (excystment).

2005 *Tintinnopsis cylindrica* - Kamiyama and Matsuyama, J. Plankton Res. 27: 307 (ingestion rate).

Non *Tintinnopsis cylindrica* n. sp. - Daday, 1892, Természetr. Füz. 15: 201 (junior homonym; now *Tintinnopsis cylindrata* Kofoid and Campbell, 1929).

Non *Tintinnopsis cylindrica* Daday - Entz, 1905, Áll. Közl. 4: 204 (now *Tintinnopsis cylindrata* Kofoid and Campbell, 1929).

Non *Tintinnopsis cylindrica* (Daday) - Entz, 1909a, Math. naturw. Ber. Ung. 25: 204 (now *Tintinnopsis cylindrata* Kofoid and Campbell, 1929).

Non *Tintinnopsis cylindrica* Daday - Entz, 1909b, Arch. Protistenk. 15: 118 (now *Tintinnopsis cylindrata* Kofoid and Campbell, 1929).

Non *Tintinnopsis cylindrica* Daday - Jaczó, 1940, Fragm. faun. hung. 3: 59 (now *Tintinnopsis cylindrata* Kofoid and Campbell, 1929).

Non *Tintinnopsis cylindrica* sp. n. - Meunier, 1910, Campagne Arctique de 1907: 140 (junior homonym; now *Tintinnopsis spiralis* Kofoid and Campbell, 1929).

Neotype material

Neotypified from plankton of the mixo-polyhaline basin (54°32′58″ N, 08°52′59″ E) in the Beltringharder Koog, as (i) no type material is available, (ii) the original description lacks many morphologic features, and (iii) the species has several proposed subjective synonyms.

Improved diagnosis (based on data from the type and neotype population)

Lorica on average 150-240 μm long and 45-50 μm wide orally, with agglutinated particles; Pasteur pipette-shaped, *viz.*, cylindroidal for on average 65-75% of total length, posteriorly tapered, merging into straight cylindroidal process ~ 20 μm long and 10-15 μm wide. Cell on average 125-210 × 40-45 μm and elongate obconical, highly contractile. 2 macronuclear nodules and 2 micronuclei. Ventral kinety commences anterior to right ciliary field, consists of ~ 36 monokinetids. On average 11 kineties in right and 10 in left ciliary field, all composed of monokinetids and one anterior dikinetid, except for second and third ciliary row with two anterior dikinetids. About 36 dikinetids in dorsal kinety and 26 in posterior kinety, with a cilium only at each posterior basal body. Lateral ciliary field composed of ~ 11 monokinetidal kineties. On average 22 collar membranelles of which 4 extend into buccal cavity; single buccal membranelle. Marine and brackish waters.

Description of polder specimens

Loricae 75-220 μm long and 34-56 μm wide orally after preservation with Lugol's iodine solution; Pasteur pipette-shaped, *viz.*, cylindroidal for about two thirds of total length, anterior end transversely truncate, posteriorly tapered, merging into cylindroidal process. Process aborally open and usually transversely truncate, straight, 8-11 μm in diameter but highly variable in length possibly because it easily breaks off (Table 1). Matrix hyaline, incrustrated to various degrees by particles of non-biogenic origin (probably silt particles), diatom frustules and their fragments, and green globular organisms; no distinct spiralled or annulated structures recognizable (Figs 1a, d, e; 3a-e).

Fully extended cells 75-185 × 30-55 μm *in vivo*, elongate obconical, body proper gradually merges into slender, wrinkled stalk, attached to tapered portion of lorica (Figs 1a; 2c, d; 3a); disturbed or preserved cells contracted by ~ 40% and almost ellipsoidal (Figs 1b, c; 2a, b; 3b, d; Table 1). One ellipsoidal macronuclear nodule each in anterior and posterior cell half, with some large (~ 4 μm across) and several small (1-2 μm across) dark inclusions (probably nucleoli). Micronuclei adjacent to macronuclear nodules, globular, faintly impregnated with protargol. No contractile vacuole recognized. Cytopyge near mid-body. Myonemes not impregnated. Accessory combs rarely recognized *in vivo* (Fig. 3a), while striae, tentaculoids, and capsules not recognizable. Cytoplasm colourless, finely granulated, contains food vacuoles with coccal organisms (4-9 μm across) as well as centric (5-8 μm across) and pennate (10-16 × 2-3 μm) diatoms. Swims slowly (~ 0.1 mm s^{-1}) forward, twitches back on obstacles. Disturbed specimens retract quickly (< 1 sec) into posterior portion of lorica, with motionless collar membranelles bent to centre of peristomial field (Fig. 3b); lorica abandonment never observed. When inconvenience stops, specimens slowly (> 1 min) extend and spread out the collar membranelles almost perpendicularly (Fig. 1a).

General pattern of somatic ciliature as described in 'Terminology' (Figs 1b, c, f). Length of kineties and number of kinetids usually highly variable possibly due to basal body proliferation or resorption in postdividers (see below; Table 1). Ventral kinety commences anterior to second or third kinety of right ciliary field, performs distinct leftward curvature, terminating near anterior end of posterior kinety, composed of densely spaced monokinetids; cilia decrease in length from ~ 11 μm in anterior portion to 3-4 μm in posterior. Kineties of right ciliary field composed of monokinetids and one anterior dikinetid, except for its first and second kinety that probably have two dikinetids anteriorly; cilia 2-4 μm long, except for the 9-11 μm long anteriormost dikinetidal cilia (soies, Fauré-Fremiet 1924), often apparently absent in posteriormost kinetids. Dorsal kinety commences at same level as right and left ciliary field and curves leftwards to base of stalk; cilia ~ 10 μm long and only at each posterior dikinetidal basal body. Posterior kinety commences in second quarter of cell posterior to last or penultimate kinety of lateral ciliary field and curves rightwards to base of stalk; cilia 6-7 μm long and only at each posterior dikinetidal basal body. Kineties of left ciliary field composed of monokinetids and one anterior dikinetid, almost gradually elongated from left to right; cilia 2-4 μm long, except for the 9-11 μm long anteriormost dikinetidal cilia (soies, Fauré-Fremiet 1924), often apparently absent in posteriormost kinetids. Kineties of lateral ciliary field commence ~ 1 μm anterior to those of left and right ciliary field, densely spaced and slightly curved, except for the rightmost kinety that extends parallel to the distinctly curved ventral kinety, 8-10 μm long (n = 6), composed of closely spaced monokinetids with cilia 2-4 μm long. Longitudinal argyrophilic fibres connect kinetids in ciliary rows.

Oral apparatus occupies anterior cell portion, perpendicular to main cell axis. Collar membranelles form closed spiral on peristomial rim, 1-2 μm apart, composed of three rows of basal bodies with cilia up to 25-30 μm long (Figs 1a-c; 3a). Two argyrophilic fibre bundles extend from each collar membranelle rightwards and leftwards, merging into a horizontally orientated circular fibre underneath the membranellar zone. Another argyrophilic fibre bundle commences at the left half of the circular fibre and extends posteriorly, terminating between the posterior and dorsal kinety (Fig. 1c). Eccentric buccal cavity contains one buccal membranelle and the proximal portions of four elongated collar membranelles, each associated with a longitudinal argyrophilic fibre bundle extending to the posterior quarter of cell proper (Fig. 1b). Endoral membrane inconspicuous, as apparently short and restricted to the buccal cavity.

Ontogenesis

Only few sufficiently impregnated division stages were found in the preparations (Figs 2a, b; 3f-h). Stomatogenesis commences with the apokinetal development of a small, cuneate field of basal bodies posterior to the lateral ciliary field. The oral primordium sinks into a subsurface pouch and membranelles differentiate. The posterior portion of the oral primordium performs a distinct rightwards curvature until the opisthe’s right side faces the proter’s ventral side. The endoral membrane is apparently very short and entirely located in the buccal cavity. In middle dividers, the proter’s ciliary fields are elongated compared to morphostatic specimens: the left field by ~ 80%, the right field by ~ 50%, and the lateral field by ~ 240%. In the opisthe, the right field is about one third shorter than in morphostatic specimens, whereas the lateral field is almost of same length; length of the left ciliary field is not recognizable. The ventral kinety curves along the lower right margin of the oral primordium. One replication band each traverses the macronuclear nodules. Only when the new oral apparatus evaginates, the two nodules fuse. Loricae embracing a resting cyst were not found.

DISCUSSION

Comparison of populations

The loricae from the type population are longer than those of the polder specimens (243 μm *vs.* 75-220 μm), while the oral diameter is almost identical (45 μm *vs.* 48 μm; Daday 1887). According to Laval-Peuto and Brownlee (1986), the oral diameter of a lorica is the least variable dimension and a taxonomically reliable character, whereas its length increases during lorica formation. Hence, the identification of the polder specimens with *Tintinnopsis cylindrica* is beyond reasonable doubt, especially, as Daday (1887) observed a similar number of collar membranelles and a similar position of the two macronuclear nodules. Schweyer (1909) recognized tentaculoids which were not found in the polder specimens; however, these organelles are probably contractile (Laval-Peuto 1994) and their absence should thus not be overestimated.

The literature data concerning the lorica dimensions of *T. cylindrica* and its synonyms fall into a size range of 105-300 × 33-60 μm (Brandt 1907; Okamura 1907; Laackmann 1913; Rossolimo 1922; Wailes 1925, 1943; Hada 1932a, c, 1937; Marshall 1934; Orsi 1936; Balech 1948, 1951; Biernacka 1948; Silva 1952; Cosper 1972; Gold and Morales 1975; Bakker and Phaff 1976; Kršinić 1980; Rampi and Zattera 1982; Stoecker *et al*. 1983; Yoo *et al*. 1988; Lipej 1992).

Comparison with similar species

There are several species and subspecies from marine and brackish waters which might be synonyms of *Tintinnopsis cylindrica*: *T. davidoffii* with two globular macronuclear nodules in posterior cell half; *T. davidoffii* var. *longicauda* and *T. curvicauda* with a curved lorica process (Daday 1887); *T. pseudocylindrica* with irregular aboral opening (Hada 1964); *T. fracta* with an obliquely truncate lorica process (Brandt 1906, 1907); *T. coronata* with an irregularly expanded oral lorica rim (Kofoid and Campbell 1929); *T. levigata* with a lorica 50-70 × 20-30 μm in size (Wailes 1925); *T. platensis* without agglutinated particles at the lorica process (Cunha and Fonseca 1917); *T. aperta* (Brandt 1906, 1907), *T. lindeni* (Daday 1887), *T. panamensis*, and *T. tocantinensis* (Kofoid and Campbell 1929) with a bulbous zone between the cylindroidal portion and the lorica process; *Codonella annulata* with an annulated lorica structure (Daday 1886); *C. radix* with a lorica up to 480 μm long (Imhof 1886); and *Tintinnus annulatus*, *T. helix* (Claparède and Lachmann 1859), and *T. fistularis* (Möbius 1887) with a spiralled lorica structure. The often very short descriptions of these taxa consider only or mainly lorica features, using small discrepancies in structure and shape for the establishment of a new species or variation. Although the formation of spiralled or annulated lorica structures is part of the life cycle in several tintinnids (paralorica and epilorica; Laval-Peuto 1981, 1994) and the lorica process might vary in shape and size due to environmental conditions, investigations of the cell morphology are required to justify a synonymization of the species mentioned above.

In only 16 tintinnid species, the main cytological features are known. The general ciliary pattern of *T. cylindrica* matches that of *Codonella cratera* (Foissner and Wilbert 1979), *Stenosemella lacustris* (Foissner and O'Donoghue 1990), *Codonellopsis glacialis*, *Cymatocylis calyciformis* (Petz *et al*. 1995), and the *Cymatocylis affinis/convallaria*-group (Wasik and Mikołajczyk 1994, Petz *et al*. 1995). Small and Lynn (1985), Laval-Peuto and Brownlee (1986), and Laval-Peuto (1994) provided some original or modified illustrations from Brownlee's unpublished Master and Doctoral Theses, showing protargol-impregnated tintinnids with an apparently similar ciliary pattern: *Tintinnopsis baltica*, *T. subacuta*, *Stenosemella steini*, *Favella* sp., *Climacocylis scalaroides*, and *Protorhabdonella simplex*. Furthermore, the somatic ciliature of *Tintinnopsis rapa*, *T. fimbriata*, *T. tubulosoides*, *T. campanula*, *Helicostomella subulata*, and *Leprotintinnus pellucidus* are very much alike (own observ.). Further studies are required to elucidate whether the observed subtle differences in the structure, position, and curvature of the kineties are species- or genus-specific. On the other hand, the congener *Tintinnopsis cylindrata* resembles *Tintinnidium fluviatile* and *Tintinnidium pusillum* 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). Nevertheless, its generic affiliation is not changed as the ciliary pattern of the type species of the genus *Tintinnopsis*, *T. beroidea*, is unknown.

Ontogenetic comparison

In only seven tintinnid species, ontogenesis was investigated after protargol impregnation: *Tintinnopsis* sp., *Favella* sp. (Brownlee 1983, Laval-Peuto 1994), *Tintinnopsis cylindrata*, *Tintinnidium pusillum*, *T. semiciliatum*, *Codonella cratera* (Petz and Foissner 1993), and *Cymatocylis convallaria* (Petz *et al*. 1995). *Tintinnopsis cylindrata* and the *Tintinnidium* species differ from *Tintinnopsis cylindrica* in the ciliary pattern (see above); hence, they are excluded from the following comparison.

The division stages of *T. cylindrica* match the observations on *Codonella cratera* (Petz and Foissner 1993), *Cymatocylis convallaria* (Petz *et al.* 1995), and apparently *Favella* sp. (Laval-Peuto 1994) very well in the position of the oral primordium. Likewise, the kineties of the proter are elongated and those of the opisthe are shortened compared to morphostatic specimens, indicating a resorption of basal bodies by the proter and a second round of basal body proliferation by the opisthe in late dividers or postdividers (this study, Brownlee 1983, Petz and Foissner 1993). Petz and Foissner (1993) assumed that an anteriorly elongated ventral kinety occurs only in dividers or postdividers, while we agree with Petz *et al.* (1995) in regarding it as the morphostatic state of the ciliary row.

Occurrence and ecology

The following compilation comprises merely records of *Tintinnopsis cylindrica* and the synonyms mentioned above. Note that only few of them were substantiated by morphometric data and/or illustrations (see ’Comparison of populations’) and that the morphologic variability of the species is unknown; thus, misidentifications cannot be excluded.

Daday (1887) discovered *T. cylindrica* in the Gulf of Naples. In the Mediterranean Sea and adjacent brackish water lagoons, the species was also found by several other authors (Brandt 1906, 1907; Schweyer 1909; Laackmann 1913; Orsi 1936; Rampi 1939, 1948, 1950; Margalef and Morales 1960; Kršinić 1979, 1980, 1987; Rassoulzadegan 1979; Rampi and Zattera 1982; Lakkis and Novel-Lakkis 1985; Lipej 1992; Lam-Hoai *et al.* 1997; Rougier and Lam Hoai 1997; Ounissi and Frehi 1999; Lam-Hoai and Rougier 2001; Sabancý and Koray 2001; Modigh and Castaldo 2002; Moscatello *et al.* 2004; Balk’s and Wasik 2005). Likewise, it was recorded in the North Atlantic (Wright 1907; Silva 1952; lorica of *T. cylindrica* less distinctly tapered, Cosper 1972; Gold and Morales 1975; Hargraves 1981; Stoecker *et al.* 1983; Verity 1986, 1987; Middlebrook *et al.* 1987; Sanders 1987; Gilron and Lynn 1989; Pilling *et al.* 1992; Leakey *et al.* 1993; Pierce and Turner 1994; Paulmier 1995; Tempelman and Agatha 1997; Urrutxurtu *et al.* 2003; Urrutxurtu 2004), South Atlantic (Balech 1948, 1951; Akselman and Santinelli 1989), Red Sea (Aboul-Ezz *et al.* 1995), Indian Ocean (Krishnamurthy and Santhanam 1978; Krishnamurthy *et al.* 1979, 1987; Damodara Naidu 1983; Damodara Naidu and Krishnamurthy 1985), North Pacific (Okamura 1907; Wailes 1925, 1943; Hada 1932a, b, c, 1937; Wang and Nie 1934; Konovalova and Rogachenko 1974; Yoo *et al.* 1988; Yoo and Kim 1990; Kamiyama and Aizawa 1990, 1992; Kamiyama and Tsujino 1996; Kamiyama 1997; Uye *et al.* 2000; Kamiyama *et al.* 2001; Kamiyama and Matsuyama 2005), and South Pacific (Brandt 1906, 1907; Marshall 1934; Burns 1983). *Tintinnopsis cylindrica* also occurred in the brackish waters of the Black (Rossolimo 1922) and Baltic Sea (Brandt 1906, 1907; *T. cylindrica* with exceptionally long lorica process, Biernacka 1948, 1968) and lagoons at the coast of the North Atlantic (this study, Bakker and Pauw 1975, Bakker and Phaff 1976, Bakker 1978, Agatha and Riedel-Lorjé 1997, Riedel-Lorjé *et al.* 1998), North Pacific (Hada 1937, Godhantaraman and Uye 2003), and Indian Ocean (Godhantaraman 2001, 2002). Accordingly, records substantiated by morphometric data are available from marine and brackish waters of subarctic, temperate, subtropical, and equatorial areas, while the species was apparently not found in polar regions. The spatial distribution of *T. cylindrica* might, however, change when further species or subspecies will definitely be synonymized and the morphologic variability of the species is better known.

In the polder basins, *Tintinnopsis cylindrica* was mainly recorded at salinities higher than 10‰ and temperatures above 8°C, that is, mostly during summer. It occasionally dominated the tintinnid community and had maximum abundances of ~ 4,400 individuals per litre in September 1991 and July 1992 in the mixo-polyhaline basins of the Beltringharder Koog and Speicherkoog Dithmarschen. The seasonal dynamics observed in the polder basins match the findings from other regions (Hada 1937; Bakker and Pauw 1975; Bakker and Phaff 1976; Bakker 1978; Hargraves 1981; Sanders 1987; Verity 1987; Leakey *et al.* 1993; Pierce and Turner 1994; Kamiyama and Tsujino 1996; Godhantaraman 2001, 2002).

Specimens infested by a parasitic dinoflagellate, probably *Duboscquella* sp., were occasionally found (Figs 2c-e). Hada (1932a) as well as Akselman and Santinelli (1989) described similar infection stages in *Tintinnopsis kofoidi*, whereas the infection was interpreted as sexual reproduction in the possibly synonymous species *Tintinnus helix* (Laackmann 1907). While the infection rate was apparently low in the polder basins, *Duboscquella* sp. significantly decimated ciliate stocks at the northeast coast of the USA (Coats and Heisler 1989).

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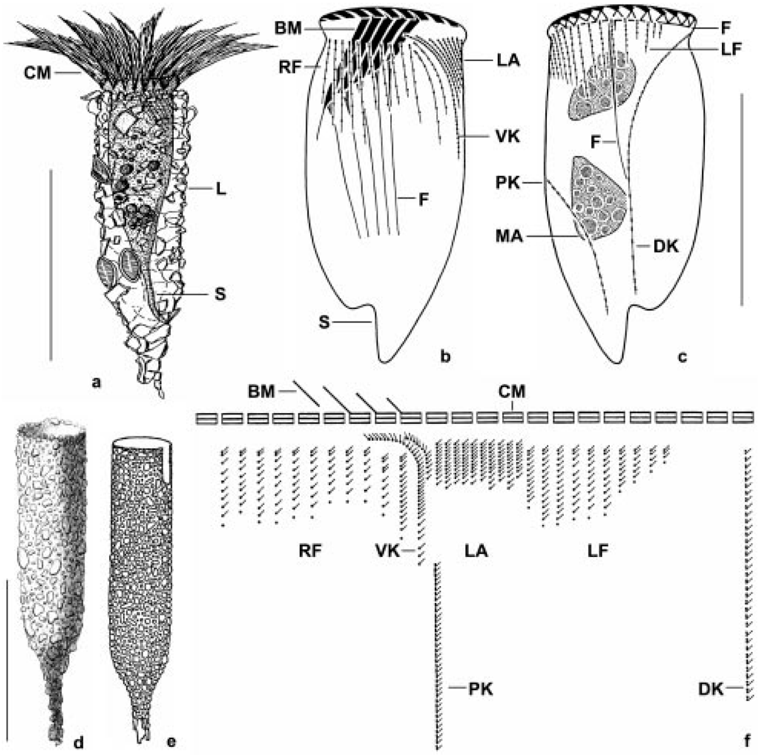
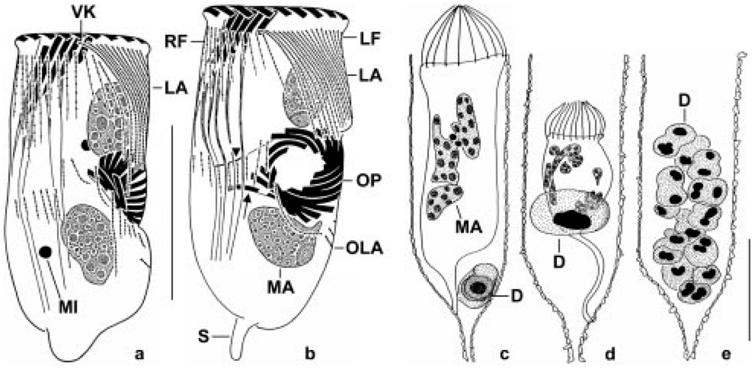


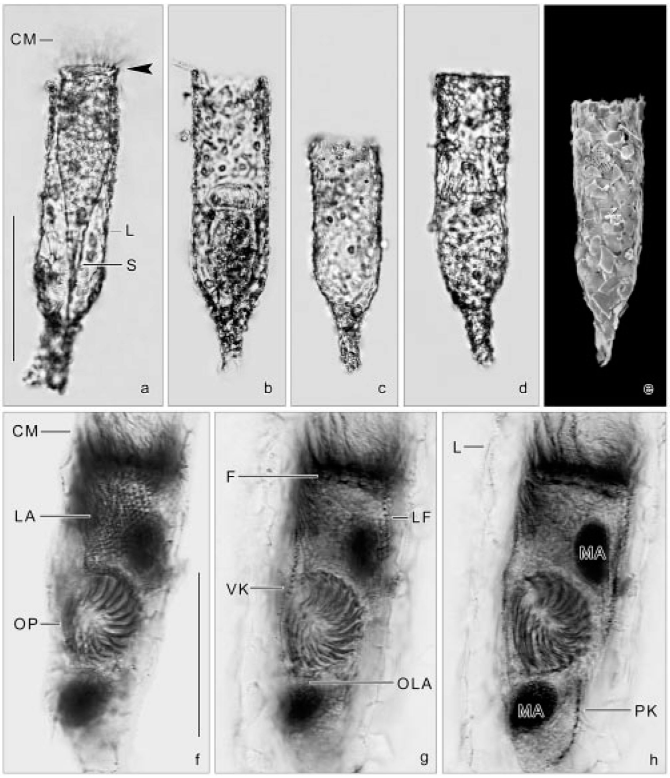
Figs 1a-f.

Tintinnopsis cylindrica (a-d, f) and a supposed synonym (e) from life (a, e), after protargol impregnation (b, c, f), and preserved with mercuric chloride (d). **a** - a representative specimen from the neotype population; **b, c** - ciliary pattern of ventral and dorsal side. Note the fibres that are associated with the oral and somatic ciliature; **d** - a lorica from the type population (from Daday 1887); **e** - *Tintinnopsis kofoidi* (from Hada 1932a); **f** - kinetal map of a morphostatic specimen. BM - buccal membranelle, CM - collar membranelles, DK - dorsal kinety, F - probably fibrillar structures, L - lorica, LA - lateral ciliary field, LF - left ciliary field, MA - macronuclear nodules, PK - posterior kinety, RF - right ciliary field, S - stalk, VK - ventral kinety. Scale bars: 100 µm (a, d, e); 50 µm (b, c).



Figs 2a-e.

Tintinnopsis cylindrica after protargol impregnation. **a, b** - ventral views of middle dividers showing the oral primordium in a subsurface pouch posterior to the proter's lateral ciliary field whose kineties are distinctly longer than in morphostatic specimens (cp. Figs 1b, c, f). Note the replication bands in the macronuclear nodules (b). Arrow marks the single buccal membranelle of the opisthe. Arrowhead denotes the short endoral membrane of the opisthe; **c-e** - lateral views of specimens in successive stages of dinoflagellate infection. The dinoflagellate completely sucks out the tintinnid cell (c, d), before it obtains the sporogenetic stage (e). Note the morphologic changes of the macronuclear nodules due to the infection (c, d). D - parasitic dinoflagellate (probably *Duboscquella* sp.), LA - proter's lateral ciliary field, LF - left ciliary field, MA - macronuclear nodules, MI - micronuclei, OLA - opisthe's lateral ciliary field, OP - oral primordium, RF - right ciliary field, S - contracted stalk, VK - ventral kinety. Scale bars: 50 μm.



Figs 3a-h.

Tintinnopsis cylindrica from life (a-d), in the scanning electron microscope (e), and after protargol impregnation (f-h). **a-d** - lateral views showing lorica variability, concerning the degree of incrustrated particles and length of the cylindroidal portion. Accessory combs (arrowhead; a) are rarely recognizable; **e** - the lorica wall has many silt particles and fragments of diatom frustules incrustrated; **f-h** - same middle divider at three focal planes. The new oral apparatus develops in a subsurface pouch posterior to the proter's lateral ciliary field. CM - collar membranelles, F - probably fibrillar structures, L - lorica, LA - proter's lateral ciliary field, LF - left ciliary field, MA - macronuclear nodules, OLA - opisthe's lateral ciliary field, OP - oral primordium, PK - posterior kinety, S - stalk, VK - ventral kinety. Scale bars: 100 μm (a-e); 50 μm (f-h).

Table 1

Tintinnopsis cylindrica morphometric data. 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, $\bar{X}$ - arithmetic mean.

Characteristics[a]	$\bar{X}$	**M**	**SD**	**SE**	**CV**	**Min**	**Max**	**n**
Lorica, total length[b]	151.3	148.0	25.1	5.2	16.6	75.0	220.0	23
Lorica, oral diameter[b]	48.4	49.0	5.2	1.1	10.8	34.0	56.0	23
Lorica length:oral diameter, ratio[b]	3.2	3.0	0.6	0.1	19.4	1.6	5.2	23
Lorica, length of cylindroidal portion[b]	98.1	95.0	18.1	4.7	18.4	69.0	144.0	15
Lorica, length of tapered portion[b]	26.2	28.0	8.5	2.2	32.6	6.0	38.0	15
Lorica, process length[b]	22.1	20.0	9.7	2.4	43.9	0.0	38.0	15
Lorica, process diameter[b]	10.1	10.0	0.7	0.2	7.3	8.0	11.0	15
Cell, length	71.0	68.5	12.8	2.6	18.0	52.0	89.0	24
Cell, width	31.7	32.5	6.2	1.3	19.5	22.0	48.0	24
Macronuclei, length	15.6	16.0	4.5	1.0	29.2	9.0	23.0	19
Macronuclei, width	8.1	8.0	2.3	0.5	28.2	3.0	12.0	19
Macronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	19
Micronuclei, diameter	2.0	2.0	0.7	0.2	34.0	1.0	3.0	14
Micronuclei, number	2.0	2.0	0.0	0.0	0.0	2.0	2.0	14
Ventral kinety, length[c]	22.1	23.0	3.7	1.4	16.8	17.0	28.0	7
Ventral kinety, number of kinetids	35.8	33.0	12.3	5.5	34.4	25.0	55.0	5
Dorsal kinety, length[c]	46.8	43.5	9.4	4.7	20.2	40.0	60.0	4
Dorsal kinety, number of kinetids	36.1	36.0	9.6	3.6	26.5	25.0	55.0	7
Posterior kinety, length[c]	33.4	31.0	14.6	6.5	43.7	19.0	50.0	5
Posterior kinety, number of kinetids	26.1	21.0	10.7	3.6	41.0	15.0	45.0	9
Left ciliary field, number of kineties	10.4	11.0	1.5	0.5	14.5	8.0	12.0	8
1. kinety in left field, length	2.4	2.0	0.7	0.3	31.3	2.0	4.0	8
1. kinety in left field, number of kinetids	2.9	3.0	0.6	0.2	22.3	2.0	4.0	8
2. kinety in left field, length	3.9	4.0	1.6	0.6	42.4	2.0	7.0	8
2. kinety in left field, number of kinetids	3.9	3.5	2.0	0.7	50.6	2.0	8.0	8

Characteristics[a]	$\overline{X}$	M	SD	SE	CV	Min	Max	n
3. kinety in left field, length	5.8	5.0	1.2	0.4	20.3	5.0	8.0	8
3. kinety in left field, number of kinetids	5.5	5.0	1.1	0.4	19.4	4.0	7.0	8
4. kinety in left field, length	8.3	8.5	2.9	1.0	35.3	3.0	12.0	8
4. kinety in left field, number of kinetids	7.9	8.0	2.6	0.9	33.6	3.0	11.0	8
5. kinety in left field, length	9.8	10.0	2.5	0.9	26.1	6.0	15.0	8
5. kinety in left field, number of kinetids	9.8	9.5	2.0	0.7	20.3	7.0	13.0	8
6. kinety in left field, length	10.6	9.5	2.8	1.0	26.6	8.0	16.0	8
6. kinety in left field, number of kinetids	10.1	10.0	1.6	0.6	16.2	8.0	13.0	8
7. kinety in left field, length	11.1	9.0	4.2	1.5	37.7	8.0	20.0	8
7. kinety in left field, number of kinetids	10.1	9.5	2.7	1.0	27.1	7.0	16.0	8
8. kinety in left field, length	11.5	9.5	4.8	1.7	41.3	8.0	19.0	8
8. kinety in left field, number of kinetids	11.5	10.5	4.0	1.4	35.1	7.0	18.0	8
9. kinety in left field, length	11.7	11.0	4.5	1.7	38.7	6.0	18.0	7
9. kinety in left field, number of kinetids	12.0	12.0	4.4	1.7	36.6	7.0	18.0	7
10. kinety in left field, length	11.4	8.0	5.6	2.5	49.5	6.0	18.0	5
10. kinety in left field, number of kinetids	11.0	10.0	3.4	1.5	30.8	7.0	15.0	5
11. kinety in left field, length	10.6	10.0	4.8	2.2	45.5	5.0	16.0	5
11. kinety in left field, number of kinetids	10.6	9.0	3.6	1.6	34.4	7.0	15.0	5
12. kinety in left field, length	11.5	-	-	-	-	9.0	14.0	2
12. kinety in left field, number of kinetids	11.0	-	-	-	-	8.0	14.0	2
Lateral ciliary field, number of kineties	11.1	10.0	2.9	1.1	25.6	8.0	16.0	7
Right ciliary field, number of kineties	10.6	11.0	1.3	0.5	12.0	9.0	12.0	7
1. kinety of right field, length	16.3	15.0	3.9	1.6	24.1	13.0	23.0	6
1. kinety of right field, number of kinetids	14.3	14.0	4.1	1.4	28.5	9.0	19.0	8
2. kinety of right field, length	11.0	10.5	2.8	1.1	25.1	7.0	15.0	6
2. kinety of right field, number of kinetids	7.3	7.0	1.8	0.7	25.3	5.0	11.0	8
3. kinety of right field, length	9.6	9.0	2.3	0.9	24.0	7.0	14.0	7
3. kinety of right field, number of kinetids	6.4	6.0	1.7	0.6	26.4	5.0	9.0	8
4. kinety of right field, length	9.5	9.5	2.4	1.0	25.6	6.0	13.0	6
4. kinety of right field, number of kinetids	6.8	6.0	2.1	0.8	31.4	5.0	10.0	8
5. kinety of right field, length	10.3	9.5	3.8	1.5	36.6	5.0	16.0	6

Characteristics[a]	$\bar{X}$	M	SD	SE	CV	Min	Max	n
5. kinety of right field, number of kinetids	6.6	6.0	2.4	0.8	36.0	4.0	11.0	8
6. kinety of right field, length	13.2	14.0	3.2	1.3	24.2	8.0	17.0	6
6. kinety of right field, number of kinetids	8.4	8.0	2.8	1.0	33.1	5.0	13.0	8
7. kinety of right field, length	13.4	14.0	3.8	1.7	28.2	9.0	17.0	5
7. kinety of right field, number of kinetids	8.6	8.0	3.2	1.2	37.4	6.0	14.0	7
8. kinety of right field, length	14.4	17.0	4.5	2.0	31.3	9.0	18.0	5
8. kinety of right field, number of kinetids	9.1	7.0	3.8	1.4	41.6	6.0	15.0	7
9. kinety of right field, length	13.5	12.5	3.3	1.7	24.6	11.0	18.0	4
9. kinety of right field, number of kinetids	10.3	9.5	3.6	1.8	35.1	7.0	15.0	4
10. kinety of right field, length	12.0	11.0	2.6	1.5	22.0	10.0	15.0	3
10. kinety of right field, number of kinetids	9.0	8.0	2.6	1.5	29.4	7.0	12.0	3
11. kinety of right field, length	15.0	-	-	-	-	-	-	1
11. kinety of right field, number of kinetids	8.0	-	-	-	-	-	-	1
12. kinety of right field, length	10.5	-	-	-	-	9.0	12.0	2
12. kinety of right field, number of kinetids	8.0	-	-	-	-	7.0	9.0	2
Collar membranelles, number[d]	21.7	22.5	1.8	0.7	8.1	19.0	23.0	6
Buccal membranelle, number	1.0	1.0	0.0	0.0	0.0	1.0	1.0	18

[a] Data are based, if not stated otherwise, on protargol-impregnated and mounted specimens from field material

[b] material preserved with Lugol’s iodine solution

[c] measured as cord of organelle

[d] counted in properly orientated morphostatic specimens or oral primordia of middle dividers.