Hydrobiologia vol. 50, 2, pag. 101-111, 1976

TINTINNIDA FROM COASTAL WATERS OF THE S.W.-NETHERLANDS I. THE GENUS TINTINNOPSIS STEIN.

C. BAKKER & W. J. PHAFF

Delta Institute Hydrobiological Research, Yerseke, The Netherlands, communication no. 127

Received February 1, 1975

Keywords: lorica characteristics, phenotypic variability, environmental conditions.

Introduction

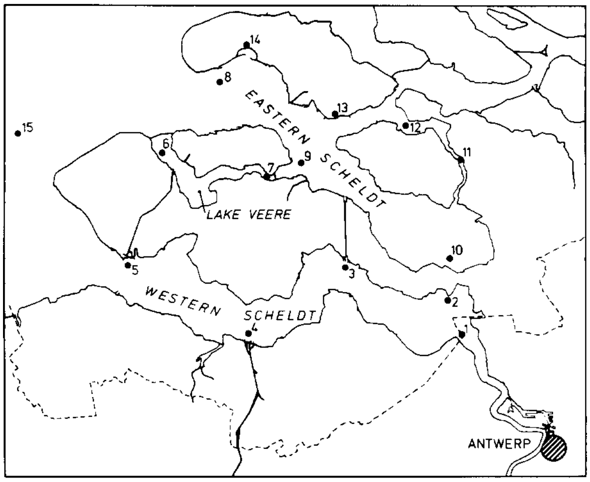
Most authors have based their investigations of Tintinnid systematics on the well known 'Conspectus' of Kofoid & Campbell (1929). In this work all characteristics used for separation of the taxa are derived from the lorica, this structure showing a remarkable adherence to type (Kofoid & Campbell, 1939).

However, Brandt (1906) already admitted that a classification only based on lorica shape and structure was incomplete and demonstrated artificial features especially in relation to the highly variable loricae of neritic species. Consequently, Laackmann (1908) and Merkle (1909) studied the protozoan cells of several Tintinnid species as well and included reproduction phenomena. Particularly Hofker (1931) stressed the significance of cell studies. His investigations enabled him to compose a key based on lorica as well as on cell structures. He made important observations in relation to the different ways of building up the lorica by *Tintinnopsis campanula*. This species showed a large variability in one and the same sample. Hofker argued that loricae may be constructed by cells of threefold origin: 1. after binary fission the upper daughtercell, keeping the old peristome, has to build up a new bowl initially constructed as a circular structure. 2. sometimes a cell is loosing its old lorica and is bound to make a new one: in this case, Hofker stated, the lorica may be constructed along the whole lateral surface of the animal. 3. finally, new cells may develop from resting stages and are therefore forced to build new loricae too. Moreover, environmental conditions may differ during lorica construction. After binary fission the old lorica is maintained: consequently, a number of loricae of different age is present in course of time, developed during different conditions of water temperature, salinity and water movement. Changes in salinity e.g., provoking osmoregulatory activities of the cells, might lead to temporary changes in body form, resulting in aberrant shape of the new lorica. Notably the aboral end of *Tintinnopsis beroidea* and *T. campanula* loricae is varying strongly in relation to its shape. Therefore it is not surprising that all transitions have been found from sharply pointed to evenly rounded aboral portions of *T. beroidea* (fig. 2-3). In the same way the development of the *bütschlii*- and *cyathus*-forms of *T. campanula* (fig. 9) is to be understood: Hofker observed that swarming *T. campanula* without lorica were rounded and built new *bütschlii*- or *cyathus*-like bowls. The upper daughtercell developing after binary fission, on the other hand, is aborally pointed originally, forming a typical *campanula*- like lorica with pedicel.

Not only the shape of the aboral part, but also the lorica length is extremely variable. Gold (1969), culturing *Favella*, demonstrated that in ageing cultures length decreased strongly in comparison to that of specimens from natural plankton samples. Oral diameter, on the other hand, appeared nearly constant. Halme & Lukkarinen (1960) measured hundreds of loricae of *Tintinnopsis lobiancoi* Daday and also found a great constancy of oral diameter.

We had the opportunity to study a large material from several stations of the sea arms, estuaries, larger and smaller brackish inland waters of the S.W.-Netherlands during approx. 5 years (see Map). The large variability of lorica shape, dimensions and structure, stressed the

Dr. W. Junk b.v. Publishers - The Hague, The Netherlands



Map of the area investigated with sampling localities.

necessity never to identify species examining only a few specimens, but to study in each sample as many specimens as possible. During periods of peak abundance dense populations were sampled: such samples appeared particularly suitable to establish specific limits of variability. Extensive studies of large numbers of loricae before describing a species were also made by Rossolimo (1926) and Halme & Lukkarinen (1960). In coastal waters of the temperate zone species of the families Codonellidae (genus *Tintinnopsis*) and Codonellopsidae (genus *Stenosemella*) predominate. In this first paper we have treated only the *Tintinnopsis* species. All figures have been drawn after measuring the oral diameter, length, maximum diameter a.s.o. Dimensions were plotted and lorica outlines were sketched; finally figures were completed with all details (incl. encrustation).

Description of the species

a. T. baltica Brandt. (fig. 1a-d).

The characteristic shape of a typical *T. baltica* is presented in fig. 1a. The lorica shows a flaring mouth, nuchal constriction, inflated bowl and conical pointed aboral end, the latter sometimes being slightly convex at one side and slightly concave at the other side. The oral rim may be denticulate.

The variability of this species is large. Many loricae have the appearance of fig. 1b and c, showing the enlargement of the bowl closer to the aboral end than the specimen of fig. 1a. Sometimes individuals are found as pictured in fig. 1d, lacking any enlargement of the house suborally and gradually narrowing in aboral direction. The specimens of fig. 1b and c sometimes show annulation.

Dimensions: oral diameter: 36-48μ, maximum width of the bowl 36-50μ; length 55-106μ. These data agree with those given by Brandt (1906) and Silva (1950). Balech (1948) studied material from Atlantic Ocean waters off Uruguay and found smaller dimensions (oral diameter: 30-40μ; maximum diameter of the bowl: 28-35μ; length 42-72μ), apparently owing to the prevailing higher water temperature in this subtropical region.

The range of variability demonstrated in fig. 1a-d was already established by earlier authors. Fig. 1a corresponds very well with Brandt's (1906) fig. 6, pl. 15; with Balech's (1948) fig. 22, pl. 3 and fig. 44, pl. 4; and with Silva's (1950) fig. 2, pl. 1. The most common form of the species, fig. 1b and c, is shown too by Brandt's (1906) fig. 9, pl. 15 and by Silva's (1950) fig. 5, pl. 1. Finally, the rather aberrant shape of fig. 1d corresponds with Brandt's (1906) fig. 15, pl. 15. We did not observe Brandt's (1905) specimens of *T. baltica* with strongly elongated collar (his fig. 4, pl. 16).

Hofker (1931) wrongly considered *T. baltica* an elongated *T. fimbriata.* We were not able to discover any transitional stage between *T. fimbriata* and *T. baltica* in the Western Scheldt estuary where dense, partly overlapping populations occur. *T. baltica* is a polyhalobe species extending in the mesohaline zone, whereas *T. fimbriata* is a true brackish water species, characterizing the mesohaline part of the estuary and extending into the lower reaches of the polyhaline zone. *T. baltica* Brandt and *T. fimbriata* Meunier appear to differ markedly in shape (compare figs. 1 with 7), dimensions and salinity preference.

Jörgensen (1927) supposed *T. vasculum* Meunier, *T. strigosa* Meunier and *T. turbo* Meunier to be identical with *T. baltica.* This may be justified, in our opinion, in

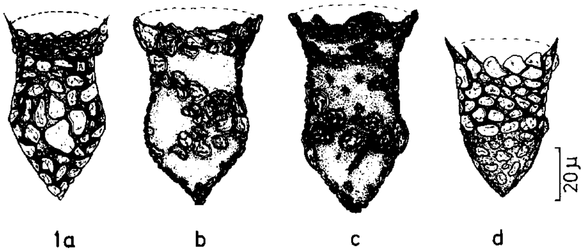


Fig. 1. Tintinnopsis baltica Brandt (1a, b, c from the Western Scheldt, loc. 3, 5; 1d from the Eastern Scheldt, loc. 9).

relation to *T. vasculum* and *T. strigosa. T. vasculum* however lacks a flaring mouth, is enlarged in its upper half and is aborally rounded. *T. strigosa,* on the other hand, does indeed resemble *T. baltica.* These two species (*T. vasculum* and *strigosa*) are described by Meunier (1919) from a few specimens only; therefore they are too insufficiently known to be maintained as distinct species. *T. turbo,* on the contrary, we consider a valid species (see pg. 12).

Finally the position of *T. nitida* Brandt and *T. sinuata* Brandt has to be discussed in relation to *T. baltica.* Marshall's (1969) figure 43, pl. 2 representing *T. nitida,* no doubt belongs to *T. baltica.* Brandt's (1906) original figures 5 and 10, pl. 15, however differ markedly from Marshall's one. His *T. nitida* therefore may be a valid species. *T. sinuata* Brandt is larger, more elongated (vase-shaped) and shows inflation of the bowl above the middle (Brandt, 1906, fig. 3, 4, pl. 15). According to Jörgensen (1905) *T. nitida* varies strongly and shows transitions to *T. sinuata* as indicated by his fig. 116 pl. 18. Our preliminary conclusion is that *T. nitida* and *T. sinuata* have to be united. Inclusion however of this species into *T. baltica* seems not yet justified.

b. Tintinnopsis beroidea Stein (fig. 2-8)

The difficulties of the exact delimination of systematic entities within the genus *Tintinnopsis* are well illustrated by the figs. 2a-h and 3a-f. The loricae of both series have been found in small polyhaline inland waters. The specimens of fig. 2 were sampled in winter (8-2-'72) those of fig. 3 in summer (22-8-'72). They differ mainly in width of oral diameter: 50-60µ (average 53,5µ) in the winter series, 40-42,5µ in the summer series. Dimensions of the lorica may partly depend on water temperature. Mostly species are larger in the colder parts of their range (Marshall, 1969). Equally a species occurring throughout the year may reach larger dimensions in winter than during summer. As usual lengths of loricae of both series varied much more than oral diameters: the length range of series 1 was 60-135µ, of series 2: 50-110µ.

We assign both series to the same species as the largest portion of specimens (60-70%) was characterized by the identical appearance of fig. 2d and 3b. The constancy in width of oral diameter (notably in series 2) excluded the possibility of the presence of different species in both series.

The great variability of the species in both series is demonstrated by several characteristics. Annulation was sometimes clearly visible in the summer forms (fig. 3a), but in most cases not or hardly demonstrated (fig. 3e). In the winter forms annulation was not seen at all. Slight annulation however may be easily overlooked when the encrustation with particles becomes denser (Halme and Lukkarinen, 1960), which was indeed the case in the winter forms (compare figs. 2 and 3). Some summer forms showed gradual narrowing (fig. 3f) in oral direction, in some cases followed by widening of the mouth (fig. 3d). Often the aboral part of the lorica was spherical (30-40%, fig. 1c, f, 3a, c, e,) giving the species a *T. lobiancoi* appearance. Moreover the species demonstrated several times a slight widening of the rounded aboral part (fig. 2a, e, 3a, d, e). The most common appearance however is shown in figs. 1d and 3b: lorica aborally bluntly pointed, typically for *T. beroidea* Stein.

Our assignement of the species to *T. beroidea* Stein is based on the following considerations:

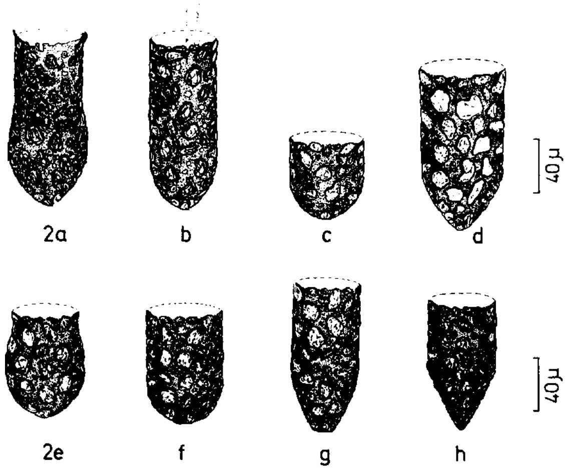


Fig. 2. Tintinnopsis beroidea Stein (from Inlaag 1953, loc. 13).

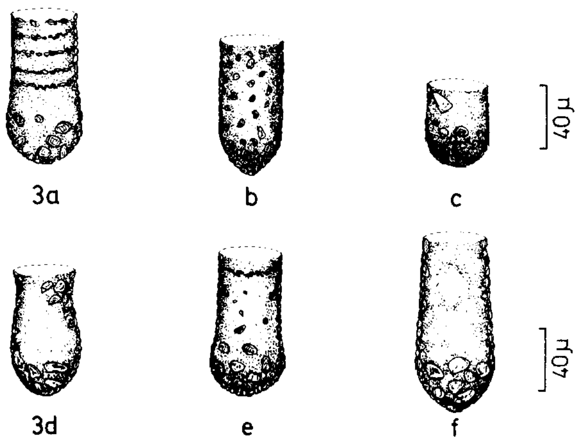


Fig. 3. Tintinnopsis beroidea Stein (from Schelphoek, loc. 14).

1. The fairly large average oral diameter (40-54μ) is in agreement with the dimensions given by Daday (1887): 45-50μ and Entz Sr. (1884): 50-60μ. Often however smaller widths are given: 18-36μ (Marshall, 1969); 30-42μ (Jörgensen, 1927). Smaller diameters (range 20-40μ) were generally found in the forms occuring in coastal seawater and the larger inland polyhaline waters (Lake Veere). These specimens are pictured in fig. 4.

2. Jörgensen (1927, fig. 5) described *T. beroidea* Stein according to Entz Sr. (1884). He was followed by Kofoid & Campbell (1929). The typical appearance of *T. beroidea* Stein em. Entz Sr. em. Jörgensen (cylindrical lorica above conical aboral end) is shown by 60-70% of our specimens.

3. Also the *T. beroidea* figures of Daday (1887) are impressive by their variability. Besides the species this author distinguished the varieties-*acuminata*, -*plagiostoma* and -*compressa*. His description of species and varieties strikingly agrees with our figures. Daday's species (Pl. 19, fig. 2, 14) covers our aborally rounded specimens: figs. 2b, 2c and 3c (Kofoid & Campbell, 1929: *T. rotundata*. Jörgensen). Daday's var. *acuminata* (Pl. 19, fig. 4) is identical with the type (Kofoid & Campbell, 1929, p. 28). Some of our specimens resemble Daday's var. *plagiostoma* (Pl. 19. fig. 3), though he is giving a second figure too (Pl. 19, fig. 6) showing a much wider mouth. Kofoid & Campbell (1929) raise this variety to species, but notice that this form is perhaps only a flattened *T. beroidea* Stein. This form was also figured by Entz Sr (1884, pl. 24, fig. 1). The var. *compressa* Daday finally (Pl. 19, fig. 7-9), raised also to species by Kofoid & Campbell (1929), is rounded aborally and shows a slight nuchal constriction, according to our figures 2e and 3d. This latter form resembles *T. lohmanni* Laackman (1908) which Kofoid & Campbell (1929) considered to be based on incomplete loricae and was synonimized by these authors with *T. subacuta* Jörgensen (= *T. lobiancoi* Daday, see p. 107).

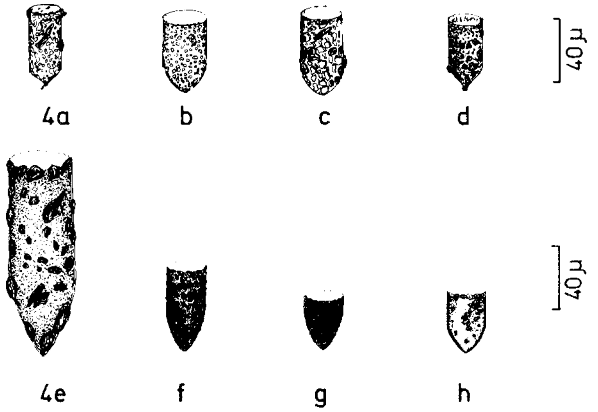


Fig. 4. Tintinnopsis beroidea Stein (4a, b, c, d, f, g from Lake Veere, loc. 6, 7; 4e from coastal seawater, loc. 15; 4h from Inlaag 1953, loc. 13).

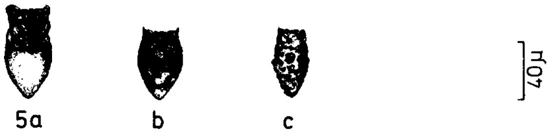


Fig. 5. Tintinnopsis beroidea Stein (5a from Lake Veere, loc. 7; 5b from the Eastern Scheldt, loc. 11; 5c from the Western Scheldt, loc. 3).

Daday rightly decided to a great variability of *T. beroidea*. He had the disposal of a very rich material from the Mediterranean (Gulf of Napels), sampled during 8 months. Perhaps he was impressed (as the present authors) by the nearly constant oral diameter (45-50μ) of most of his specimens (only for his species he mentions lower values: 27-45μ). Our samples too consisted of dense suspensions of *T. beroidea*. Such samples are very suitable to establish specific variability ranges.

Jörgensen (1912) used Brandt's (1906) fig. 5, pl. 16 (identified by Brandt as *T. beroidea* Stein) to describe *T. parvula*. This form was smaller and more slender than *T. beroidea*. The main difference from the latter was the slightly constricted oral part of the lorica. The bowl is widest in its middle part. The conical aboral portion is bluntly pointed, with an angle of ± 60°, see fig. 5. Dimensions: oral diameter: 18-26μ; maximum width: 24-32μ; length: 49-65μ. Brandt (1906) measured an oral diameter of 24μ, v. Breemen (1905): idem 24-28μ; Meunier (1929, fig. 28, pl. 22, identified as *T. beroidea*) idem: 14-20μ; Schulz (1965): idem 21-22μ. Kofoid & Campbell (1929) united *T. fusus* Meunier with *T. parvula*. *T. parvula* occurs in the Baltic, along the norwegian coast, in the southern North Sea and adjacent sea-arms and estuaries and in polyhaline inland waters (Lake Veere).

So far, separation of *T. parvula* from *T. beroidea* seems justified. Rossolimo (1926) however, figured twenty somewhat larger specimens of a species from the Kara Sea assigned to *T. beroidea*, the oral diameter varying from 31-38μ and showing partly *T. parvula* shape: see fig. 6 (derived from Rossolimo). These figures demonstrate convincingly a series of transitional stages between *T. parvula* and *T. beroidea*. We have to conclude, therefore, that *T. parvula* cannot be maintained as a distinct species.

6

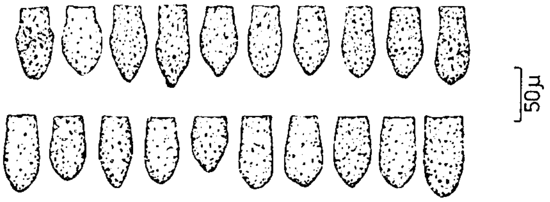


Fig. 6. T. beroidea Stein, after Rossolimo (1926).

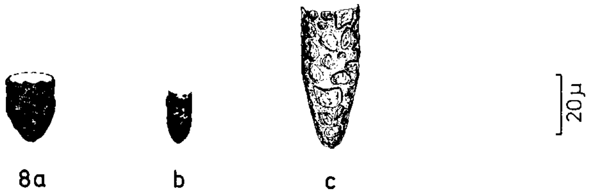


Fig. 8. Tintinnopsis beroidea Stein (8a from Lake Veere, loc. 6, 8b from Schelphoek, loc. 14, 8c from the Eastern Scheldt, loc. 12).

Sometimes the *parvula*-forms are clearly tapering to the aboral end (fig. 7a) and then approach *T. rapa* Meunier. This latter form, being only slightly narrower (fig. 7b), thus may fall within the *beroidea-parvula* series too.

Finally, we put together all very small cylindrical loricae, having an oral diameter of ± 15μ (Hofker, 1922, fig. 81; van Breemen, 1905, fig. 16; Lohmann, 1908, fig. 12, Pl. 17; Meunier, 1919, fig. 21, Pl. 22), and showing a slightly pointed aboral end, as *T. nana* Lohmann. Our smallest specimen even measured 8μ, oral diameter (fig. 8b). *T. minuta* Wailes (fig. 8a) differs from this species only in relation to length and the shorter and more rounded aboral end. These characters, again, appear very variable and therefore are insufficient to maintain *T. minuta* as a distinct species. Kofoid & Campbell (1929) already identified *T. fistularis* Meunier as *T. nana.* Clear separation however of *T. nana* from larger species, notably *T. beroidea,* is not possible, because not only *T. nana* has a -*beroidea* shape, but also there is a gradual transition of -*nana*-to-*beroidea*-dimensions. Smallest *beroidea*-loricae may show oral diameters below 20μ; thus, the boundary between *T. beroidea* and *T. nana* is quite arbitrary. We named the specimen of fig. 8c *T. nana* owing to its elongated conical aboral end, but we might classify this form as well as *T. beroidea* in view of the high degree of variability of the shape of the aboral end of the latter species.

On the other hand it seems reasonable to suppose that the minute forms, although -*beroidea*-like in appearance, are in fact not *T. beroidea.* But the evidence cannot be given on the basis of differences in lorica structure and -dimensions. Culture experiments and subsequent investigation of the protozoan cells may reveal eventual real differences between *nana*-and *beroidea*-forms.

Fig. 7. Tintinnopsis beroidea Stein (7a from the Eastern Scheldt, loc. 10, 7b from Lake Veere, loc. 7).

c. T. campanula (Ehrbg.) Daday (fig. 9a-g)

The variability of this common species is very large as was demonstrated by Hofker (1931). This author includes the following forms into *T. campanula: T. bütschlii* Daday, *T. cincta* (Clap & Lachm.) Daday, *T. cyathus* Daday, *T. elongata* Daday, *T. infundibulum* Daday, *T. lindeni* Daday and *T. urniger* (Entz Sr) Daday. All these species were collected together in the Bay of Naples. Also Jörgensen (1899, 1927) identified *T. bütschlii, T. cincta* and *T. cyathus,* occurring in the North Sea and the Baltic, with *T. campanula.* Already van Breemen (1905) dealt with a *T. campanula-cincta-bütschlii*-series. Marshall (1969) supposed that *T. major* Meunier (Arctic, Norwegian Sea, Baltic) too may belong to this group. We agree with these authors and refer to Hofker (1931) for ample argumentation. *T. ecaudata* Kofoid & Campbell (Norwegian Sea) was already described by Brandt (1906) as *T. campanula* var. a.

Except the characteristic-*campanula*-forms (fig. 9a-c), we found-*major*-(fig. 9d-e) and-*bütschlii*-(fig. 9f) -specimens. Fig. 9g represents a developmental stage of a characteristic *campanula.* The lorica of the typical form is campanulate and provided with a widely flaring mouth and a stout pedicel (fig. 9a-c). Even this characteristic form shows a large variability, as demonstrated by a series of figures from Brandt (1906). The bowl is enlarging gradually to the oral part. The oral region may show a more or less clear annulation (fig. 9d). The encrustation with particles may be dense and rather regular (fig. 9a) or mainly limited to the aboral part with pedicel (fig. 9b, c, g). *Major*-and-*bütschlii*-forms demonstrated sparse and irregular encrustation (fig. 9d-f). Transition between bowl and pedicel may proceed gradually (fig. 9a) or abruptly (fig. 9b). Pedicel runs mostly straight but sometimes shows torsion (Brandt, 1906; Meunier, 1919). Specimens without pedicel may be

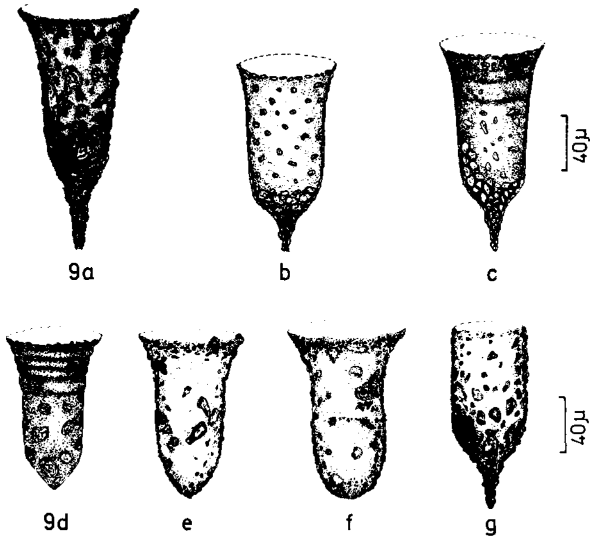


Fig. 9. Tintinnopsis campanula (Ehrbg) Daday (9a, e, f, g from the Western Scheldt, loc. 4, 2, 1; 9b, c, d, from the Eastern Scheldt, loc. 8, 9).

evenly rounded aborally (*bütschlii*-forms, fig. 9 f; *cyathus*-forms) or angular (*major*-forms, fig. 9d, e; *cincta*-forms). *Bütschlii*-forms have a more flaring mouth than *cyathus*-forms; *cincta*-forms are nearly cylindrical throughout their length. For figures of *cyathus*- and *cincta*-forms: see Marshall (1969). Therefore diagnosis of *T. campanula* cannot be based on presence of a pedicel. Hofker (1931) gave a satisfactory explanation for the origin of forms without pedicel (see introduction).

Dimensions: Maximum oral diameter: 70-88μ; diameter ± halfway the lorica: 40-56μ; length including pedicel: 135-172μ; length without pedicel: 110-130μ.

Occurrance: North Sea, Baltic, Mediteranean Sea, Atlantic Ocean (Jörgensen, 1927; Hofker, 1931; Marshall, 1969). In the Western Scheldt estuary the species is commonly found throughout the polyhaline and within the α-mesohaline zone, decreasing rapidly in the brackish water. These data are in agreement with those of Hofker (1922, 1931) and van Breemen (1905), tracing the species in the northern, more saline parts of the former Zuiderzee only (not below 8‰ Cl') and with those of Schulz (1965) of the Elbe estuary. *T. campanula* is a summer form: maximum abundance occurring during the period of July to October (30-40/l, salinity 14,3-17,2‰ Cl'). We could not yet demonstrate the species in Lake Veere, though chlorinity in summer may rise from 10 to 14‰.

d. T. cylindrica Daday (fig. 10)

According to Kofoid & Campbell (1929) we base the identification of this species on the original description of Daday's (1887) *T. davidoffi var. cylindrica* (Daday), pl. 19, fig. 24).

T. cylindrica is characterized by an elongated lorica, the anterior part being cylindrical for 75-80% of the total length. The aboral part narrows to a stout pedicel, slihgtly varying in length and width. Transition of the cylindrical part of the lorica into the pedicel proceeds often gradually but sometimes abruptly. Encrustation with coarse particles is especially seen in the aboral part and pedicel. In Lake Veere the greater part of the lorica is covered with very small particles (clay particles and μ-cells). The oral diameter of our specimens is strikingly constant in time and space, varying only between 35-42, most loricae measured 36 diam. Length varied from 120-223 μ.

The species occurs in Eastern Scheldt, Western Scheldt and Lake Veere, prefering salinities higher than 10‰ Cl'. Highest numbers are reached in summer.

e. T. fimbriata Meunier (fig. 11 a-c)

T. fimbriata is a very characteristic species, showing a comparatively slight variability. Brandt (1906) figured an undescribed species (figs. 5, 7, Pl. 17 and fig. 10, Pl. 18), doubtless identical with *T. fimbriata* Meunier (Hofker, 1931). Kofoid & Cambell (1929) wrongly described this form as a new species: *T. meunieri.*

The campanulate lorica narrows into a strong nuchal constriction. The mouth is flaring to nearly the diameter of the bowl. The oral rim is characteristically ragged. The aboral end is always pointed (fig. 11a), sometimes very stoutly (fig. 11b), sometimes only slighty (fig. 11c). Lorica densely encrusted with coarse particles, a typical

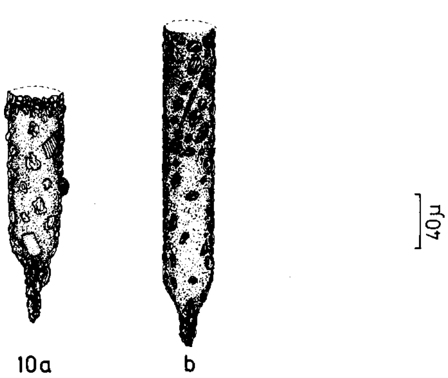


Fig. 10. Tintinnopsis cylindrica Daday (10a from the Eastern Scheldt, loc. 10; 10b from Lake Veere, loc. 7).

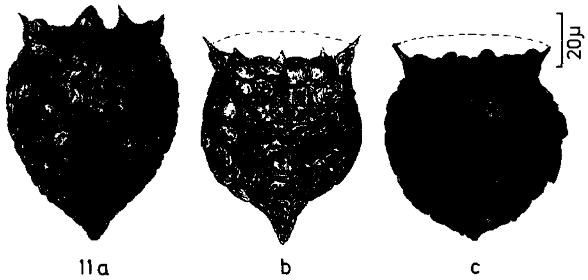


Fig. 11. Tintinnopsis fimbriata Meunier (from the Western Scheldt, loc. 1, 2, 3).

phenomenon for *Tintinnopsis*-species occurring in turbulent estuarine tidal waters with high suspended matter contents.

Dimensions: oral diameter: 44-68μ; maximum width of the bowl: 48-68μ; length 56-88μ. Average values show the tendency of decreasing dimensions when water temperature is rising. During July 1974, water temp. 17,7-19,2 °C, average dimensions were (36 specimens): oral diameter: 55μ; maximum width: 61μ; length: 74μ. After a month, August 1974, water temp. 19,5-20,4°C, average values were (57 specimens): oral diameter: 52,5μ: maximum width: 58μ; length: 71.5μ.

Observations of Hofker (1931), indicating that specimens grew longer when salinity increased were not confirmed by our data. Measurements of 57 specimens from 3 stations with different chlorinities (7,6; 10,6; 12,2‰) resulted in a nearly constant ratio of length to maximum width (1,25; 1,26; 1,23 respectively).

Hofker (1931) stated that *T. baltica* Brandt may be identical with *T. fimbriata*. After our opinion this is not justified: see p. 102.

Meunier (1919) described the species from brackish inland waters in Belgium, occurring abundantly there. In coastal waters on the other hand he found the species sparsely, in agreement with Hofker (1922) and with our observations. We found incidental *T. fimbriata* in the polyhaline zone of the Western Scheldt estuary. We did not observe the species in the eu-polyhaline Eastern Scheldt. Brandt (1906) found the species in the Kiel Bay and the Kaiser Wilhelm Canal. *T. fimbriata* proves to be a character species of the (mixo) mesohaline zone of the Western Scheldt estuary during summer (Bakker & De Pauw, 1975). The species occurred abundantly too in the south western (mesohaline) part of the former Zuiderzee (Hofker, 1922; 1931). According to Schulz (1961; 1965) the species lives in the Elbe estuary too, but not in great numbers.

f. T. lobiancoi Daday (figs. 12 a-d, 13)

According to the original description of Daday (1887), *T. lobiancoi* is a cylindrical, elongated species of large length (270 μ) aborally evenly rounded and showing an oral diameter similar to that of the lorica: 45μ. Most data agree in relation to the width of the oral diameter. A large material from the Baltic (Gulf of Finland) was thoroughly investigated by Halme & Lukkarinen (1960). They established a range of 30-55 μ oral diameter, 90% of the loricae however falling within a range of 35-45 μ. Some other data: Brandt (1906): 40-50 μ; Biernacka (1948): 46-50 μ; van Breemen (1905): 45 μ; Meunier (1910): 36-40 μ; own measurements; 37-47 μ. Length varies from 30-300 μ, (Halme & Lukkarinen); 220-390 μ (Brandt); 156-170 μ (van Breemen); 100-140 μ (Meunier); own measurements: 144-210 μ.

The species shows a large variability. Jörgensen (1927) considered *T. lobiancoi* Daday and *T. tubulosa* Levander distinct species, *T. tubulosa* differing from *T. lobiancoi* by annulation and aboral widening of the lorica. Merkle (1909) however, gave a figure of *T. lobiancoi* with very clear annulation. Notably Halme & Lukkarinen demonstrated convincingly that *tubulosa*- and *lobiancoi*-appearance occurred in the same material, showing all possible intergradations. In their samples about a third of all specimens showed *lobiancoi*-appearance, the remainder demonstrating all a more or less enlarged aboral part, often slightly pointed, resembling the *tubulosa* form. Our material (fig. 12 a-d) was never *tubulosa*-like. So far as we encountered specimens with widened aboral end of the lorica, we had to assign these forms to *T. beroidea* Stein (see fig. 2a, e; 3a, d, e). We never found *T. lobiancoi* in great abundance and so we could not compose a series of this species comparable with that of Halme and Lukkarinen. In fig. 13, derived from these authors, we choose 13 specimens of their series of 100 representing several

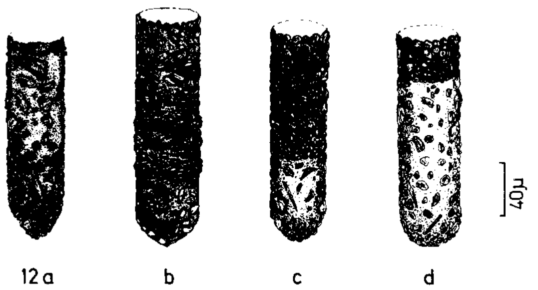


Fig. 12. Tintinnopsis lobiancoi Daday (12a from the Western Scheldt, loc. 5; 12b from the Eastern Scheldt, loc. 11; 12c, d from coastal seawater, loc. 15).

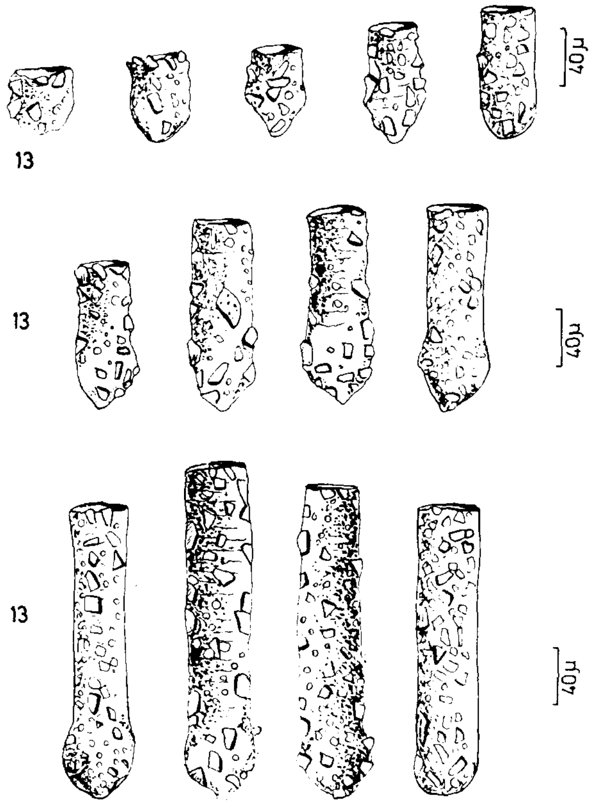


Fig. 13. Tintinnopsis lobiancoi Daday, after Halme & Lukkarinen (1960).

developmental and adult stages of *T. lobiancoi.* They consider the following species belonging to the *lobiancoi*-series: *T. tubulosa* Levander, *T. karajacensis* Brandt, *T. subacuta* Jörgensen, *T. tubulosoides* Meunier, *T. pistillum* Kofoid & Campbell, *T. rotundata* Jörgensen, *T. lata* Meunier, *T. strigosa* Meunier, *T. turbo* Meunier, *T. baltica* Brandt. After our opinion *T. turbo* and *T. baltica* are well defined species (see p. 108 and 102) not to be confused with developmental stages of *T. lobiancoi,* although resembling these stages. *T. strigosa* may be identical with *T. baltica* (Jörgensen, 1927; see p. 103). As to the remainder of the above mentioned species, we agree with Halme & Lukkarinen. Brandt (1906) already stated that his *T. kacajacensis* only differed from *T. lobiancoi* in relaton to its smaller dimensions. *T. macropus* Meunier and *T. lohmanni* Laackman appear to belong to this series too: Kofoid & Campbell (1929) ranged these forms already under *T. subacuta* Jörgensen. Finally, the series has to be classified as *T. lobiancoi* Daday, this species name having priority, and not as *T. tubulosa* Levander as Halme & Lukkarinen incorrectly did.

In our area the species occurs in high-salinity waters and in the polyhaline estuarine zone. Penetration into the mesohaline zone, however, is possible.

g. T. turbo Meunier (fig. 14 a-f)

The lorica shows maximum width in its middle or upper part and narrows (sometimes abruptly: fig. 10 a, b) to the oral portion consisting of a short cylindrical collar. The conical aboral end is rounded or bluntly pointed. The house, is strongly encrusted with large particles.

The original description of Meunier (1919) is rather incomplete and has been based on a few specimens. The sharply pointed aboral end in his figure (fig. 27, pl. 22) has not been observed by any author. Brandt (1906) described and figured (fig. 3 pl. 16) a form as *T. nucula* Fol?, which was identified by Kofoid & Campbell (1929) as *T. turbo.* This form shows a somewhat more swollen appearance than Meunier's species. Schulz's (1965) microphotograph of *T. turbo* (fig. 4, pl. 2) is characterized by a conical aboral part with almost straight contours resembling our fig. 9 f. Schulz had the opportunity, to study a large material as well as we had.

Dimensions: oral diameter: 29-40 μ, average 35 μ; maximum width: 45-54 μ, average 48 μ; length 64-81 μ, average 69 μ. Schulz (1965) measured an average oral diameter of 33 μ, maximum width of 51 μ, and length of 66 μ.

Hofker (1922) identified a much larger species from the former brackish Zuiderzee (oral diameter: 55-60 μ;

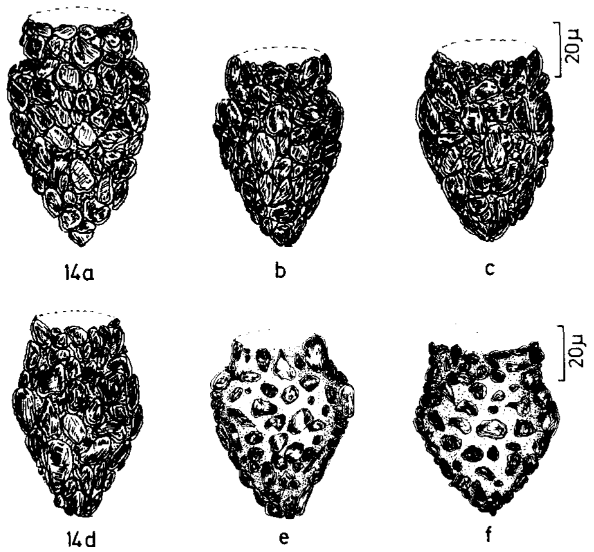


Fig. 14. Tintinnopsis turbo Meunier (from the Western Scheldt, loc. 3).

maximum width: 70-78 μ; length: 100-115 μ) as *T. turbo* and later (1931) as *T. lohmanni* Laackmann (synonimized by Kofoid & Campbell, 1929, with *T. subacuta* Jörgensen = *T. lobiancoi* Daday according to Halme & Lukkarinen, 1960). The shape of the lorica represented by Hofker's (1931) fig. 12 b, however, approaches Meunier's (1919) description and not Laackman's (1906).

Fig. 12a, on the other hand, shows an elongated oral part with somewhat increasing diameter of the oral rim and cannot be classified, in our opinion, as *T. turbo*. Hofker's (1931) fig. 13, finally, resembles to some extent our fig. 9 f and Schulz' (1965) fig. 4, pl. 2.

We noted already (p. 11) that Halme & Lukkarinen (1960) synonimized numerous species with *T. lobiancoi* Daday, a.o. *T. turbo*.

Examining their figures we feel that the smallest specimens may look *turbo*-like (see our fig. 13), but in fact are developmental stages with incomplete loricae and thus *T. turbo* must not be identified with these forms.

T. turbo is a character species of the oligohaline (Schulz, 1965), and the mesohaline zone (Bakker & De Pauw, 1975) of the estuaries of Elbe and Western Scheldt resp. The species occurs throughout the year, demonstrating peaks in spring and summer.

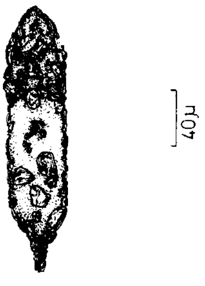
Discussion

Evidently the way of development of the lorica may differ strongly, according to the developmental phase during which the animal has built its lorica and also according to the prevailing environmental conditions (see introduction). In this way the large phenotypic variability of the lorica of one species in the same sample is established. The important observations of Hofker (1931) have strongly contributed to a better understanding of the possible causes of lorica variability. It is reasonable to suppose that particularly coastal seawater and brackish inland waters offer good opportunities for the development of great variation in Tintinnid species, owing to the strong fluctuations occurring in the chemical and physical environment and to the presence of estuarine gradient situations. Therefore it is not justified to use the term 'Formenkreis' in this case. A 'Formenkreis' is defined (Mayr, 1965) as an aggregate of geographically representative (allopatric) species and subspecies. In his discussion about polytypic species (= Formenkreise) Mayr, citing Döderlein (1902) and Tortonese (1950) argues that most marine animals indeed should be united into comprehensive polytypic species, but that sometimes the subspecies are merely individual variants. Brandt (1896) compared *Tintinnopsis* loricae from different geographical regions, describing related forms as distinct species but uniting these species into 'Formenkreise'. Without excluding the possibility of geographic variability in *Tintinnopsis* species, we should like to attach the greatest importance to individual variation here too.

Of course we have to consider the possible occurrence of lorica variability on a genetic base. Environmental changes during late stages of conjugation caused permanent morphological changes of *Paramaecium* spec. (Jollos, from Kudo, 1966). Recombination of nuclear materials might be effected in such a way that the genotype is altered (Kudo).

Finally we may mention eventual hybridization as a cause of phenotypic variability. We made a single observation of a possible conjugation of *Tintinnopsis cylindrica* and *T. beroidea* (fig. 15). We could not demonstrate, however, that conjugation really had taken place, and, if so, that the hybrides might prove viable. Kudo (1966), discussing experiments to realize conjugation between different species of *Paramaecium*, states that species of this genus are incompatible with one other.

Thus individual phenotypic variability, geographic variability and genotypic changes of the protozoan cell may all be responsible for the large variability in lorica shape. However, differences in lorica shape should not primarily be related to (sub) specific (genotypic) differences between the Tintinnid cells. Individual phenotypic variation evidently plays an all important role in local populations. Therefore it is not justified in our opinion, to describe new species from a material consisting of only one or a few specimens, as Meunier (1910, 1919) did. Kofoid & Campbell (1929) ignore this aspect in their con-



15

Fig. 15. Tintinnopsis cylindrica Daday and T. beroidea Stein: conjugation? (from the Western Scheldt, loc. 4).

spectus and consequently have not escaped to unacceptable splitting of species; many inadequately known forms or different forms from a coherent group have been raised to species.

Studying separate specimens from our (figs. 2 and 3) and Rossolimo's (fig. 6) *beroidea* material, one may identify these forms easily with different described species. The aspect of individual variation in building of the lorica deserves full attention of all workers on Tintinnid systematics. Classification has to be based on investigation of a large material. Ultimately, problems of lorica development and shape may definitely be solved by culturing. Combination of field investigations and laboratory experiments would appear most fruitfull. Renewed attention to full life cycles (Corliss, 1961) might lead to a base for revision of present-day classifications.

Summary

The species of the Tintinnid genus *Tintinnopsis* Stein, occurring in the coastal waters of the SW.-Netherlands, are figured and described. We demonstrated a large variability of several species in relation to the shape of the lorica. Nearly all lorica characters appeared to vary considerably, particularly the shape of the aboral portion of some species (*T. beroidea* Stein). The oral diameter of the lorica, on the other hand, varied much less. The many forms were classified into 7 species only: *T. baltica* *Brandt, T. beroidea* Stein, *T. campanula* (Ehrbg) Daday, *T. cylindrica* Daday, *T. fimbriata* Meunier, *T. lobiancoi* Daday, *T. turbo* Meunier. Loricae of some species demonstrated extreme variability, notably those of *T. beroidea.* Others on the contrary, appeared rather constant: *T. cylindrica, T. fimbriata.* Very strong individual variation was demonstrated in local populations (fig. 2 and 3). Therefore it is not justified to describe new species from sparse material. For descriptive work, especially on neritic Tintinnids, investigations of a great number of specimens is advocated.

Acknowledgements

We thank mr. J. v. d. Ende for his assistance in the reproduction of the figures.

References

Bakker, C. & N. de Pauw. 1975. Comparison of brackish water plankton assemblages of identical salinity ranges in estuarine tidal and stagnant environments. II Zooplankton Neth. J. Sea Res. 9 (2): 145-165.

Balech, E. 1948. Tintinnoinea de Atlantida (R. O. del Uruguay) (Protozoa Ciliata oligotr.). Comun. Museo Argent. Cienc. Nat., Ser. Cienc. Zool. 7.

Biernacka, I. 1948. Tintinnoinea in the Gulf of Gdansk and adjoining waters. Bull. Lab. Marit. Gdynia anc.-Bull. Stat. Marit. Mel. 4.

Brandt, K. 1896. Die Tintinnen. Bibliotheca Zoologica 20 (2).

Brandt, K. 1906-07. Die Tintinnen der Plankton-Expedition. Ergebn. Plankton-Exp. 3 (La). (mit Tafelerklärungen und Atlas).

Breemen, P. J. van. 1905. Plankton van Noordzee en Zuiderzee. Diss. Amsterdam.

Corliss, J. O. 1961. The Ciliated Protozoa. Int. Ser. Monogr. on pure and appl. biol. vol. 7. Pergamon Press, Oxford.

Daday, E. v. 1887. Monographie der Familie der Tintinnoideen. Mitt. zool. Stat. Naepel 7: 473-591.

De Pauw, N. 1975. Bijdrage tot de kennis van milieu en plankton in het Westerschelde-estuarium. Diss. Gent.

Entz, sen., G. 1884. Uber Infusorien des Golfes von Neapel. Mitt. zool. Stat. Neapel 5:

Gold, K. 1969. Tintinnida: feeding experiments and lorica development. J. Protozool. 16: 507-509.

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. Ann. Zool. Soc. Zool. Bot. Fenn. Vanamo 22 (2): 1-24.

Hofker, J. 1922. De Protozoën. In: Flora en Fauna der Zuiderzee, red. H. C. Redeke, p. 127-183.

Hofker, J. 1931. Studien über Tintinnoidea. Arch. f. Protistenk. 75: 315-402.

Jörgensen, E. 1899. Uber die Tintinnodeen der norwegischen Westküste. Bergens Mus. Aarb. 2.

Jörgensen, E. 1905. The protist plankton and the diatoms in bottom samples. In: O. Nordgaard: hydrographical and biological investigations in norwegian fjords. Bergens Museum.

Jörgensen, E. 1927. Ciliata, Tintinnidae. In: Die Tierwelt der Nord- und Ostsee. Tl. II C: 1-28.

Kofoid, C. A. & Campbell, A. S. 1929. A conspectus of the marine and freshwater 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. Publ. in Zool. 34: 1-403.

Kofoid, C. A. & Campbell, A. S. 1939. The ciliata: the Tintinnoinea. Bull. Mus. Comp. Zool. Harvard 84: 1-473.

Kudo, R. 1966. Protozoology. 5th ed. CC. Thomas publ., Springfield U.S.A.

Laackmann, H. 1908. Ungeschlechtliche und geslechtliche Fortplanzung der Tintinnen. Wiss. Meeresunters. N.F. 10 (Abt. Kiel): 15-37.

Lohmann, H. 1908. Untersuchungen zur Feststellung des vollständigen Gehalts des Meeres an Plankton. Wiss. Meeresunters. N.F. 10 (Abt. Kiel): 129-370.

Marshall, S. M. 1969. Protozoa Tintinnida. Zooplanktonsheet 117. C.P.I.E.M.

Mayr, E. 1965. Animal species and evolution. 2nd pr. Belknapp Press Harvard U.S.A.

Merkle, H. 1909. Untersuchungen an Tintinnodeen der Ost- und Nordsee. Diss. Kiel.

Meunier, A. 1910. Microplankton des mers de Barents et de Kara. Campagne Arct. Duc d'Orleans, 1907.

Meunier, A. 1919. Microplankton de la mer Flamande. 4. Les Tintinnides etc. Mém. Mus. Roy. Hist. Nat. Belg. 8 (2): 1-59.

Rossolimo, L. L. 1926. Planktische Infusorien des Karischen Meeres. Ber. Wiss. Meeresinst. 2 (1): 63-77.

Schulz, H. 1961. Qualitative und quantitative Planktonuntersuchungen im Elbe-Aestuar. Arch. Hydrobiol./Suppl. 26: 5-105.

Schulz, H. 1965. Die Tintinnoinea des Elbe-Aestuars. Arch. Fischereiwiss. 14: 216-225.

Silva, E, de Sousa, e. 1950. Les Tintinnides de la Baie de Cascais (Portugal). Bull. Inst. Océanogr. Monaco no. 979: 1-28.