ISSN 0704-3716

CANADIAN TRANSLATION OF FISHERIES AND AQUATIC SCIENCES

No. 4561

Studies on tintinnoidea

by J. Hofker

Original Title: Studien uber tintinnoidea

From: Arch. Protistenkd. 75: 315-402, 1931

Translated by the Translation Bureau (YM)
Multilingual Services Division
Department of the Secretary of State of Canada

Department of Fisheries and Oceans
Marine Ecology Laboratory
Dartmouth, N.S.

1979

125 pages typescript

DEPARTMENT OF THE SECRETARY OF STATE
TRANSLATION BUREAU

MULTILINGUAL SERVICES DIVISION

CANADA

SECRÉTARIAT D'ÉTAT
BUREAU DES TRADUCTIONS

DIVISION DES SERVICES MULTILINGUES

CTFAS 4561

TRANSLATED FROM – TRADUCTION DE	INTO – EN
German	English

AUTHOR – AUTEUR

J. Hofker

TITLE IN ENGLISH – TITRE ANGLAIS

Studies on Tintinnoidea

TITLE IN FOREIGN LANGUAGE (TRANSLITERATE FOREIGN CHARACTERS)
TITRE EN LANGUE ÉTRANGÈRE (TRANSCRIRE EN CARACTÈRES ROMAINS)

Studien über Tintinnoidea

REFERENCE IN FOREIGN LANGUAGE (NAME OF BOOK OR PUBLICATION) IN FULL. TRANSLITERATE FOREIGN CHARACTERS.
RÉFÉRENCE EN LANGUE ÉTRANGÈRE (NOM DU LIVRE OU PUBLICATION), AU COMPLET, TRANSCRIRE EN CARACTÈRES ROMAINS.

Archiv für Protistenkunde

REFERENCE IN ENGLISH – RÉFÉRENCE EN ANGLAIS

Archive for Protistology

PUBLISHER – ÉDITEUR	DATE OF PUBLICATION / DATE DE PUBLICATION			PAGE NUMBERS IN ORIGINAL / NUMÉROS DES PAGES DANS L'ORIGINAL
not shown	YEAR / ANNÉE	VOLUME	ISSUE NO. / NUMÉRO	315–402
PLACE OF PUBLICATION / LIEU DE PUBLICATION				NUMBER OF TYPED PAGES / NOMBRE DE PAGES DACTYLOGRAPHIÉES
not shown	1931	75		125

REQUESTING DEPARTMENT / MINISTÈRE-CLIENT: DFO

TRANSLATION BUREAU NO. / NOTRE DOSSIER N°: 1846283

BRANCH OR DIVISION / DIRECTION OU DIVISION: Sc. Inf. and Publ. Br.

TRANSLATOR (INITIALS) / TRADUCTEUR (INITIALES): Y.M.

PERSON REQUESTING / DEMANDÉ PAR: A.T. Reid

YOUR NUMBER / VOTRE DOSSIER N°:

AUG / AOUT 22 1979

DATE OF REQUEST / DATE DE LA DEMANDE: 2/4/79

UNEDITED TRANSLATION
For information only
TRADUCTION NON REVISÉE
Information seulement

SOS-200-10-6 (REV. 2/68)
7530-21-029-5333

Secretary of State / Secrétariat d'État

MULTILINGUAL SERVICES DIVISION / DIVISION DES SERVICES MULTILINGUES

Client's No. — Nº du client	Department — Ministère	Division/Branch — Division/Direction	City — Ville
	DFO	Sc. Inf. and Publ. Br.	Dartmouth, N.S.
Bureau No. — Nº du bureau	**Language — Langue**	**Translator (Initials) — Traducteur (initiales)**	
1846283	German	Y.M.	AUG AOUT 22 1979

Studies on Tintinnoidea

by

Dr. J. Hofker

Den Haag, Holland

A fairly large number of works on Tintinnoidea exist already (the 'Conspectus' of this important family of ciliates, published in 1929, already lists 232 references, although this list is not even complete - for instance, most of the literature published in the Dutch language is missing), but there are still gaps in the knowledge regarding their taxonomic position and further subdivisions as well as regarding the anatomy of the various species. Many researchers who have concerned themselves only with the planktonic composition of the ocean, have described many species of which only the housings have become known because the cell bodies could not be studied, frequently as a result of inadequate fixation. But Brandt (1907, p. 14 and 15) has already stressed:' nothing reliable is known for some typical species (e.g. Cytharocylis cassis and all its related forms) about the vegetative condition of the cell, the number and arrangement of the nuclei and secondary nuclei, and of the vacuoles, and about the number of adoral ciliate lamellae ...', 'Basic for the system of the family of Tintinnoidea, as for any other group of animals, must be the knowledge of the cell and its reproductive processes. The exclusive consideration of the housings and their structural properties can only lead to an artificial system'.

Although the more recent research has produced much that was still unknown at the time of Brandt's monograph, very much has still remained totally unclear. This state of affairs has induced me to study thiy interesting family more closely. 316

Most of the material was collected by myself. It comes from the North Sea (Scheveningen, zoological station at Den Helder), from the Zuider Zee (field trips of the 'Nederlandsche Dierkundige Vereeniging (Dutch zoological society)'), and from the Gulf of Naples (stazione zoologica di Napoli).

Due to the very varied origin, the material consisted of fairly many, and mostly very important, species. It was collected at very different times, and in different years (Scheveningen: 1917-1931; Den Helder: 1921, 1929; Zuider Zee: 1919-1920, 1928-1930; Naples: 1930, February to May).

Methodology. As I mentioned above, many authors considered only the housings for their research. Only a few more recent workers (Geza Entz jr., Laackmann, Campbell) are a laudable exception. But since particularly the formalin method used by plankton researchers yields very poor results, I have tried to find a simple process which would allow the very delicate cells of the Tintinnids to be well preserved and which could also be used on scientific expeditions. I have described this method in detail elsewhere (1930) but would like to reiterate here the most important points relating to (the preservation of) Tintinnids.

A concentrated solution can be manufactured as follows: combine a saturated solution of trichloracetic acid (Merck) in distilled water with an equal quantity of glacial acetic acid.

5ml of this concentrate (more does no harm but less has a macerating effect) is added to 1000 ml of the seawater which contains the plankton to be investigated, and the mixture quickly stirred vigorously with a glass rod. The plankton soon collects at the bottom of the vessel, and the excess liquid can be poured off after one hour, frequently even sooner. This liquid should be replaced by 70 % alcohol in which the plankton can be kept further.

In this way the Tintinnids are preserved without deformation due to energetic contraction, and the finest structural characteristics of the protoplast become visible. The organelles remain completely unchanged, and in swimming samples extend very nicely out of the housing. This preservation method further has the great advantage that

the material is suitable for all staining methods, as I had stressed already in 1921. Even the fine structure of the nucleic elements is perfectly preserved. 317

I have stained the material with Ehrlich's hematoxylin, boracic carmine, ferric hematoxylin according to Heidenhain, and with the staining method according to Borrel. Iron hematoxylin is particularly suitable for sections which I made with the usual paraffin method. Ehrlich's hematoxylin is useful especially for complete specimens, particularly when the nuclei are to be stained. I have described the various staining methods in detail in my paper mentioned earlier (1930).

The various species which I have studied permit me to find a wealth of new facts. These facts, in the overall context can give us a clearer picture regarding the many questions which are still open. I will therefore deal individually with each of the species observed by myself, before discussing the general results.

Systematic Section

In this description of the species, I shall use the nomenclature and classifications of the Kofoid-Campbell Conspectus (1929), only for clarity. I shall only later subject the taxonomy to a closer critical scrutiny.

1. Tintinnidium incertum Brandt (Fig. 1)

I have repeatedly found this species in the centrifuged plankton from the Zuider Zee, and was thus able to study it fairly closely. It appears often in large masses, from July until September, particularly also in the brackish water. It also occurred a few times in large numbers in the vicinity of Scheveningen during July (1917). The wall of the lorica is thick, more or less flexible, and yellowish. The surface contains a number of small, strongly refractive particles; occasionally there is also a hint of primary alveoli. The cross section of the loricae is elliptical, with the result that they appear much narrower in a side

view than in a front view. They are open on one side, but on the opposite side, one of the wider sidewalls more and more approaches the other until they merge into one. This has the effect of an oblique tapering of this pointed side. The animals are attached at one point at the adoral side, 318
and another point on the wall at the center of the shell. They usually have 16 oral organelles but I counted only 12 in some instances[1]. There is always a single macro-nucleus, frequently with a desmose; there is always only a single albeit small micro-nucleus which is very small and can often be made visible in staining only with difficulty. Length of the housings 100 to 269µm; width at the widest point 30 to 60µm.

The identification of the species found in the Zuider Zee caused some difficulties because the various authors had found this species only sporadically.

The species illustrated by Brandt is probably identical with the one described here, but the species described by Busch is probably also synonymus with it. Busch at any rate did not take into account my description (1922) or he would not have given a new name (Tintinnidium primitivum).

Bibliographical Notes

Brandt, K. (190)): Tintinn. plankton expedition, p. 442, plate 31, Fig. 6-7

Hofker, J. (1922): Flora and fauna of the Zuider Zee, p. 169, Fig. 76

Busch, W. (1923): Verhandlungen der deutschen Zoologischen Gesellschaft (Proceedings of the German Zoological Society), Volume 28, p.71;

Archive for Protistology, 1925, Volume 53, p. 183-190, Fig. A-D.

Kofoid, C.A. and Campbell, A.S. (1929): Conspectus, p. 15, Fig. 3, p.11, Fig. 7

1) The number of organelles of the tintinnids is relatively easily determined by one of two methods. Either slight pressure is applied on the glass cover so that the animals in Canada balsam are made to cant and their peristome goes into a horizontal position, or one observes animals which are about to divide, and which have formed a second peristome laterally.

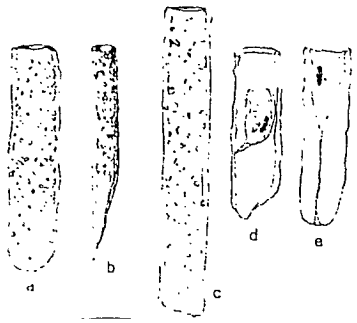


Fig. 1: Tintinnidium incertum Brandt.
a) Top view, b) side view of shell, c) very large shell, d) cell; Technique: Acid. trichl. Ehrlich's hem., Canada balsam. Magnification 200:1.

According to observations by Busch the shell is said to form simultaneously from the contents of a large number of vacuoles which are said to be located on the surface of the cell.
It is curious that this species which is so common in the Zuider Zee also seems to be frequent in tropical oceans; this is also the case with other types of organisms of the Zuider Zee (cf. my paper: Faunistic observations in the Zuider Zee, Zeitschrift für Morphologie und Ökologie der Tiere (Journal of morphology and ecology of animals, , 1930, Volume 18, p. 214-216). But I must stress that I have found the species fairly frequently at the North Sea coast (Scheveningen). 319

2. Tintinnidium mucicola
(Claparede et Lachmann) V. Daday

This species is still very inaccurately known (the finds mentioned by different authors are most likely not all of the same species). It was observed by myself a few times

in the vicinity of Scheveningen and in the harbour of den Helder. It never occurred in larger quantities, and I cannot say anything regarding its internal structure. It is quite possible that Tintinnidium fluviatile is closely related to the species encountered by myself. The detailed investigations of Faure-Fremiet's have shown that Tintinnidium fluviatile Stein has only one macro-nucleus. According to Laackmann (1906), Tintinnidium mucicola from the Bay of Kiel has '2 round nuclei and 2 small secondary nuclei of 1µm size'. He also reports that its distribution in plankton is irregular and never very frequent.

Another 'species' observed by myself a few times in Naples (early March 1930) was a form which was almost indistinguishable (Fig. 2) from the Tintinnidium mucicola from the Bay of Kiel which Laackmann described. It also shows two macronuclei and two secondary nuclei. It is very likely that it is identical with the species Tintinnidium neapolitanum v. Daday (1887, p. 522) because the collar described by v. Daday, as such formations on shells of tintinnids always do, may have its origin in external conditions or reproductive phases of the animals. The adoral ciliate zone contained 12 organelles: division proceeds fully analogously to that of the other Tintinnoidea, with the formation of a new peristome at one side of the animal. On living animals I was also able to clearly observe lamellae at the inside bases of the organelles. On the side closest to the mouth and at a slight angle, a row of long cilia runs down along the cell to the cytopyge. These cilia serve to transport foreign particles towards the edge of the lorica and attach them to the outside. On the opposite side, I observed a few rows of very fine cilia. These cilia are engaged in the construction of the lorica (Fig. 3). 320

If we consider the finer details of the cell we must admit after all that 'Tintinnidium' fluviatile Stein (with few rows of subadoral cilia and a single macro-nucleus,

Faure-Fremiet), Tintinnidium lacustris which also does not have an adoral row of cilia (Faure-Fremiet), usually containing two macro-nuclei (Entz jr., 1909, p. 160), 'Tintinnidium' neapolitanum v. Daday studied in detail by myself, and Tintinnidium incertum Brandt hardly form a natural unit. And we must realize that the presence of a gelatinous lorica has no taxonomic value. I shall return to this question later.

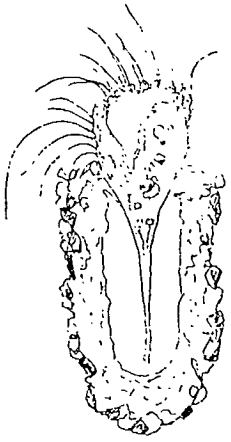


Fig. 2: Tintinnidium neapolitanum v. Daday. Drawn to life. Magnified 325:1 319

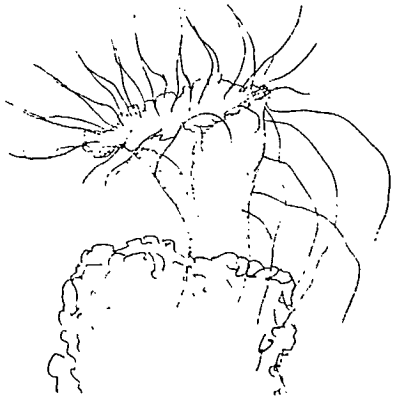


Fig. 3: Tintinnidium neapolitanum v. Daday. The lateral row of cilia is engaged in the accumulation of foreign particles on the lorica. Magnified 325:1. 320

3. Leprotintinnus bottnicus (Nordquist) Jörgensen (Fig.4)

The loricae are cylindrical and slim, narrowing towards the adoral side, where they are frequently thicker on one side than on the other, and thus skewed: the adoral side is usually open. The oral end is usally clearly ringed.

The cell is elongated, and always attached at the side wall of the lorica: two macro-nuclei are present, frequently exhibiting the desmose. The micronuclei are tiny, and lie in a pair in the vicinity of the macronuclei. The number of organelles is unknown to me. Length of the shell: 130 to 192 µm; largest width 24 to 30µm.

The skewed shells frequently suggest Tintinnopsis fracta Brandt (Brandt, Plankton Expedition, Plate 23, Fig. 10). The specimens found by myself in the Zuider Zee also have the ringed anterior shell section in common with Tintinnopsis fracta.

Van Breemen (1905, p. 56) reports that the posterior parts of the shells that he found in the Zuider Zee never exhibit the widening which Levander found in shells collected in the Baltic sea. But a number of shells which I caught in the vicinity of the mouth of the Ketel (river) clearly show a widening of the posterior end. They approximate thus Brandt's species Tintinnopsis pellucida (l.c. Plate 23, Fig. 14). 321

Tintinnopsis bottnica was found by van Breemen only in the Zuider Zee proper, never in the Waddensee (mud flats). I did find them, however, strangely enough, at the North Sea cost, in the vicinity of Scheveningen, but always rarely.

Bibliographical Notes

Tintinnus bottnicus Nordquist; Medd. Soc. Flora Fauna Fennica, 1890, Vol. 17, p. 126, Fig. 5

Codonella bottnica Levander, Acta Soc. Flora Fauna Fennica, 1894, Vol. 12, p.89, Plate 3, Fig.7.

Tintinnopsis bottnica Levander, Acta Soc. Flora Fauna Fennica, 1901, Vol. 20, p.8,14, 15,17,19,28,33; Hofker,l.c.,p.170, Fig. 78

Leprotintinnus bottnicus Jörgensen, Skr.Schw. Hydrog.Biol. Komm., 1912, Volume 4, p.4

Further: Kofoid-Campbell, Conspectus, 1920, p.17, Fig. 11.

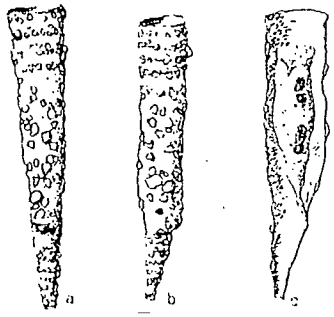


Fig. 4: Leprotintinnus bottnicus (Nordquist)
a Front view, b side view, c cell;
technique: Ehrlich's hem., Canada balsam.
Magnification 300:1.

4. Tintinnopsis fimbriata Meunier (Fig. 5)

The lorica is very beautifully bell-shaped and ends in a short strong spine. The casing bulges in the centre, like Codonella ventricosa, and narrows again somewhat towards the mouth. At the oral end it opens into a ragged wide oral rim. Where the wall widens into the oral rim it almost always thickens quite considerably. Length of the lorica: 64µm; 55µm broad.

The cell is fairly large when extended and just fits into the opening of the shell. Two macronuclei which usually exhibit the desmose are located on one side of the cell, and two macronuclei are often difficult to stain.

The organelles are somewhat pointed, rather small, and usually clearly set off from the body, but not to the same degree as in Tintinnopsis campanula. There are 18 of them (Fig. 6b). 322

The cell body is always attached to the lorica at its aboral pole.

The species was found in large quantities in the Zuider Zee by myself and also by van Breemen (Tintinnopsis sp., 1905, p.59-60). It forms a very important part of the plankton during the summer months there, particularly in the southwestern part of the Zuider Zee.

The species is not very variable but it was possible to detect a variability in the shell which indicates that some shells described by other authors probably belong to this species.

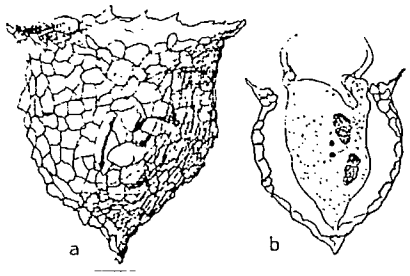


Fig. 5: Tintinnopsis fimbriata Meunier
a shell, magnification 350:1; b cell, magnification 300:1; technique: acid. trichl. Ehrlich's hem., Canada balsam

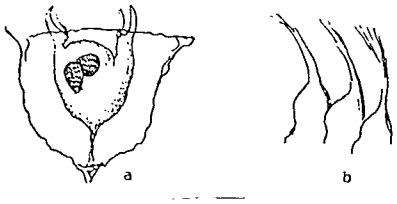


Fig. 6: Tintinnopsis fimbriata Meunier
a swimming individual, magnification 250:1; b organelle, from a Canada balsam preparation, magnification 675:1.

The shells found by Meunier come from an area of brackish water in the vicinity of Nieuwendamme (Belgium). Levander (and later Brandt as well) found this species in the Bay of Kiel but he described it erroneously as Tintinnopsis ventricosa. Brandt does not agree with this view (Brandt, Plankton Expedition, 1907, Plate 17, Figs. 5 and 7; Plate 18, Fig. 10), but in his opinion there are not sufficient grounds for creating a new species. Kofoid-Campbell associated Brandt's illustration with the name Tintinnopsis meunieri.

He writes:

> „Lorica very stout campanulate, 1,25 oral diameters in length: oral rein very ragged and irregular; collar flaring to the diameter of the bowl, inverted conical (90 %); bowl globuse: aboral region convex conical (90 %): aboral horn subconical, 0,11 oral diameter in length: oral end truncate: wall of rather coarse, subuniform secondary areas. Length 75 μ.
>
> The type locality is the Kaiser Wilhelm Canal."

This description corresponds entirely to that which I would apply to Tintinnopsis fimbriata. 323

I shall still prove my contention that Tintinnopsis meunieri Kofoid et Campbell is only synonymus with Tintinnopsis fimbriata Meunier. This species then seems to be characteristic for isolated areas of brackish water in the vicinity of the North Sea. Its main area of distribution seems to be in the Zuider Zee.

Bibliographical Notes:

Meunier, A. (1919): Microplankton of the Flemish Sea. IV. Report of the Royal Museum for Natural History of Belgium, 1919, p. 13, Plate 22, Figs. 38-39.

Kofoid C.A. and Campbell, A.S.: Conspectus Univ. of Calif. Publ. Zool. Vol. 34, p. 40, Fig. 59 (does not permit the typical form of the lorica to be recognized).

I was able to study extensive material of this interesting species. This material was collected during the draining work by the Commission for investigating the biology of the Zuider Zee. Most of the plankton specimens were studied in toto in Canada balsam but a few hundred individuals were analysed on sections.

The first thing I noticed was that the housings of the animals are not quite the same in the different parts of the Zuider Zee. In some parts, the animals generally have a short lorica, in other parts a slightly more elongated one. The habitus of the first is compatible with 'Tintinnopsis meunieri' Kofoid-Campbell while that of the latter appear often to be identical with Tintinnopsis fimbriata Meunier typus and even with Tintinnopsis baltica Brandt.

Several different factors appear to contribute to the cause of this variation in the form of the lorica. The salt content may be the first important factor. I have measured the length of the loricae of different samples and have reached the following conclusions.

The samples were all preserved by the same method and variations resulting from shrinkage due to preservation are therefore eliminated.

Sample I. Commission site 132, in the vicinity of the 'Roggebot', August 29. 1929. The water temperature was 18°C, the chlorine content 0.48 % . 49 loricae were measured. The largest measured 44 units. 324

Sample II. Commission site 133, level with 'de Knar', August 29, 1929. The water temperature was 19°C, the chlorine content 0.59 % . 81 loricae were measured with the maximum approximately 45 units.

Sample III. Commission site 139, in the vicinity of Edam, August 30, 1929. The water temperature was 18°C, the chlorine content 0.69 % . 82 loricae were measured. The maximum at this site was 49 units.

More exact measurements with more material are still being made, but are not published here. But the above data are already sufficient for demonstrating that in this non-uniform part of the Zuider Zee there are probably different clones of Tintinnopsis fimbriata with a greater (preliminary) mean length of the lorica when the salt content is higher.

Other factors also play a role. This follows from the preliminary analysis of a sample which had a particularly low salt content:

Sample IV. Commissionsite 74, at the level of the'Roggebot', September 4, 1928. The temperature was 18°C but the chlorine content only 0.29 %. 60 loricae were measured. The maximum was near 46, thus higher than that measured at the same site in the same season, the following year, but where the salt content was higher. The contributing factors cannot be named with certainty yet and more accurate statistical investigations may possibly provide an explanation; but we can already conclude that the variations in the loricae of a single species occurring in a small region may be described as considerable. Particularly the length of the loricae (but also their diameter as I shall show elsewhere) is very variable and seems to be subject to external influences. This is how the many 'varieties' of Tintinnoid species originated which were unfortunately elevated to the rank of species by Kofoid and Campbell (I had already occasion to argue against this species-making: Die Naturwissenschaften (Natural Sciences) 1930, issue 18, p. 395-396). We shall also have occasion in the present paper to point out repeatedly that the species which are based on only a few specimens have no real value, and that whole series of 'species' like Tintinnopsis cyathus Daday, Tintinnopsis bütschlii Daday, Tintinnopsis inpundibulum Daday, Tintinnopsis campanula Daday and many others can only be interpreted as the remote members of different clones of a single species. 325

The 'species' Tintinnopsis fimbriata Meunier, Tintinnopsis baltica Brandt, Tintinnopsis denticulata Kofoid-Campbell, Tintinnopsis meunieri Kofoid-Campbell are also good examples of this completely arbitrary collection of specious species. On this occasion I must point out that Fig. 49 of Kofoid-Campbell, given as the typical figure for Tintinnopsis fimbriata Meunier, is really the somewhat aberrant form of this species, given by Meunier as Fig. 39 whose collar is only slightly fringed. But the figure given as typical by Meunier (Meunier, Plate 21, Fig. 38) is not shown in Kofoid-Campbell although this is the figure which corresponds to the most common form of the shell of Tintinnopsis fimbriata, as indicated by Meunier.

We know that Brandt thinks he can recognize in most of the particles which cover the shells of the Tintinnopsis loricae a fine structure which he interprets as primary alveoli. He bases this observation also on the investigations of R. Biedermann, 1893, who described such a structure in other genera (Dictyocysta, Codonella). Brandt also thinks that most of the socalled foreign particles on the shell of Tintinnopsis species are products secreted by the cell, and therefore exhibit this structure. But I studied a large number of shells of Tintinnopsis fimbriata on very thin microtome sections, and have never been able to detect such a structure in the foreign particles. Rather, most of these particles which are immutable in acids and alkalis turned out to be quartz grains under polarised light. This explains why they have no primary alveolar structure. They are thus real foreign particles, and I am at a loss to understand Brandt's illustrations. It is possible that a few of the foreign particles of Tintinnopsis fimbriata are of an organic nature, but not the majority.

As I hope to be able to prove elsewhere (Tintinnopsis fimbriata is such a fragile species that it is very difficult to observe it alive over any length of time) the

oral collar of any species of Tintinnopsis, especially in view of the attached foreign particles, is not useable as a proper species characteristic. Even the species 326
found in the Zuider Zee which here probably has its major distribution, frequently exhibits considerable variations in the formation of the collar part, especially its degree of raggedness, which was also already pointed out by Meunier. If we look more closely at the known Tintinnoidea of the earth, we find immediately that only very few known species exhibit the typical structure of the lorica of Tintinnopsis fimbriata. Only one species, Tintinnopsis Schotti Brandt, shows the same characteristics, the same somewhat thicker collar part of the lorica, the same shape, only somewhat stouter and, strangely, without fringes. Since this latter characteristic is only of secondary rank, this species seems to be the closest to Tintinnopsis fimbriata after all. But Tintinnopsis Schotti was found at the west coast of Borneo. This is even more remarkable when we consider that there are several other types of organisms which are found in the Zuider Zee and whose nearest relatives have been found in tropical (and frequently Pacific) regions. I had already occasion in another work (1930, Faunistische Beobachtungen in der Zuidersee während der Trockenlegung, (Faunistic observations in the Zuider Zee during the drainage operation), Zeitschrift für Morphologie und Ökologie der Tiere (Journal for morphology and ecology of animals), Volume 18, p. 214-216) to briefly discuss some of these actually tropical species, and there I have also voiced the opinion that the East-Indian Company was responsible for this strange society in the Zuider Zee. Tintinnopsis fimbriata is another example of an endemic species whose closest relatives are in tropical waters. It does of course not correspond to Tintinnopsis Schotti in every detail: the conditions in the Zuider Zee which differ absolutely from those of the tropical seas have left their traces in this Tintinnopsis fimbriata. But I would like to mention that the shells of these two species

differ only in two characteristics: in the size (Schotti is formed somewhat more robust) and the oral rim. But these two particularities are always variable quantities in Tintinnoidea, and it is very easily possible that in the Zuider Zee natural selection has favoured among the total population of the species Tintinnopsis Schotti, a tribe which has now been given the species name Tintinnopsis fimbriata. Following these considerations then, Tintinnopsis fimbriata would just be identical with Tintinnopsis Schotti especially since the fringed edge (a secondary characteristic, formed as a result of activities of the animals) is not a certain species characteristic.

In this connection I have to refer to a critique which 327
Dr. Schuurmans Steckhoven (1931) has offered against my work just cited.

In my work, I also put forth the nematode Tricoma Steineri DeMann as a typical example: DeMann has described this species in the Zuider Zee in his work on the nematodes of the Zuider Zee (Flora and Fauna of the Zuider Zee, p. 259-260), and stated that it differs in only very minor characteristics from another species (Tricoma intermedia Steiner) which is known at the Gold Coast (Africa) where Dutch merchant vessels used to visit frequently in earlier times.

Schuurmans Steckhoven now tries to weaken my arguments by saying (p. 662): 'If Hofker had wanted to, he would doubtlessly have known that ubiquity is very common among nematodes, that in fact most genera of nematodes are ubiquitous, and that it is not proper to pick a single species from the many hundreds of species, in order to support this hypothesis. He should have known, furthermore, that the genus Tricoma was defined in Naples by Cobb while Allgen has proved, which also is clear from the literature that a fairly large number of Tricoma species occur in northern latitudes.'

Mr. Schuurmans-Steckhoven could now equally well start this polemics in regard to the case of Tintinnopsis fimbriata which I just analysed in more detail. It seems to be appropriate therefore at this juncture to illuminate Schuurmans-Steckhoven's comments more closely. We can see immediately that there are many genera of organisms (Tintinnopsis!) which are ubiquitous since most sea organisms belong to ubiquitous families. But are the species also ubiquitous? Only this question is of importance here. Within the genus Tintinnopsis there are very many northern species and many of these, quite naturally, also occur in the Zuider Zee. But here is this 'one single species', Tintinnopsis fimbriata whose nearest relatives are in the Pacific. This is what has to be explained; the fact that there are many northern species of the genus Tintinnopsis, or that the genus Tintinnopsis was actually first discovered in northern regions, has very little to do with the subject. The only crucial point is this: there is a species in the Zuider Zee whose nearest relative is tropical. And it even turns out that the Zuider Zee species constitutes probably only a 'geographical variant' of the tropical species (which is also very easily imaginable of Tricoma steineri DeMann). Indeed, when we now actually find that there are several such species (I know altogether 10 of them now), we have a real problem in front of us which it is well worth the trouble considering and, if possible, solving. One does not get away with the words (Schuurmans Steckhoven): 'This information is sufficient to show that the genus Tricoma is nothing less than tropical or Pacific, and must be considered as a normal ubiquitous genus. A verification of the other examples given by Hofker in support of his contention, seems to be desirable'. 328

Regarding the finer structure of the shell, let me add that the oral rim is very typical and has elsewhere been found only in Tintinnopsis Schotti. While the interior surface of the wall narrows somewhat towards the mouth, the outside surfaces actually bends outward, making it a

Y-shape in vertical section (Fig. 5b). The shells of dividing animals exhibit a strong accumulation of foreign material on this rim which has the effect that such shells frequently carry a veritable dam of foreign particles. In a few instances I found this dam formed into a lid but I could unfortunately not fix this material, and know no details of their contents (Fig. 9).

A rather large stalk bulges up in the centre of the ciliate spiral. It appears to be indented slightly on one side where the rather deep mouth of the cell is located. The organelles of the oral spiral are planted in a distinct peristomial rim: they begin at the base with a lamella which rapidly narrows and finally ends in the organelle which is somewhat fringed at the top (Fig. 6b). The organelles which reach into the mouth are somewhat more stoutly developed. Study of the peristomial rim on sections reveals, particularly directly below the organelles, a large quantity of very fine grains which are already visible in unstained preparations, and which stand out sharply with iron hematoxylin (Fig. 7). These grains also lie together in great quantities under the stalk, but on the side opposite the mouth. A pulsating vacuole seems to lie in the aboral half of the cell; it opens to the outside through a preformed canal (see the first of the three sections of Fig. 7). The major source of food in the Zuider Zee seems to be Ebria tripartita (Fig. 8).

The macronuclei correspond to the normal conditions in Tintinnoidea; the micronuclei are frequently surrounded by a light halo (shrinkage halo?). 329

Division appears to occur normally during the night. At any rate, I found very few (animals in) stages of division during the day.

Those which I did find exhibit the normal typus: first, the macronuclei with desmose join and finally form a single elongate sausage-like nucleus (this nucleus nestles

Fig. 7: Tintinnopsis fimbriata Meunier
Three sections of a specimen which clearly exhibits the fine grains of the collar. The collar of the lorica is also clearly shown. Technique: Trichloracetic acid, ironhematoxylin, paraffine sections, magnification 435:1.

Fig. 8: Tintinnopsis fimbriata Meunier
Section of an animal feeding on Ebria.
Technique: see Fig. 7; magnification 435:1

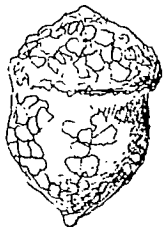


Fig. 9: Tintinnopsis fimbriata Meunier
Individual having developed a lid-like top.
Magnification 325:1.

very closely to the newly forming ciliate spiral); then the micronuclei divide, and finally the macronucleus as well. These two macronuclei are about to divide a second time when the final phase of the division of the whole cell takes place.

The animals in most samples looked quite healthy and lively (when observed alive), but there were also some samples which contained many animals with abnormalities of the protoplasm. These samples always contained very many empty shells, and they were usually found on warm summer days. When such samples are fixed and stained, and examined more closely, very typical aberrations are found. Since the micronuclei in normal cells were always very clearly visible with the methods I use, I noticed immediately that the micronuclei in the abnormal individuals often exhibited differences in number and stainability. While they are usually not surrounded by the hyaline halo, they frequently had one in these samples. But what is more 330
important is that the cell often appears to be smaller than usual, and in such cases small globular objects lie beside the animal in the lorica (Fig. 10). Something special seems to be taking place here since the excrements are usually very rapidly conveyed outside by the animals. Many of these animals which had such globules, exhibited division phases of the micronuclei, there frequently being three or four of them present, while no division of the macronuclei was evident. But often only one micronucleus was found, often also none at all. In some cases I was able to see an indentation at the aboral side of these animals which was filled with a small lump of protoplasm which clearly had a body very similar to a micronucleus. Finally, one finds loricae which contains 8 to 10 such globules and a larger lump of protoplasm, often still with vestigial cilia, which surrounds two marconuclei (Fig. 11). This must be considered to be the final phase of the strange process which I think I am able to reconstruct as follows.

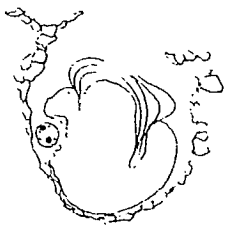


Fig. 10: Tintinnopsis fimbriata Meunier
Section of an animal with adjoining 'globular body'. Technique: as Fig. 7. Magnification 435:1.

Conditions still unknown to us trigger successive divisions of the micronuclei in Tintinnopsis fimbriata. These micronuclei surround themselves with protoplasma, bud off from the cell, and round out into small globular bodies which remain lying in the lorica. The animal eventually looses its micronuclei entirely, and subsequently dies. No parasitation of the globules inside the animals has ever been observed so that it is certain that these objects have nothing in common with the parasitic dinoflagellates Dubosquella tintinnicola found by Chatton (1929); they also do not at all possess the nuclei structure which is typical for dinoflagellates. But the process described here has many points in common with that described by Campbell (1926): Karyoclastis Tintinni. But it is also very easily possible that all the described formations are decomposition phenomena in the sense of a 'granular decomposition' which has been found in many infusorians. However, we know very little about the cause of this process although it has also been observed in tintinnoids by other authors (Campbell, l.c. p. 218). 331

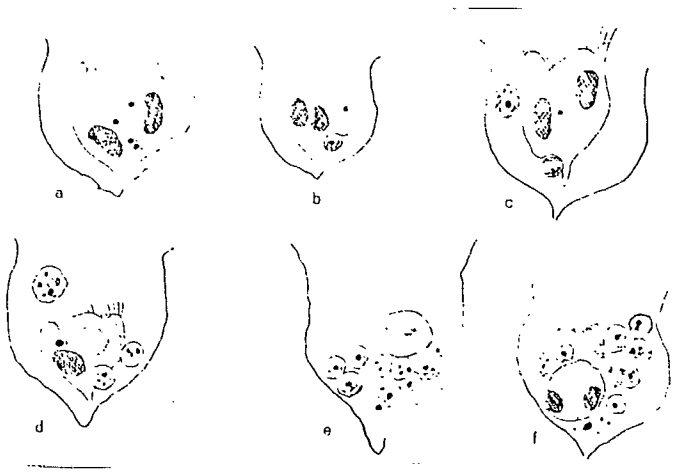


Fig. 11: Tintinnopsis fimbriata Meunier
Different phases of the formation of the 'globular body'. Technique: Trichloracetic acid. Ehrlich's hematoxylin. Magnification 325:1.

6. Tintinnopsis Iohmanni Lackmann (Fig. 12)

The lorica consists of two clearly distinguishable parts: a rather globuse housing which bottoms out in a blunt, entirely hollow point, and a stretched collar which does not widen and whose diameter is clearly somewhat less than that of the living compartment. The wall is covered with small, densely crowding, irregular particles providing an obvious means of differentiating them from Tintinnopsis tubulosa where they occur in the same sample; they are not only larger but also much less translucent. Length of the lorica: 80 to 115µm; length of the living compartment 332
60µm; width of the chamber: 60 to 78µm; length of the collar 15 to 50µm; width of the collar: 50 to 60µm.

The number of ciliate lamellae is 20 in all cases which I investigated. They are narrow and lie fairly close together. The two macronuclei usually show clearly a desmose (Fig. 14), usually have a long stretched form but less pronounced than is commonly the case in many other Tintinnoidea. There are also phases where they appear rounded in which case the desmose is not detectable. The two micronuclei are clearly

visible; their diameter ranges from 1 to 4 µm, and they are almost always nestled close to the micronucleus[+]. The cell is rather large and, withdrawn, fills the larger part of the spacious living compartment.

In 1922 I described (Flora and Fauna of the Zuider Zee, p. 175, Fig. 84) this species as Tintinnopsis turbo Meunier. It is possible that it is identical with the form described by Meunier. But the species Tintinnopsis lohmanni described by Laackmann also fits perfectly. I had pointed out even then the coincidence of these two species but had decided on the name Tintinnopsis turbo because, according to my investigations of 1920-1921, the species seemed to occur in the Zuider Zee only from June until October, and not during the winter months which Laackmann claims for the Bay of Kiel. But later finds lead me to conclude now that the species occurs in the Zuider Zee throughout the year, although it is most plentiful in late summer in the plankton samples, and frequently constitutes a considerable proportion of the plankton in the entire Zuider Zee. The species was found on the coast of Belgium by Meunier (although always in small amounts, and Meunier describes it only very incompletely while his illustration also suggests schematisation). It was found by Brandt in the Bay of Kiel.

It is certain that the species now precisely described by me, differs considerably from Tintinnopsis tubulosa which I was also able to study in the Zuider Zee. But Kofoid and Campbell nevertheless put it, together with most forms interpreted as Tintinnopsis tubulosa by other authors, under Tintinnopsis subacuta Jörgensen, a species established by Jörgensen. I must oppose this view vigorously; because I was able to observe several dividing specimens with the longest collars that I ever found (50µm long), but they never had the strongly elongated collars which are characteristic for 333
Nordquist's Tintinnopsis subacuta from the Gulf of Bothnia. But these dividing individuals must after all have fully

[+] Translator's Note: probably a printing error; should be 'macronucleus'.

matured loricae, and I cannot concur with the words of Kofoid and Campbell (p. 48): 'Tintinnopsis lohmanni Laackmann, Tintinnopsis macropus Meunier, and Tintinnopsis sp. Brandt are based on incomplete loricae'.

Thus we must stress categorically that the species from the Zuider Zee described here is identical with:
Tintinnopsis nucula Fol. Brandt (1906, Plankton Expedition, Plate 16, Fig. 3, Kaiser-Wilhelm Kanal),

Tintinnopsis sp. Brandt (1906, Plankton Expedition, Plate 17, Figs. 1 and 3, Kiel Fjord).

Tintinnopsis lohmanni Laackmann (1906, Bericht der Kommission für wissenschaftliche Untersuchung N.F. (?) (Report of the commission for the scientific investigation of N.F.), Volume 10, Section Kiel, p. 20; Plate 1 Fig. 10,11; Plate 2, Fig. 23, Bay of Kiel).

Tintinnopsis turbo Meunier (1919, Flemish Sea, p. 26, Plate 12, Fig. 27, Flemish coast; Hofker, Flora and Fauna of the Zuider Zee, p. 175, Fig. 84).

There is still the possibility that Tintinnopsis subacuta Jörgensen is also identical with Tintinnopsis lohmanni but most illustrations are too indistinct to be quite sure.

In some samples from the Zuider Zee Tintinnopsis lohmanni was found together with Tintinnopsis fimbriata, in other samples together with Tintinnopsis tubulosa, in large amounts, which made it possible to delimit these three species from each other very clearly. Tintinnopsis fimbriata always has the flared rim, Tintinnopsis lohmanni the globuse living compartment and heavy agglutination, but Tintinnopsis tubulosa has a living compartment which is not or only indistinctly differentiated from the collar part. The width of Tintinnopsis tubulosa in the Zuider Zee is furthermore always less than that of Tintinnopsis lohmanni. In the same magnification made with Abbe's drawing mirror, two outlines, one of Tintinnopsis lohmanni, the other of Tintinnopsis tubulosa, have widths of 57 and 47 mm respectively. 334

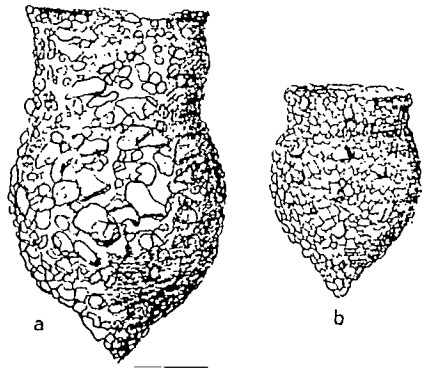


Fig. 12: Tintinnopsis lohmanni Laackmann. Two types of lorica. a magnification 387 1/2:1, b magnification 250:1. 331

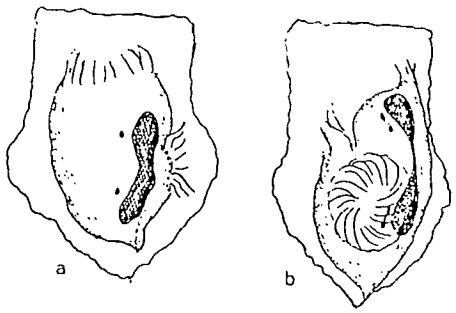


Fig. 13: Tintinnopsis lohmanni Lackmann Stages of division a beginning of division, b micronuclei divide as well. Technique: Trichloracetic acid, Ehrlich's hematoxylin. Magnification 325:1. 333

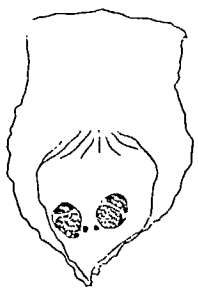


Fig. 14: Tintinnopsis lohmanni Laackmann Normal specimen. Technique: Trichloracetic acid, Ehrlich's hematoxylin. Magnification 325:1.

I have only little more to add (Fig. 13). I was able to determine the following regarding the division process: After the second spiral of organelles has formed on the side of the animal, the worm-shaped macronucleus which is now the only one approaches this spiral closely. In a second phase that I have found, the macronucleus is in the form of dumb-bells while the micronuclei have just completed their division. The division of the micronuclei thus seems to precede the division of the macronucleus.

Tintinnopsis beroidea Stein (Fig. 15)

The lorica is small, pointed at the bottom or with a more rounded point, joined to a globuse part, usually without concave transition, and a slight constriction above, either with a small indentation or gradual. The neck is usually strongly developed, clearly ringed, but sometimes missing entirely, resulting in large variations in overall length.

The lorica is more or less densely covered with foreign particles. Length 55 to 105µm; width of the actual lorica 40µm; width of the neck 33 to 35µm.

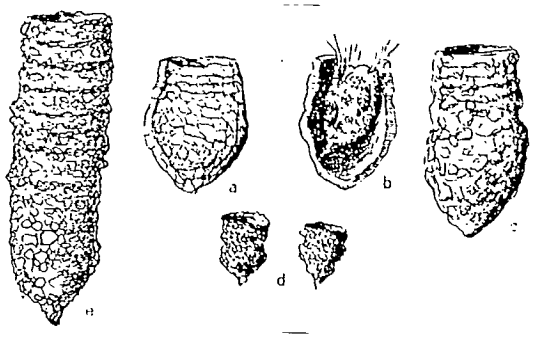


Fig. 15: Tintinnopsis beroidea Stein
Loricae and cells from the Zuider Zee.
a and b without neck, magnification 500:1;
c normally fully grown specimen, magnification 500:1; d forms which perhaps belong to the 'subspecies' parvula Jörgensen, magnified 180:1;
e individual with very long neck and sharp point, magnification 400:1.

The cell is rather compact and is attached in the side of the base section of the lorica, through a thin pedicle (Fig. 15b). The number of adoral membranelles is 16. Two macronuclei can be observed in the vegetative state; two micronuclei lie in close proximity to these. 335

In the specimens which I found in the Zuider Zee as well as those which I was able to study in Naples, the walls of the lorica was very thick. The individual foreign bodies were arranged in such a way that they join like building blocks and so are responsible for the even thickness of the wall; this is for instance not the case in Tintinnopsis fimbriata.

I found Tintinnopsis beroidea in the Zuider Zee on frequent occasions. It occurs here in masses particularly in spring and is during this period (February to May) almost the only tintinnoid species in this region. But later in the year it is also always present among the other species in the Zuider Zee. It can be found throughout the Zuider Zee from March until October, even in the vicinity of Amsterdam where I found it in September 1921 in conjugation.

In Naples I found it during March and April, often in large amounts; Brandt as well (1907) reports it at Naples, similarly Entz and Daday. It seems to be one of the more frequent species there as well.

I myself observed the species repeatedly in the North Sea (Scheveningen), particularly during Spring; van Breemen also (1905, p. 55) reports it from the North Sea coast (Helder, Waddensee). It is also reported to be common at the coast of Norway and in the Baltic Sea (Brandt, 1907 p. 138).

In Naples I had left a plankton sample overnight and kept it alive with the electrical stirrer. In the morning I found specimens in this sample which swam around without lorica but were encircled at the oral end by a wide belt which was already adorned with detritus relicts, and which obviously showed the beginning formation of the new shell (Fig. 16). On the previous evening the sample contained

almost exclusively animals of Tintinnopsis beroidea in all phases of division (Fig.17). This division always took place in long-stretched loricae. Just when the separation in the vicinity of the newly formed peristome begins, the macronucleus forms into a dumb-bell shape while the two micronuclei are in the process of division. Here too, then, 336
a merging of the two macronuclei took place before fission starts (Figs. 17a and b).

Another phase which I was able to study in Helder in August 1929 apparently precedes the stage described above: I found the new peristome already completely formed, beside it two macronuclei, both with desmoses which separated each of the two nuclei into a larger lighter staining and a smaller darker staining part. It seems then that here as well the desmose changes location before combination of the macronuclei takes place.

Important were the observations which I made late at night on March 7, 1930 in Naples (11 p.m.). Many of the Tintinnopsis beroidea in the sample collected at 9 p.m. exhibited a far advanced stage of division. The macronucleus was already split and the products of this division were about to divide again. Two micronuclei could be found at the same time.

It then appeared that the upper half (neck part) of the mother lorica surrounded the emerging individual and separated from the mother lorica along a softened perimeter. This is probably the effect which creates the 'rings' of the new individuals (Figs. 17c and d).

Some of the animals were also studied in longitudinal section (stained with hematoxylin according to Heidenhain). The organelles exhibited a fairly complex habitus. They carry combs along the inside while the outside is smooth with a 337
band which stains darker. The peristomial ring ('the collar' according to G. Entz jr. 1907, p. 134) on which they stand is full of granules which colour it dark. The mouth is a shallow, narrow indentation, the pistil is only weakly developed. A distinct row of relatively short cilia runs

down along the side furthest removed from the mouth; the cilia are associated with a row of basal granules (Fig. 17A). The wall of the lorica shows no signs of primitive alveoli in section as were described by Brandt (p. 132). I did not find them on the living material either. Geza Entz jr. (1907, p.106) was also unable to detect them.

Stein claims that rows of cilia extend along the entire body surface of Tintinnopsis beroidea. Entz jr. (p. 149) also claims to have observed these cilia both on the living animal and in sections.

The conjugation of Tintinnopsis beroidea seems to be readily accessible to observation. Laackmann at any rate illustrated a few phases (1906, Figs. 51 and 52). I was also able to study some of these phases in Naples in stained specimens. One partner contained three micronuclei while the other had five, or both partners had four each. The final stage (after separation) is, according to Laackmann's observations, that the individual has two micronuclei. It is thus possible that a fusion of the micronuclei has taken place. 338

The literature on Tintinnopsis beroidea is extremely rich but also rather confused because many other species were probably taken for Tintinnopsis beroidea. For instance Kofoid and Campbell (1929, p. 28 where most of the literature is listed: we are only missing references to van Breemen, 1907 and Hofker, 1922, p. 173, Fig. 82a-d) hold the view that one should strictly differentiate between Tintinnopsis beroidea Stein, emend. Entz jr., emend. Jörgensen and Tintinnopsis parvula Jörgensen. If this assumption were correct, the animals found in the Zuider Zee would probably have to be identified as Tintinnopsis parvula while the specimens from Naples would no doubt be included among Tintinnopsis beroidea emend. But I believe that the differences are too minor after all, and only relate to the lorica; we should abstain from this differentiation until cell characteristics can be drawn upon. But such cell differences

will probably not be detectable; at least I did not find them. I found 'Tintinnopsis parvula' frequently during the summer months at den Helder and in the vicinity of Scheveningen.

Fig. 16: Tintinnopsis beroidea Stein 335
Young animal in the process of building a new shell. Magnification 400:1.

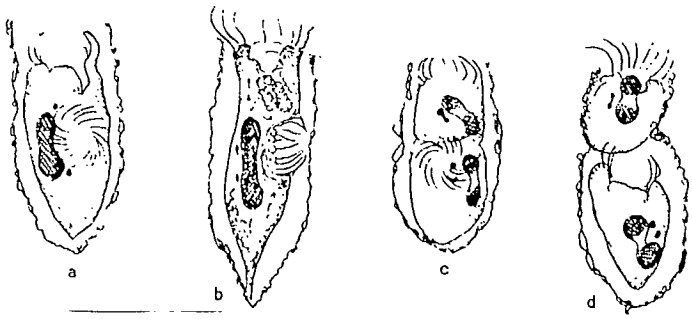


Fig. 17: Tintinnopsis beroidea Stein 336
Various phases of division; from the Gulf of Naples. Technique: trichloracetic acid, Ehrlich's hematoxylin
a start of division, simple macronucleus
b division of the macronuclei;
c separation
d the animal which swims away surrounds itself with the neck part of the mother lorica which forms the 'ring'. Magnification 400:1.

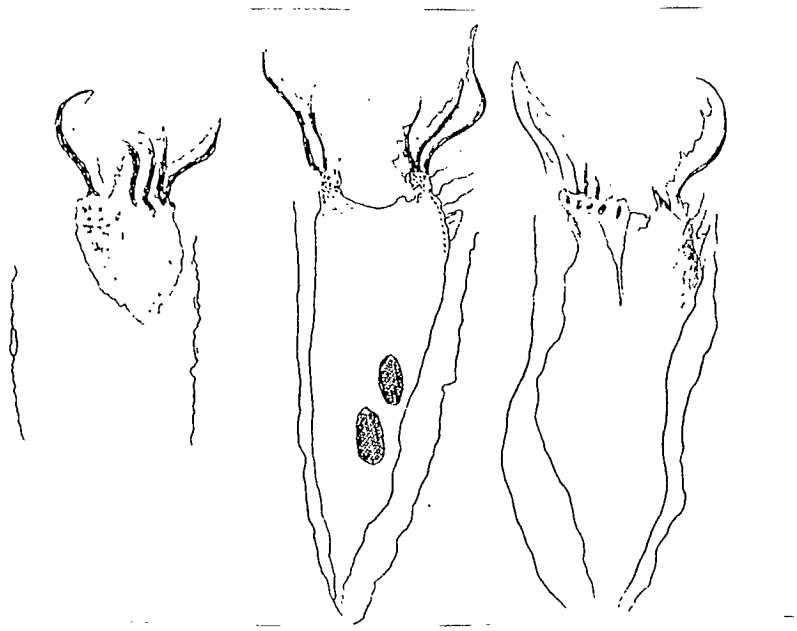


Fig. 17A: Tintinnopsis beroidea Stein
Three successive longitudinal sections through the cell. Technique: trichloracetic acid, iron hematoxylin, paraffin. The organelles show a darkly tinged band along their outside; basal bodies of the lateral row of cilia (centre figure). Magnification 625:1. 337

7. Tintinnopsis tubulosa Levander (Fig. 18)

Loricae rather long, either rounded bottom or with a small point. The wall of the lorica is thin and relatively sparsely covered with foreign particles with the result that some portions of the lorica are naked. Most of the loricae in the North Sea are not pointed, but those in the Zuider Zee usually are. The neck part is only very slightly narrower compared with the living compartment. The longer loricae are ringed irregularly. 338

The length of the lorica varies widely: 65 to 100µm; width of the bowl 49.5 to 52.5µm; width of the neck 45 to 49µm. The cell is stretched fairly long when the animal is swimming, and is usually attached at the bottom of the lorica. Two macronuclei and two micronuclei. 339
Contractile vacuole in the posterior part of the animal.

This form was found quite frequently in the Zuider Zee, both in the salty and the brackish part of this bay, but never in the same large quantities as Tintinnopsis fimbriata or Tintinnopsis beroidea.

It could be mistaken for Codonella lacustris forma laevis Entz, because of its habitus; but I do not believe that it is identical. At any rate, it is a true Tintinnopsis because the 'Schliessaparat' (interlocking circle of membranelles) is completely missing, and the wall structure is also different. Faure-Fremiet has already said this for the typical sweet water species Tintinnopsis lacustris (1924, p. 89). Kofoid-Campbell gather under Tintinnopsis tubulosa Levander emnd. only those forms which lack the aboral point. The other forms are classified by these authors (p. 48) as Tintinnopsis tubulosoides Meunier and Tintinnopsis subacuta Jörgensen. The latter is also assumed to include Tintinnopsis lohmanni Laackmann; I have already made the point that this is erroneus since it is not true that Tintinnopsis lohmanni is based on incomplete loricae. But this would mean that these animals which surely belong to one and the same species would have to be named Tintinnopsis tubulosoides in one case and Tintinnopsis subacuta in the other, because the loricae from the Zuider Zee sometimes have a clearly globuse living compartment, and sometimes a stretched lorica. It seems to me preferable then not to maintain this disitinction, especially since I was able to observe many animals from the North Sea which were identical with the 'species' Tintinnopsis tubulosoides established by Meunier, together with loricae which clearly had a pointed bttom.

Fig. 18: Tintinnopsis tubulosa Levander.
Two forms from the Zuider Zee. Magnification 300:1

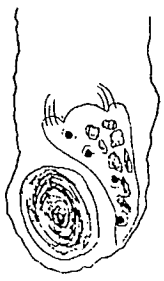


Fig. 18A: Tintinnopsis tubulosa Levander
Abnormal individual which contains a large body of a concentric structure in the lorica; has a degenerated macronucleus and four micronuclei; from the Zuider Zee. Magnification 300:1.

I come to the conclusion then that Tintinnopsis tubulosoides Meunier (also Tintinnopsis karajacensis Brandt partim) and Tintinnopsis subacuta can only be synonyms of Tintinnopsis subacuta Levander. 340

Bibliographical Notes

Levander, K.M. (1900): Acta Soc. Fauna Flora Fenn., Volume 18, p. 18-19, Fig. 4-5.

Hofker, J. (1922): Fauna and Flora of the Zuider Zee, p. 174, Fig. 83

Kofoid and Campbell (1929): Conspectus p. 47-49, Figs. 66, 39,74; here also most of the literature references.

8. Tintinnopsis nana Lohman (Fig. 19)

Lorica very small, 30 to 45µm long, 12-15µm broad, bottom usually bluntly rounded or conically pointed, either heavily agglutinated or covered with only few foreign particles. Two macronuclei, two micronuclei. The animals leave their loricae very early when the environment becomes unfavourable. As a result, only empty loricae are often found in plankton catches. Only more frequently encountered in centrifuged plankton. It is a species of which still only little is known. It occurs frequently in the spring in the catches in the North Sea (Scheveningen), was found by myself repeatedly in the salty part of the Zuider Zee from June until September, by Lohman in the Bay of Kiel, and also by van Breemen in the Zuider Zee. It is probably identical with Tintinnopsis fistularis Meunier under which name I described it in the Zuider Zee (1922, p.1173, Fig. 81), although van Goor denies this identity (1923, p.168). It is quite likely that such small tintinnoids have also been found elsewhere but were only observed now and then because of their small size. In particular Tintinnopsis minuta Wailes which was raised to the rank of a separate species by Kofoid-Campbell probably also belongs to Tintinnopsis nana. The differences are at any rate not very pronounced, and nothing is known about the cell of tnis Tintinnopsis minuta so that great caution seems to be appropriate.

Bibliographical Notes

Kofoid-Campbell (1929): Conspectus p. 40-41, Fig. 15 and 16

Hofker, J. (1922): Flora and Fauna of the Zuider Zee, p. 173, Fig. 81.

Van Goor, A.C.J. (1923): p.167-168.

Fig. 19: Tintinnopsis nana Lohman
Several specimens from the Zuider Zee.
Magnification 300:1.

9. Tintinnopsis campanula (Ehrbg.) (Figs. 20 and 21)

I was able to study this typically neritic species in many stages and in quantities of thousands: it is one of the most frequent species in the northern part of the Zuider Zee, in Helder, in the vicinity of Scheveningen, and finally also in the Gulf of Naples. 341

For reasons to be discussed below I also include in the species Tintinnopsis campanula the forms cincta, bütschlii, campanella, cyathus etc. which are described by Brandt and others as variants, by Kofoid-Campbell as separate species. This will also be evident from my description. 342

In the ordinary form, the lorica has the form of a Christmas bell. The hollow stem is joined rather abruptly to the living compartment proper which has a globuse posterior part and gradually ends in a more or less developed flare. This flare consists of a spiral band. The wall of the shell is relatively thin with many foreign particles attached, particularly on the flare.

Often it is possible to encounter differently developed forms in the same sample: but the'normal' form is never absent as far as I have noticed (and Brandt also notices it). Occasionally the flare is only very weakly developed and only a rather straight neck part is observed. In these forms particularly the flare often has a rim bent inward

which was first observed by Geza Entz jr. (1909, Plate 8, Fig. 8). The wide rim then often carries a large number of foreign particles which gives the effect of a thick opaque collar around the lorica. This form was named Tintinnopsis infundibulum Daday and cincta (Clap. et Lachm.). In other cases, the pointed bottom is absent, giving the shell a completely rounded aspect. This form is called Tintinnopsis bütschlii when it has a wide flare, and Tintinnopsis cyathus when the flare is less fully developed.

The cell is relatively small, especially when it is withdrawn, and occupies only part of the living compartment. Swimming, it forms a long stalk which is almost always attached near the tip. The number of organelles is always 20. The peristomial rim surrounds a mobile pistil which often twitches lively; the collar is fairly high.

The organelles are broad blades, three times as high as they 343
are wide, with a pointed triangular shape. The peristomial rim carries several rows of very long cilia on its outside which are situated circumorally. They are generally longer than the organelles. Between the organelles themselves we find, alternating with these, peculiar club-like formations which are probably homologous with the 'cover lamellae' of G. Entz jr. They seem to be capable of being drawn in (Figs. 22 and 23).

On the side closest to the buccal cavity an oblique row of rather stout cilia runs along the body, from the long cilia to the cytopyge. On the opposite side there is a papilla which is located below the row of long cilia.

I shall name the proper organelles arranged spirally 344
around the mouth the adoral organelles. The long, thin cilia outside the adoral ring I call circumperistomial cilia. The club-like objects will be called clavicles, and the rows of stouter cilia which run from the cytopyge upwards I shall call lateral ciliate band. The papilla is called lateral papilla.

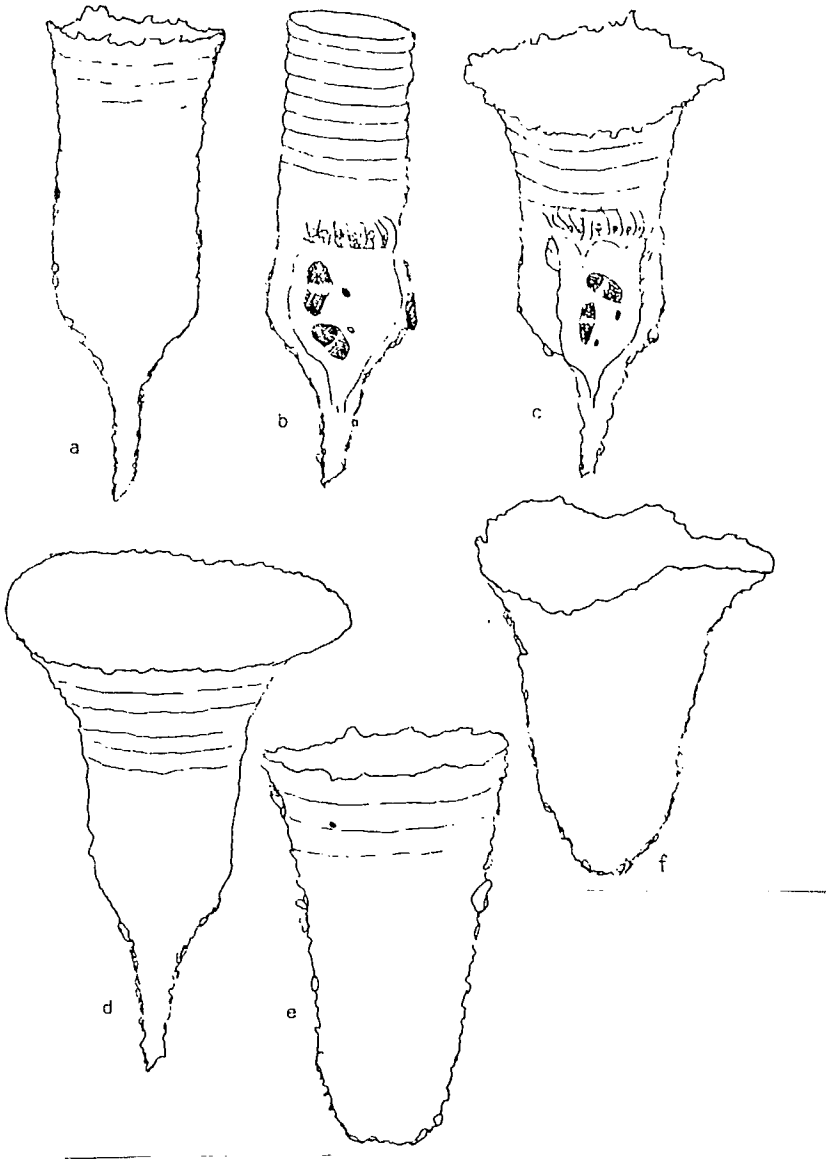


Fig. 20: Tintinnopsis campanula (Ehrbg). 341
Six different forms such as were found together in a single plankton sample at Naples (March 27, 1930).
a var. elongata v. Daday,
b var. lindeni v. Daday,
c campanula s.s. Ehrbg.,
d var. cincta v. Daday,
e var. cyathus v. Daday,
f var. bütschlii v. Daday.

Magnification 325:1.

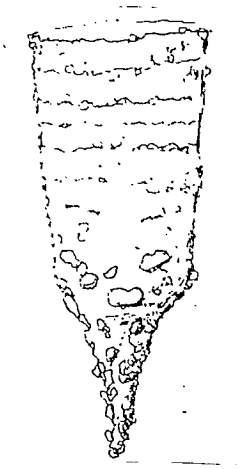


Fig. 21: Tintinnopsis campanula (Ehrbg.) 342
The form described by Entz sr. as Tintinnopsis urniger. Gulf of Naples. March 5, 1930.
Magnification 325:1.

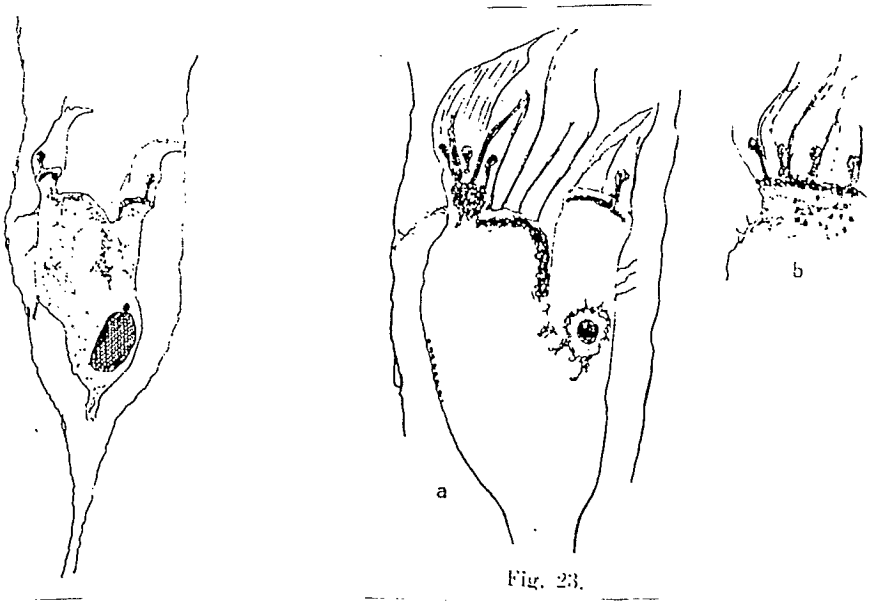


Fig. 23.

Fig. 22: Tintinnopsis campanula (Ehrbg.). 343
Longitudinal section of an animal with micro- and macronucleus, organelles, associated combs, and hint of a lateral row of cilia. Parts of the 'neuromotorium' can also be seen, as dark granulation. Technique: trichloracetic acid, iron hematoxylin, paraffin; Magnification 425:1.

Fig. 23: Tintinnopsis campanula (Ehrbg.)
a Longitudinal section showing the arrangement of the organelles, dark staining of the pistil, lateral row of cilia (basal bodies) and micronucleus.
b Tangential section throught the peristomial rim, with organelles, associated combs (small clubs), 'neuromotoric' granulation.
Both sections: Magnification 625:1, technique as Fig. 22.

Tintinnopsis campanula (often together with those forms interpreted by me as variants) occurs in the Zuider Zee only in the salty northern part, during July and August. Here it appears in the typical campanula form while the specimens caught at the same time in the North Sea (Scheveningen) were identical with Tintinnopsis cincta described by Brandt. In den Helder I observed Tintinnopsis campanula in the spring as in the summer (but it appears to be found in the largest amounts during the summer months there). I found many forms, often mixed together, mostly Tintinnopsis campanula and Tintinnopsis bütschlii. I was able to observe the same thing in Naples where I found together: Tintinnopsis urniger, Tintinnopsis cyathus, Tintinnopsis bütschlii, Tintinnopsis campanula, Tintinnopsis infundibulum, Tintinnopsis cincta, Tintinnopsis lindeni (e.g. on March 27, 1930). Other authors too found this whole assemblage there (Daday).

The species (with its various forms) is known in the Atlantic Ocen, the Mediterranean, and the Baltic Sea.

The literature is referenced best in the Conspectus by Kofoid and Campbell, p. 29 (Tintinnopsis bütschlii Daday), p. 30 (Tintinnopsis campanula (Ehrbg.) Daday emend.), p.31 (Tintinnopsis cincta (Clap. et Lachm.) Daday emend.), p.32, Tintinnopsis cyathus Daday emend.). Brandt also (1907, Plankton Expedition p. 146) lists the more important literature up to 1907. I would also like to mention my own work (1922, Flora and Fauna of the Zuider Zee, p. 177, Fig. 86).

Comparing the size of the lorica with that of the cell we immediately notice the large difference between them: the body is small and tumbles around in the spacious lorica, continuously twisting and turning around its pedicle. We cannot help asking how this small body was able to build the spacious lorica. This question entered my head each time I observed Tintinnopsis campanula. I believe to have solved

it completely now. (See also my remarks in my article: The formation of the tests of Tintinnidae; Tijdschrift der Nederlands Dierkundig Vereeniging (Journal of the Dutch Zoological Society), Series 3, Volume 2, 1931, p.4 and 5; also Fig. 24).

First of all, I have to point out the following. When we 345
study the fission of the tintinnids we have to conclude that of the two individuals emerging from the fission, one obtains the new peristome but the old lorica while the other retains the old peristome but must by necessity form a new lorica.

We would further like to point out a fact known to researchers of tintinnids: that the animals frequently leave their lorica and swim about freely. Do these animals after they have left their old shell also form a new lorica? It is likely that they do. Finally it is said that tintinnids form permanent spores. The new animals growing from the spores also must build new loricae. By this reasoning it becomes clear that one may expect different forms, especially different starting forms of the lorica which the animals in each of these cases must build. Thus different forms of loricae may be expected in a single species. Now this in fact is the case with Tintinnopsis campanula, a species which has been studied sufficiently. We do find different forms here at the same time. Only, I must clarify once and for all, that only the original part of the shell is relevant in these considerations since the part which has the spiral rings is only sculpted later by the animal living in the lorica.

In Naples I was able to differentiate three forms with respect to the lower part of the lorica:

a) One form which is known as Tintinnopsis elongata Daday in the literature (see Kofoid-Campbell, p.34, Fig. 80). The hollow point is quite spacious, the lorica does not broaden quickly above this until, with progressing age of the shell (spiral strips!) it gradually increases in width without forming a flare.

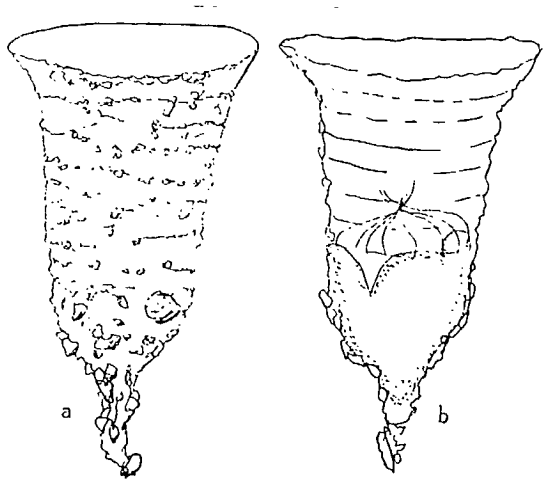


Fig. 24: Tintinnopsis campanula (Ehrbg.)
This drawing shows how the size of the animal's body corresponds to the size of the ringed part of the lorica.
a) Outside of lorica,
b) the same lorica with withdrawn body shown.
Coast of Holland, near den Helder.
Magnification 325:1.

346

These animals showed no signs of a recent fission (desmose was present.) and my guess is now that these animals without loricae are individuals which for whatever reason had left their normal (Tintinnopsis campanula-) lorica (an effect frequently enough observed in the laboratory), and were now in the process of forming a new shell. This new shell was structured like that of Tintinnopsis bütschlii because of the oropetal direction of construction, and the rounding of the freely swimming animals: this is the reason why there were many individuals of this 'species' in the plankton.

348

We thus reach the important conclusion that the subspecies which possess Tintinnopsis campanula-like primary loricae (the ones named under b) and those which possess

This accumulation usually coincides with the formation of an interior collar as described earlier. But it is now very well possible that this interior collar and the accumulation of material merely serve to supply the material for the largest part of the primary lorica if we can call the lower part of the shell that for now. The duaghter animal separates from the mother animal which remains in the shell, and fits inside this interior collar; the latter separates from the flare and forms the upper part (Meuniers' 'ring') of the new test. The lower part is subsequently formed by secretions of the body. And since this part of the body has a pointed shape as a result of the fission, most Tintinnopsis tests also develop a more or less pronounced pointed form, as is the case with Tintinnopsis campanula. It might very well be true to say that the formation of the posterior end of the primary casing starts later in species which as a rule do not develop a pointed bottom (which is probably very rarely the case in Tintinnopsis) than in the species where a point is the rule, so that in those species the bottom part of the cell has had a chance to round itself out. It is also possible that in these species, as in the Stenosomella-species to be discussed below, the body as a result of its density becomes round quickly once the separation is complete.

But then I have also observed another phenomenon. On July 11, 1921 I found a very large number of Tintinnopsis bütschlii in plankton from the vicinity of Scheveningen (North Sea). And not only in Scheveningen, in Den Helder as well (on July 21, 1921) very many animals of this 'subspecies' were found. And curiously, among these individuals covered with loricae there were many ciliates the structure of whose bodies perfectly matched that of Tintinnopsis campanula but which had no loricae. They had the normal complement of nuclei (two micronuclei and two macronuclei, the latter usually with desmose). Most of these individuals had a strongly diffractive pellicle which contained clearly visible 'foreign particles', particularly at the usually blunt posterior end (Fig. 24A).

b) one form which differs from the first in that the hollow point appears to be less spacious; the lorica grows rapidly in width like a chalice, then less rapidly until it suddenly widens into a flare. It is called Tintinnopsis campanula if the flare is wide, Tintinnopsis infundibulum if it is less broad.

c) the forms where the lorica does not have a pointed bottom. They are known as Tintinnopsis bütschlii when they have a wide flare, Tintinnopsis cyathus with a less pronounced flare.

At the zoological station of Den Helder I was able one evening in the summer of 1929 to catch a large number of 346
Tintinnopsis campanula (It was a very cold summer, and the temperature was favourable for keeping tintinnids alive for a prolonged period). I put them in open containers under a bell-glass, and noticed that, as is usually the case in the evening, quite many animals were in the process of dividing as evidenced by the formation of second lateral peristomes. On the following morning most of the tintinnids were still very much alive and were merrily swimming around. But particularly at the water surface there were many individuals which were surrounded by a short lorica completely identical to the lower end of the lorica of a Tintinnopsis campanula. It was just as if the part formed by the spiral strip was missing. I thought that they were adolescent specimens, and was able to totally confirm this observation in Naples where an electric stirring apparatus was available to myself. There are still two things we must remember. First, it is easily observed that the body of Tintinnopsis campanula, contracted but not fixed (which more or less reduces its size) fits precisely into the space which is formed by that part of the lorica which is found at the bottom, and not formed by the spiral band; this means it is the primary part (Fig. 24).

Secondly, when observing dividing individuals of Tintinnopsis campanula one very often finds fairly large accumulations of detritus material along the adoral rim.

Tintinnopsis bütschlii-like primary loricae (those named under c) are probably the result of a difference in the time of formation of the shell (the first after fission, the second after leaving their old loricae), and are not the result of a difference in hereditary factors. At the same time we must also account for the fact that after fission (which almost always takes place during the night) one half lives in the old lorica, the other half in a new one. But this new lorica may be formed under entirely different circumstances (temperature, water movement, salt content (rain., etc.) than the old lorica which may frequently be quite old indeed. These circumstances may also increase the variability of the primary lorica. Does this perhaps explain the shells mentioned under a? Or did they originate from permanent spores? At any rate, it is sufficiently evident that it is not proper to give species names to the various forms of shells, something the more recent autnors are only doing too readily. This is not the first occasion where the various forms, Tintinnopsis campanula, Tintinnopsis bütschlii, Tintinnopsis cincta, and Tintinnopsis cyathus are understood to be subspecies of a single species. Hansen-Ostenfeld (1916) already advocated this view. I must refute Faure-Fremiet's opinion that adoral lip and body cilia constitute important differences between Tintinnopsis bütschlii and Tintinnopsis campanula, perhaps because the body cilia are very variable and contractile, and the lips show only very minor differences.

The formation of that part of the shell which consists of the spiral band, seems to take place somewhat later. The comparatively very few loricae which give an unfinished impression seem to point to the fact that the formation of 349
this part takes place in a single manipulation.
In Naples I saw on a few occasions animals which slowly rotated around their axes inside the lorica while they were completely stretched. At the edge of the - possibly not completely finished - lorica, the lateral papilla

mentioned earlier seemed to secrete a slimy substance which seemed to harden very rapidly in the water. It was forming an irregular margin along the edge of the lorica. Were these animals in the process of forming the spiral margin? In this case the lateral papilla seems to have a function.

Finally I must mention another observation which I made in Naples, regarding the accumulation of foreign particles on the outside of the shell. I described it before (Tijdschrift der Nederlands Dierkundige Vereeniging (Journal of the Dutch Zoological Society), 1931, Series 3, Volume 2, p. 148, Figs. 10-12); I quote:

' The just released fecal ball is not carried away by the lateral band of cilia because they do not reach as far as the cytopyge, but it remains lying there, covered all around by a sticky substance. A strip is formed from the same sticky, somewhat grainy substance, probably a secretion of the pellicular layer. This strip reaches all the way to the row of lateral cilia.'

' Suddenly the animal bends, fully stretched, against the side opposite the row of lateral cilia. As a result, the strip which is now solidified is grabbed by the long circumoral cilia and pushed through the mouth of the shell. The animal then leans over toward the opposite edge of the shell, and the strip is brought along the outside of the shell. The still sticky substance then cements the fecal ball to a point on the casing'(Fig. 25).

Fig. 24A: Tintinnopsis campanula (Ehrbg.)
Freely swimming individual, in the process of forming a new lorica. Coast of Holland, July 1921. Technique:Trichloracetic acid, Ehrlich's hematoxylin. Magnified 325:1.

The lorica stains light pink with the method of Borrel: but many of the 'foreign particles' stain dark red: they do not join together, something which (genuinely) foreign particles generally do. I conclude from this that these red-staining bodies are of organic origin. This is not strange at all since we know already that the fecal balls are cemented together by a gelatinous, certainly pellicular substance. This also explains at the same time why for instance Brandt found the primary alveoli on most of the foreign particles of the Tintinnopsis species (1907, p. 127): the genuine foreign particles are after all completely covered by an organic cement, and this substance has undergone a solidification process which has as a result the 350
alveolar structure. When these loricae are more highly magnified one discovers that the tip of the point of the lorica remains open. This would doubtlessly be important for the taxonomy. I was, however, unable to detect primary alveoli such as Brandt is reported to have found, not even in the organic foreign particles. The ringed structure of the neck section is only very weakly differentiated by this method of staining.

Now that we have learned this and that about the lorica of Tintinnopsis campanula, let us return once more to the cell proper. First some more details on the structure of the protoplasm. Longitudinal microsections (3µm, staining with iron hematoxylin and eosin) have shown that the clavicles stain rather well and are very homogenous, without having a proper granular structure. A dark tinging band is visible in the adoral organelles, which carry on their outside and in the adoral peristomial rim a stainable band which in each case connects to the next organelle via a string of granules which stain slightly less dark. There is also a stainable layer of dense plasma just below the 351
surface of the pistil. I was, however, never able to detect a proper neuromotorium, not even in preparations of complete specimens.

Faure-Fremiet describes, under somatic cilia, also a clearly formed field of cilia on the aboral side of the animal. Although I was never able to unambiguously observe this field on the living animal, I did find on one section a row of basal bodies on the aboral side of the body. This row of basal bodies is identical with that illustrated by Faure-Fremiet (1924, p.91, Fig. 29), unless it is the initial stage of a daughter peristome. But I could not find the cilia which other wise were well preserved on the preparations.

Fission seems to take place in the same manner as I have described already for other Tintinnoidea. The desmose indicates the beginning of fission. Most animals which exhibit a desmose also have already the laterally developed second peristome. The desmose which starts in the center of the nucleus soon drifts towards one pole of the macronucleus until only a darkly tinging end finally remains. The macronuclei fuse at these poles and soon form a homogenous, sausage-like object with the micronuclei near the two ends. These then divide, and the division of the macronucleus also starts. In the meantime, the cell acquires a somewhat crooked hour-glass shape, with the second peristomeforming the upper end of the lower part. After the two micronuclei have divided, a second division of the two recently formed macronuclei takes place. Everything looks as though the micronuclei are divided among the daughter animals in such a way that the two fragments of one micronucleus end up in one daughter while the parts of the other micronucleus are attributed to the other. Geza Entz jr., (1909,p. 162) thinks to have observed 10 to 12 micronuclei in animals which were in the process of forming a new peristome. I have searched for such evidence in my very extensive material, without success. But it is possible to find a number of formations similar to basal bodies in the vicinity of the developing peristome although they are much smaller than the micronuclei which are also clearly visible.

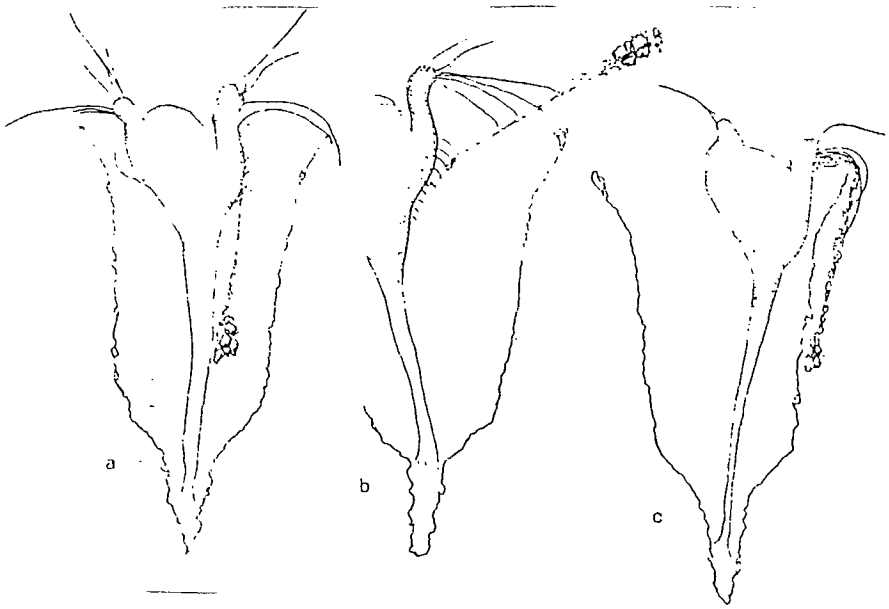


Fig. 25: Tintinnopsis campanula (Ehrbg.)
The illustrations show three consecutive phases of the attachment of foreign particles on the outside of the shell. a) The fecal ball is still inside the lorica, b) the strip of pellicular substance, including the fecal ball, is moved outside, c) the fecal ball is attached to the outside of the shell. Naples. Magnification 325:1. 350

10. Codonella galea Haeckel

I was able to study several individuals of this species in Naples. They constitute one of the most frequently occurring species in spring. 352
The loricae are relatively small (e.g. compared to Codonella nationalis and cistellula) and are always (in the Gulf of Naples) covered with foreign particles (this is not reported by Brandt, 1907, p. 89-90 with respect to his specimens).

The living compartment is clearly longer than broad, with the greatest lateral dimension slightly above the centre. It narrows a little towards the mouth (Fig. 26). As a result, the collar part is sharply separated from the living compartment itself. This collar is conical, without doubling of the oral rim, and has a very thin wall. It is always wide open, and wider at the top than at the mouth of the living compartment. There are almost always more particles deposited on the wall of the living compartment than on the collar. The collar is never ringed.

Length of living chamber:	appr.	100µm
Length of entire casing:	appr.	120µm
Width of living chamber:	appr.	75µm
Width of mouth of living chamber :	appr.	50µm
Width of mouth of collar:	appr.	70µm

A 'Schliessapparat' (set of interlocking membranellae) consisting of about twelve lamellae seems to be present in most cases. But the agglutination of the shell frequently makes it extremely difficult to observe it (the Schliessapparat). However, I also was able to detect one on living specimens.

The number of macronuclei is always eight in the vegetative state. I was unfortunately unable to determine the number of micronuclei. Geza Entz (1909, p. 163) quotes widely varying numbers, from 2 to 10, for the macronuclei. The fairly large material that I have studied definitely showed eight macronuclei in every case. According to v. Daday, the number of macronuclei ranges from 8 to 22. Brandt also (1907, p. 75) mentions eight small nuclei.

The body can stretch quite far out of the lorica, in which case it becomes very slender while the peristome always keeps the same width, and fine longitudinal lines appear on the lateral pellicle. The number of fairly stout pektinellae is probably 12 or 14 (although v. Daday mentions

18 ciliate lamellae which may very well be correct: I was not able to determine the number precisely because of the 353
'Schliessapparat'). On fully extended animals a strip of lateral cilia which are long and stout, are clearly observable. These again serve the agglutination of particles when the animal bends around the neck and attaches the feces which are whirled up by the strip (Fig. 27). When the animal is swimming, these cilia usually remain motionless and turned towards the adoral side (Fig. 28). The animal must always lean far around the oral rim in order to reach the wall of the lorica, to attach the particles. The collar consequently only rarely comes in contact with the topmost cilia which do the attaching. This explains the small number of particles which are found there (Fig. 26).

A few times I was able to observe stages of fission and noticed that fission proceeds quite similarly to that of Tintinnopsis campanula and Tintinnopsis beroidea for instance. The macronuclei merge into one body which separates into the shape of dumb-bells. Then, before the cell splits, another division takes place. At this stage there are two micronuclei and two macronuclei in each of the two newly formed individuals. The macronuclei at any rate divide a few more times until there are eight of them. The micronuclei probably behave differently and do not divide any further and thus probably remain two in number in the vegetative state although I was not able to determine this in more detail.

The literature on Codonella galea is rather confused. The species from Naples which I have described is probably not identical with Codonella lagenula Clap. et Lachm. because its dimensions are much larger. But it occurs very regularly in Naples, and, particularly with its particles, can 354
never be confused with another Codonella species. The sharply defined but never doubled collar is also very characteristic.

Fig. 26: Codonella galea Haeckel
Shell from Naples (February 25, 1930) 352
Magnification 325:1.

Fig. 27: Codonella galea Haeckel
The animal leans out of the lorica in order to 353
attach the particles with the aid of the lateral
cilia.

Fig. 28: Codonella galea Haeckel
Swimming animal. The lateral cilia are
motionless.

Kofoid and Campbell list this form as a new species under the name of Codonella aspera (Conspectus, p.55-56, Fig. 101) probably to take account of the attached particles. Their description which corresponds exactly with my own follows, and I quote:

> "Lorica stout ovate; collar 0,91 width of bowl, flaring 15°, 0,24 total length in length, slightly convex outwardly; bowl rotund ovate; aboral end rather broadly rounded, or slightly contracted; no projecting aboral point; wall often includes coarse particles. Length 85–90 μ. The type locality, is off Villefranche-sur-Mer in the Mediterranean. Occurs also in the Strait of Messina, the Mediterranean, and the California Current, off San Diego. Differs from *Codonella elongata* in more rotund bowl, less pointed aboral end, more convexity of the collar, and coarser particles included in the wall".

This separation of Codonella aspera from Codonella galea has many good points; but it must be viewed with great caution since the differences in the shells are fairly minor, and both the shape of the collar and particularly the agglutination, certainly depend very much on extraneous influences.

11. Codonella cistellula (Fol) Brandt

This characteristic species is also found in the vicinity of Naples during spring in very large quantities, but is never constant. Some times it is caught in large numbers, on the following day it may have disappeared.

The shells only rarely carry accumulations of particles, and what particles there are are generally deposited on the double rim of the collar (Fig. 29b). The wall is of a yellow hue and consists of two lamellae which are connected by alveoli. On microsections this shows up as cross links in the wall. The lorica consists of a living compartment which is more or less spherical, and a collar part which first widens and then suddenly narrows again.

At this junction a sharp ridge appears on the outside, making the rim of the collar look doubled. Fixed individuals very frequently exhibit , as a result of shrinking, a thin skin which has separated from the inside of the shell and now hangs between the wall of the shell and the cell body (Fig. 29a). This wall continues into the 'Schliessapparat' 355
(interlocking set of membranellae) without further transition. This suggests that the animal, after having formed the lorica proper, produces a second pellicular secretion which surrounds the body like a pouch and only leaves the buccal part uncovered. This pouch develops fringes at the open end, and thus forms the 'Schliessapparat' which consists of a fairly constant number of membranelles which fold inward when the animal withdraws completely inside the lorica. There are on the average twelve of these membranelles. A few times I observed animals which were in the process of tearing themselves loose from their shells. It could clearly be seen then that the pouch remained attached to the lorica at the bottom, with the result that the animal also freed itself from the bag. When the animals are observed under a cover of glass for an extended period, one can see the animal slowly withdraw into the lorica because of lack of oxygen, but the 'Schliessapparat' does not close. It actually remains wide open although slightly folded. This observation indicates that the mouth of the 'Schliessapparat' is not directly joined to the body of the animal, and that closure is very probably manipulated by the animal, probably with the aid of the circumperistomial cilia (Fig. 29b).
Biedermann (1893) already found this membrane which completely envelops the animal, and which directly continues into 356
the 'Schliessapparat' , and he described it in detail for Dictyocysta elegans (p. 11, Plate 3, Figs. 1-4).

The alveoli of the shell wall are the reason for the very typical structure of the shell which consists of more or less irregular fields. These fields differ greatly in size; the meridional region frequently has larger alveoli than

the rest, but I have also frequently observed shells which were covered by equal size fields throughout.

The number of adoral organelles on the cell is twelve; it is thus the same as the number of lamellae of the 'Schliessapparat'. It is possible that these lamellae are formed by the backs of the organelles, and that the rest of the pouch is formed by the rest of the pellicle. This at least would explain the agreement between the numbers. The cell is large and fills the living chamber almost completely when it is withdrawn. The circumoral cilia are clearly observed on the fully extended body. They play over the rim of the collar, and frequently deposit particles there. The number of macronuclei is eight, but frequently a desmose has formed which leads to an almost complete separation of the nuclear substance simulating the presence of 16 macronuclei. V. Daday was probably misled by this effect when he quotes 14 small nuclei (Brandt, 1907, p. 75). We find one or two micronuclei, but they are always vague. The shell turns a reddish violet with Borrel's staining, a collar ring is not detectable, the 'Schliessapparat' turns pink, and the protoplast reddish violet.

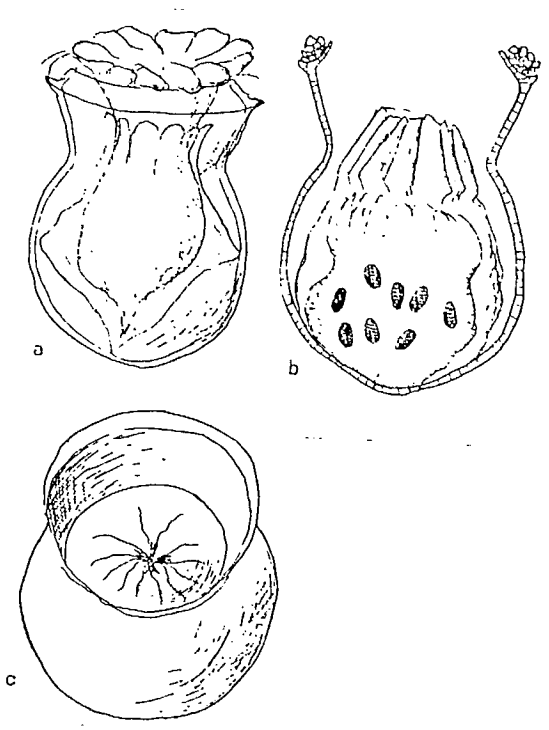


Fig. 29: Codonella cistellula (Fol) Brandt
The illustrations particularly show the detailed structure of the 'Schliessapparat'.
a) Individual, fixated with trichloracetic acid and embedded in Canada balsam. The animal is stretched, the 'Schliessapparat' is open, and the pouch part of the 'Schliessapparat' is clearly distinguished from the wall
b) animal withdrawn (with eight macronuclei), with half-closed 'Schliessapparat'. Particles are deposited on the double wall of the shell.
c) Lorica with tightly closed 'Schliessapparat' seen at an angle from above. Magnification 325:1. 355

12. Codonella nationalis Brandt (Fig. 30)

This species was fairly rare in the Gulf of Naples during the spring. The lorica is fairly similar to that of Codonella cistellula with regard to the alveoli. But the living compartment is roomier, oblong, and the collar portion is less clearly set off. Also missing is the double rim of the collar which widens only slightly before narrowing again, but without bending inwards. On microsections, the wall can be clearly seen to have a double structure. The 'Schliessapparat' (interlocking set of membranellae) is clearly visible with Borrel's method.

The number of nuclei (macronuclei) is eight, but often appears to be twice as high because of the transverse split (desmose).

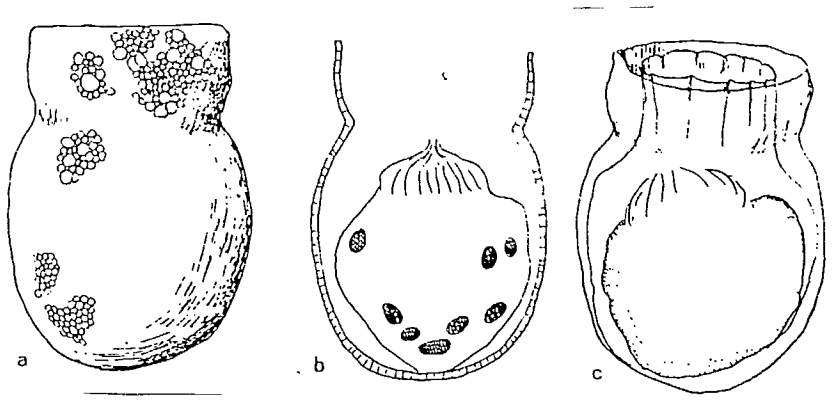


Fig. 30: Codonella nationalis Brandt
a) complete lorica, showing partially sketched structure b) optical cross section showing the eight nuclei c) shell with slightly shrunk 'Schliessapparat'.

I have carefully analysed shell and cell with Borrel's staining method. The lorica itself stains light blue, the alveolar walls on the other hand dark blue, while the 'Schliessapparat' (the entire 'pouch') stains pink red. This thus apparently consists of a totally different substance than the lorica. Around the narrower part of the shell, where the living chamber joins the collar, a ring lies on the inside of the shell. This ring, strangely enough, also stains unambiguously red. The protoplast also goes totally red, only the organelles are blue. It is therefore likely that the pouch of the 'Schliessapparat' consists of a protoplasm-like substance. The literature on the various species of the genus Codonella is collected in Brandt (1907, p.73-101), Jörgensen (1924, p.5-8), and Kofoid-Campbell (1929, p. 51-67). The latter authors have without much ado listed Brandt's variants as new species which is confusing.

13. Stenosomella ventricosa (Clap. et Lachm) (Figs. 31 and 32)

This species has recently been divided into two species by several authors: Stenosomella ventricosa (Clap. et Lachm.) and Stenosomella Steini (Jörg.). The difference between these two 'species' is actually only based on a difference in the structure of the upper part of the lorica. But I was able to compare many individuals from the Zuider Zee, from the North Sea, and from the Gulf of Naples. And these seem to me to belong to only a single species: but they would all belong to Stenosomella Steini if the new nomenclature had any value. But since this nomenclature is only based on shell characteristics, and even these appear to be trivial to say the least, I therefore think I am justified perhaps in retaining the old name Stenosomella ventricosa (Clap. et Lachm.). I must point out that the loricae from the North Sea and the Zuider Zee are always somewhat more angular at the anterior end of the living compartment than those from the Gulf of Naples. But this may well be due to geographic variations, and the value of these differences

358

should not be exaggerated. Also when we compare the size ratios of the shells from these two regions, we get the same result which I have already mentioned earlier. Because, 359
as I have explained elsewhere (Flora en Fauna der Zuiderzee Flora and Fauna of the Zuider Zee), p. 172), the mean length of the casing in the northern region is 69μm, the mean width 61μm. These two numbers are 75μm and 65μm for the Gulf of Naples. Even this then matches almost exactly. I will thus combine in my description of the lorica of Stenosomella ventricosa the characteristics of the typical northern form (= Stenosomella ventricosa) and those of the southern form (= Stenosomella Steinii).

The lorica is amphora- to heart-shaped, with a blunt point. The wall either bends abruptly towards the mouth, or bends over gradually. The opening is always formed of a hyaline substance: on this ring we again find a collar of particles, particularly in animals which are about to fission. The collar frequently seems to be somewhat flexible, and the living animal seems to be able to draw it inside with itself. The shell is covered with particles which are of organic origin, particularly on the aboral side, but which consist of quartz on the adoral side. The length of the shell (without the collar of particles) is 60 to 80μm, the greatest width 58 to 66μm.

While swimming, the body is rather long stretched, tapering to a point at the rear, and usually attached at the aboral end of the shell. But frequently the body has two cystic protrusions, and in that case is usually not attached. The cell is usually closely up against the hyaline ring of the shell. The adoral organelles on living or well fixed animals are uniformly developed, almost without fringes, and squared off at the end. Their number is 20, in single instances also 21 and 22. Viewed from the side, each organelle consists of basal element which is planted into the adoral collar of the body (peristomial rim). This basal element carries the organelle proper which bends outward, and an inside element of irregular formation which could be described as an

associated comb (Fig. 33). On the living animal one can clearly see a lateral band of cilia which runs in a spiral along the side of the body which faces the mouth (this is thus the opposite side from where it is located in the genus Tintinnopsis).

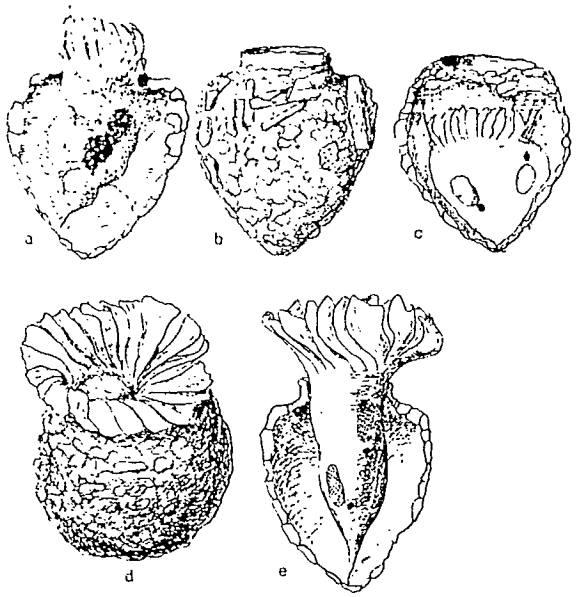


Fig. 31: Stenosomella ventricosa (Clap. et Lachm.) Individuals from the Zuider Zee, a) optical section, b) lorica, c) neckless specimen, d) animal with spread cilia, oblique view from above, e) side view, optical section. Technique: Trichloracetic acid, Ehrlich's hematoxylin. Magnification 250:1.

358

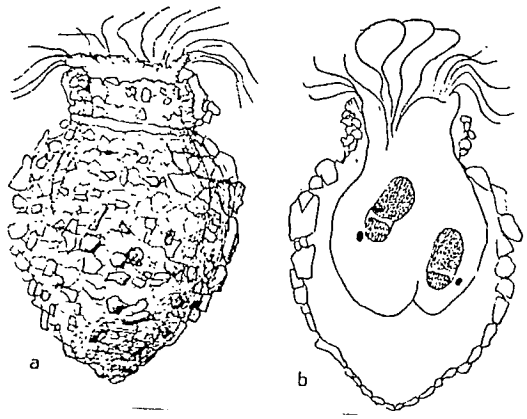


Fig. 32: Stenosomella ventricosa (Clap. et Lachmann) Individual from the Gulf of Naples. a) shell with detritus sitting on the ring, b) optical section, macronuclei with desmose. Technique as Fig. 31. Magnification 325:1.

Fig. 33: Stenosomella ventricosa Clap. et Lachmann
Single organelle, viewed from the side on a living specimen. Very much enlarged.

There are no circumoral cilia: but the peristome formes 360
a stiff rim which is clearly wider than the rest of the body. The nuclear equipment consists of two macronuclei, frequently with desmose, and two micronuclei in their vicinity. The fission of Stenosomella ventricosa (Figs. 34-36) was studied by myself in rather great detail, in Naples. I have also observed the formation of the lorica in Naples as well as in den Helder.

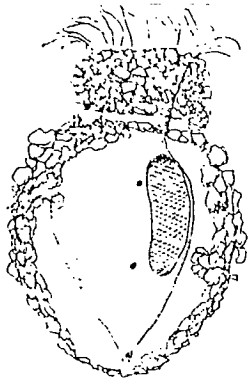


Fig. 34: Stenosomella ventricosa Clap. et Lachmann
Individual, about to divide. A thick collar of particles has formed. The macronucleus is single. Magnification 325:1.

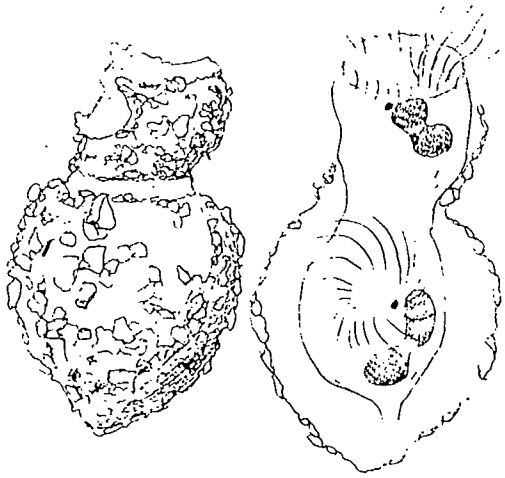


Fig. 35: Stenosomella ventricosa Clap. et Lachm. Further phase of division. The 'collar' of the lorica has widened and envelops the separating part. Magnification 325:1.

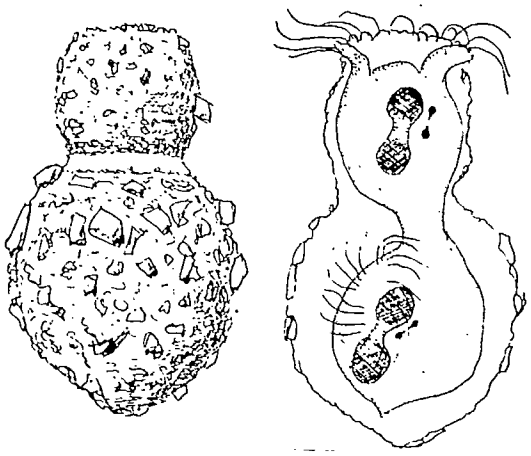


Fig. 36: Stenosomella ventricosa Clap. et Lachmann The micronuclei divide, also the fragments of the macronucleus. The cell separates and the 'collar' envelops the upper individual. Technique: trichloracetic acid, Ehrlich's hematoxylin. Magnification 325:1.

The micronuclei[+] have the desmose initially more or less in the center (Fig. 32b), and take on a very characteristic aspect when the desmose approaches one pole of the nucleus. The larger part stains little with the common 361
nucleus stains, while the other part stains the more deeply. These parts (of the two macronuclei) approach each other and merge. The desmose then disappears and a uniform nucleus is formed which nestles against the new peristome. Then this nucleus assumes an hour-glass shape and divides. One of the fragments drifts along with one of the micronuclei into the separating half of the plasma. Then both micro- and macronuclei divide before the separation of the plasma is complete. Immediately after fission, an individual thus possesses two micronuclei and two macronuclei, the latter without desmose. Geza Entz jr. (1909, p. 160) found only a single macronucleus on several occasions. He compares them with the juvenile forms of Laackmann. This is not impossible if the fission of the macronuclei is delayed under certain circumstances.

He also thinks that the micronucleus perhaps springs from the smaller part of the split macronucleus. I was still of the same opinion myself in 1921. But today we know that the micronuclei have an independent existence and cannot be derived from the macronuclei. In the conjugation too, it is the macronuclei which originate from the micronuclei rather than the opposite, according to Laackmann's studies, and in agreement with the way it is in the other ciliate families.

What is also particularly important is the way in which the newly released animal obtains its shell after the division. One frequently observes shells which have a collar of foreign material on the ring which is never covered with foreign particles. This material is actively deposited by the animals, and brought up by the lateral row of cilia.

[+] Translator's Note: Should be macronuclei; probably printing error in original.

One can always observe that these individuals which carry a collar, are in some phase of the division.

While the front half stretches, and more and more attains the shape of a typical tintinnid body, the putty-like material of the collar expands along with it, and is carried off by the new individual after separation. The collar is given final shape through further forming and stretching on the part of the cell. It seems to me that the ring is formed separately from the peristomial part.

More work is done on the shell later, when fecal parts are attached with the aid of the lateral row of cilia (Fig. 37). Here the animal leans far forward through the mouth of the shell; it also frequently bends around the edge of the shell (Fig. 38), so that particles can also be attached to the side of it. 362

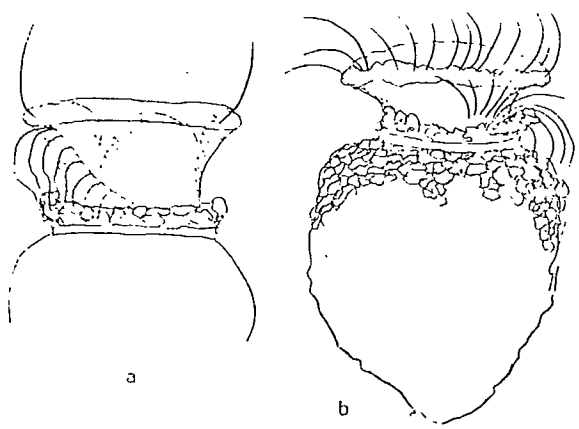


Fig. 37: Stenosomella ventricosa Clap. et Lachmann
The transport of particles towards the outside, with the aid of the row of cilia.
a) The animal works on the collar,
b) the animal deposits particles on the shell.
Drawn to life; Magnification 325:1.

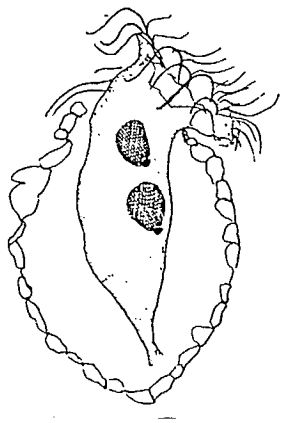


Fig. 38: Stenosomella ventricosa Clap. et Lachmann
The animal leans from the shell for the purpose of attaching particles to its side. The micronuclei are lying in recesses of the macronuclei. Technique: as in Fig. 36. Magnification 325:1.

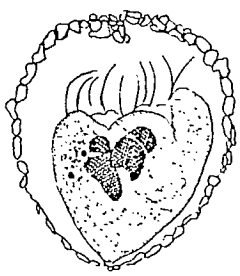


Fig. 39: Stenosomella ventricosa Clap. et Lachmann
An animal that has withdrawn into the shell and sealed the opening. Magnification 325:1.

13. Stenosomella nucula (Fol) (Fig. 40 and 41)

The typical shell of Stenosomella nucula has a narrowing mouth part under a clearly hyaline ring of some flexibility which may also be absent on occasion. The wall of the shell is sharply bent inward at the top where it forms the mouth opening. The shape of the shell is elongate with a blunted

point at the bottom. Length 35 to 55µm; width 23 to 35µm.

The body is rather elongate when extended, and possesses 363
18 organelles which are rather short and pointed, and which are not very ragged when they are preserved properly.

The two macronuclei are relatively large; the two micronuclei are difficult to stain when the animal is at rest.

Stenosomella nucula is an independent species as I have stressed already back in 1922 (Flora en Fauna der Zuider Zee, Flora and Fauna of the Zuider Zee, p. 171, Fig. 79). It is by no means always found together with Stenosomella ventricosa, because I found it along with Tintinnopsis campanula in Scheveningen. In the northern part of the Zuider Zee and in the vicinity of den Helder it is often found together with the much larger species Stenosomella ventricosa (nucula: appr. 45 by 30µm; ventricosa appr. 69 by 61µm). Also the number of organelles is 20 to 22 in Stenosomella ventricosa while it is always 18 in Stenosomella nucula.(It must be pointed out, however, that Campbell describes 22 organelles in his detailed study on Stenosomella nucula (1922). Either this number does not always stay the same, and there are tribes with a different number, or the Stenosomella nucula of the Zuider Zee is a different species than the Stenosomella nucula of the American coast which thus may also belong to Stenosomella nivalis (Meunier). A third difference is in the ratio of length to width of the lorica, at least in the Zuider Zee. This ratio is 3.2:2.3 for Stenosomella nucula and 4.9:5.2 for Stenosomella ventricosa. Stenosomella ventricosa is thus relatively more squat. In the same reference I have also pointed out that stretched loricae such as are illustrated in Brandt (1907, Plate 16, Figs. 1, 3,9,13,14) can never develop from the shells of Stenosomella nucula and probably belong to Tintinnopsis beroidea. In spite of the fact that I have given a clear description of Tintinnopsis nucula , this species was recently divided

into a number of different species by Kofoid and Campbell (Conspectus, 1929), and the name nucula reserved for a Tintinnopsis species. First , I must point out that Kofoid and Campbell did not consider my work (1922); secondly, most of the descriptions refering to 'Tintinnopsis nucula (Fol) Brandt emended' in their work (p. 41, Fig. 47) are merely reproductive stages of Stenosomella nucula equipped with collars; thirdly I must again clearly make the point that not all the illustrations of the authors which have misguided Kofoid and Campbell into establishing new species are true to nature (Meunier.); finally, I have already stressed repeatedly - and here the formation of the shell fully justifies me - that the shape of the shell will depend on external conditions, and that it is thus not proper to establish new species without hesitation, simply because of the slightly varying shape of the lorica. I am consequently convinced that Stenosomella oliva (Meunier) and Stenosomella nivalis (Meunier), both of which forms I have observed in the North Sea as well as at Naples, can only be variants of the typical species from the Bay of Kiel which Laackmann and Brandt have described.

364

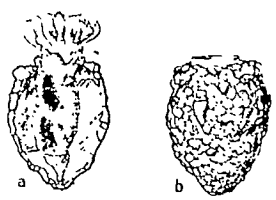


Fig. 40: Stenosomella nucula (Fol)
From the Zuider Zee. a) optical section showing the animal; from a Canada balsam preparation. b) shell. Magnification 350:1.

363

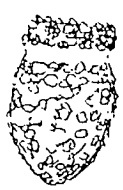


Fig. 41: Stenosomella nucula (Fol)
Shell with collar from Naples. Magnification 325:1.

Fig. 42: Stenosomella nucula (Fol).
Conjugation. Naples, February 26, 1930.
Technique: Trichloracetic acid, Ehrlich's hematoxylin. Magnification 325:1.

I cannot say to what extent Stenosomella avellana is a form which occurs in reality or whether it is only the product of Meunier's faulty drawing pen. But this 'form' also can be fully explained from external conditions.

Bibliographical Notes:

Tintinnopsis nucula Fol., H., Rec. Zool. Suisse, I. 1884, p.60 Plate 5, Fig. 13

Brandt, 1907, Plate 16, Figs. 12,13

Hofker, Flora en Fauna der Zuiderzee (Flora and Fauna of the Zuider Zee), p. 170-171, Fig. 79.

Stenosomella nucula Jörgensen, 1924, p. 95-96;1927,p.8

Stenosomella avellana (Meunier), 1919, p.30, Plate 22, Fig. 37

Stenosomella nivalis (Meunier), 1910, p.143,Plate 13, Figs. 26,27.

Stenosomella oliva (Meunier), 1910, p.144, Plate 13, Figs. 9-13, Plate 14, Fig. 6.

Kofoid and Campbell, Conspectus, 1929, p.41 (Tintinnopsis nucula), p.69 (Stenosomella avellana, Stenosomella nivalis), p.7o, Stenosomella oliva).

As I was able to determine, organisation and fission as well as the development of the shell (of Stenosomella nucula) at Naples are exactly similar to those of

Stenosomella ventricosa; everything is only proportionately smaller. I was also able to see conjugation where the two shells join at their mouth openings, and the rounded edges of the rings bend outward, resulting in a spacious combination of the two shell cavities. In this conjugations (Naples, February 26, 1930) I found a total of eight micronuclei in the two individuals (Fig. 42). 365

14. Codonellopsis morchella (Cleve)

This species was described by Brandt in three different variants: Codonellopsis morchella s.s., Codonellopsis morchella var. Schabi, and Codonellopsis morchella var. crythiaensis. The variant Schabi differs from the species proper only in the slightly larger size of the shell and a smaller number of rings on the neck. This variant has therefore only the value of a local variety. But Kofoid and Campbell set it up as a separate species, Codonellopsis Schabi (1929, p. 87, Fig. 157). I do not know why they did this.

However, the size and the small number of rings, are fairly constant for a given geographical location: I found this 'species' in the spring of 1930 (February 12 and 15, 1930) quite frequently in the plankton in the Gulf of Naples. Nevertheless it seems to be fairly rare there because I have not observed it afterwards, and also Daday, Entz and Brandt do not report it at that site.

The casing proper (without the neck part) is oblong with a wide open mouth. The largest width occurs below the center. The lorica is usually covered with very coarse grains of sand, especially on the upper half of the shell. The mouth of the shell merges into the neck part without a real narrowing. The neck part consists of 5 to 9 helical rings and usually ends in a slightly wider opening (Figs. 43 and 46).

The neck part is covered with only few particles, but its rim can be fairly heavily encrusted. On a single occasion (morning of March 9, 1930) I noticed a few living animals which had laid an enormous ring of particles around the mouth of the neck part (Fig. 45). It is possible that this ring has something to do with the fission; but I was not able to make sure of this. The wall of the neck is fairly thick.

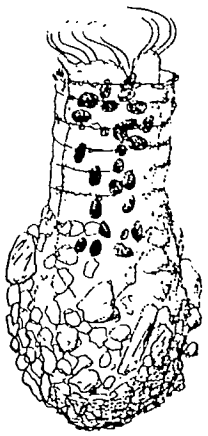


Fig. 43: Codonellopsis morchella (Cleve)
Individual in a shell, from a Canada balsam preparation. Technique: Trichloracetic acid, Ehrlich's hematoxylin. Gulf of Naples. Magnification 325:1.

The neck part is covered with only few particles, but its rim can be fairly heavily encrusted. On a single occasion (morning of March 9, 1930) I noticed a few living animals which had laid an enormous ring of particles around the mouth of the neck part (Fig. 45). It is possible that this ring has something to do with the fission; but I was not able to make sure of this. The wall of the neck is fairly thick.

366

Length of entire lorica	106 - 121µm
Width at neck	32 - 38µm
Length of neck	30 - 38µm
Largest width of living compartment	59 - 62µm
Length of living compartment	73 - 78µm

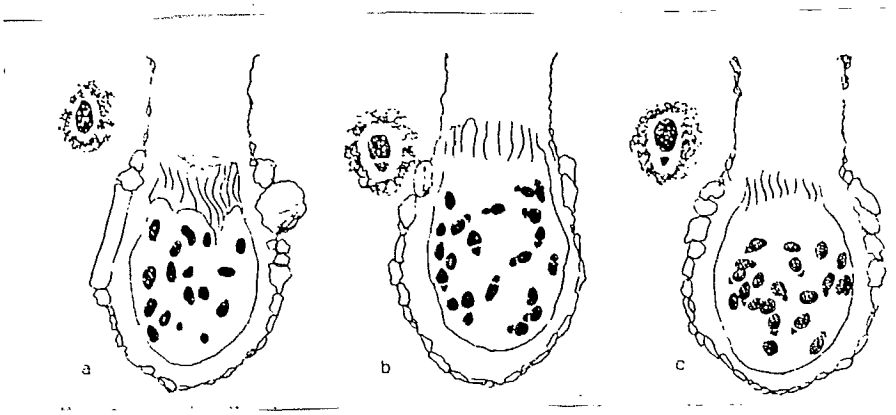


Fig. 44: Codonellopsis morchella (Cleve)
Three stages of the nucleic phase changes; from Canada balsam preparations. The small accompanying drawings illustrate the stages of each of the macronuclei in the animal in each case. Ehrlich's hematoxylin. Magnification 325:1.

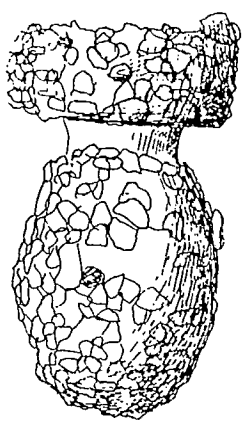


Fig. 45: Codonellopsis morchella (Cleve)
Living animal with enormous collar. Naples, March 9, 1930. Magnification 325:1.

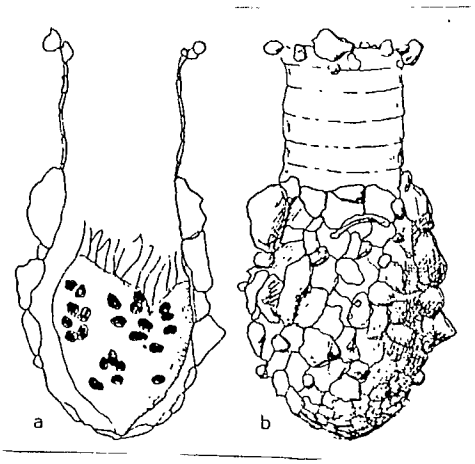


Fig. 46: Codonellopsis morchella (Cleve)
a) optical section, showing the structure of the neck part and the cell.
b) the same shell with particles on the neck.
Naples, February 15, 1930. Technique: Trichloraceti c acid, Ehrlich's hematoxylin. Magnification 325:1.

The tip of the shell is frequently totally free of particles. On tne subject of the cell I can say only very little. The number of organelles seems to be 20; 367
the number of macronuclei is very large. Usually there are about 20 of them which in most cases have a clearly visible unequal desmose. The number of macronuclei+ is probably two. Some of the specimens identified as Codonellopsis morchella by Brandt had only eight nuclei. It is strange that all nuclei in one animal exhibit the same stage of nuclear phase change, as shown in the illustrations (Fig. 44).

+ Translator's Note: Contradiction, probably printing error in original and should be 'micronuclei'.

15. Codonellopsis orthoceras (Haeckel) (Fig. 47)

This species is larger than Codonellopsis morchella, it has a long spike at the bottom, its mouth is narrower (than the chamber) and continues into a long neck. The living compartment is totally covered with foreign particles of fairly even size which render the wall almost opaque. Biedermann (1892) thinks that the foreign particles on the shell of Codonellopsis orthoceras have an organic origin, and that they really form a netlike system of secondary bracing rods. I reject this hypothesis categorically since under polarised light the shell very clearly exhibits the typical colours of small quartz grains.

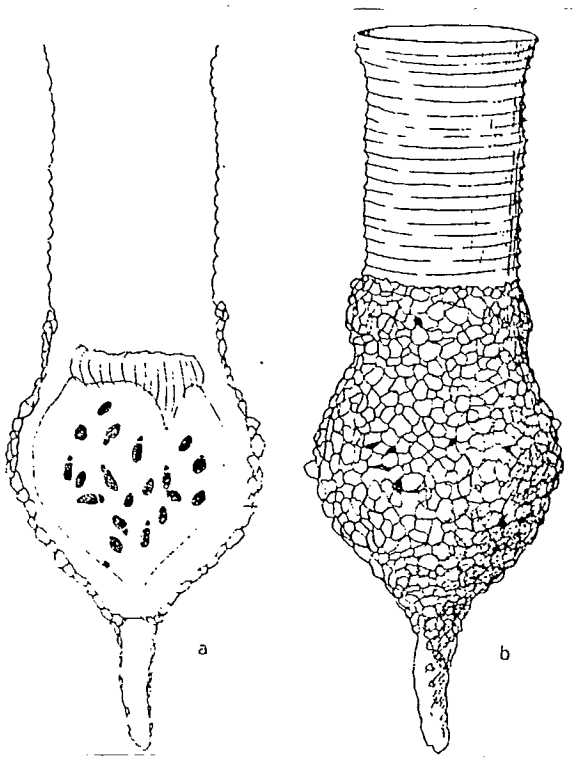


Fig. 47: Codonellopsis orthoceras (Haeckel)
From the Gulf of Naples. a) optical section of shell, b) outside of shell

The lorica is drawn out into a fairly long spike which 368
is, however, separated from the living compartment itself by a horizontal wall. The upper half of the living compartment narrows, and then directly continues into the long, finely ringed neck which in turn widens slightly at its mouth. The helix on the neck part is right-handed.

The cell body is fairly large, and is usually attached to the roof which separates the spike. When the body is withdrawn it occupies only the living compartment. But it can also stretch itself out very long. The number of organelles is 20 (only 18 according to Daday). A lateral row of cilia is located on the side farthest from the cytostome. The number of macronuclei is 18 or 20, the number of micronuclei is only two. V. Daday (1887, p.572) indicates 22 macronuclei, Entz jr. (1909, p. 163) an even larger number (25 to 50), while Brandt (1907, p. 75) mentions 22.

The literature which had been quite confused until now, has recently been reviewed critically by Kofoid-Campbell. Unfortunately, they list many forms which cannot even claim the status of varieties, as new species, both in the Morchella and the Orthoceras group. In this way 39 species just came into existence. In particular those species which are based on differences in the neck portion can be eliminated straight away since they are probably only the result of external conditions. I would like to refer here to the differences which occur for instance in the clones of Tintinnopsis fimbriata which are no greater than those of the various 'species' of Codonella orthoceras described here (Kofoid-Campbell, Conspectus, 1929, p.73-90).

The transport of the foreign particles to the outside wall of the shell occurs in the same way as has been described for Codonella galea, and which may take place in a similar way in many tintinnids which have necks. 'The animals bend their very extensible body over the long neck of the

lorica; the adoral, longer cilia of the lateral row in this way just touch the part of the lorica which is covered with particles; the fecal particles again travel along the row of cilia, and are cemented on the shell by the longer cilia, often also by the circumoral wreath. Now and then some sand grains also land on the neck part of the shell. Where an accumulation of these (in connection with the fission) has occurred at the mouth of the shell, this is always the work of the circumoral circle of cilia' (Hofker, 1931, p.148, Fig.16; also Fig. 48 in the present work). 369

We do not know yet how the spike of Codonella orthoceras is formed. It is a different phenomenon than the point of the shell of many known Tintinnopsis species because it is separated from the living compartment itself by a roof. But I believe, nevertheless, that the twelve different 'species' which Kofoid and Campbell list in their 'Conspectus' belong to one single species, Codonella orthoceras. Only exact knowledge of the structure of the lorica and the cell, can give more precise information.

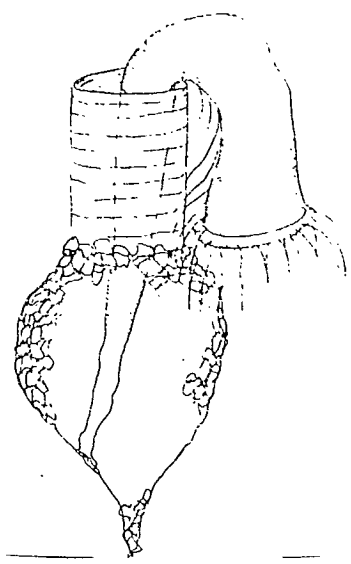


Fig. 48: Codonellopsis orthoceras (Haeckel)
The drawing illustrates an animal, drawn to life, which is busy transporting foreign particles to the outer shell surface.

Fig. 48A: Codonellopsis orthoceras (Haeckel)
Photograph of a specimen fixed in Canada balsam

15 a. Helicostomella subulata (Ehrenberg) Jörgensen emend.

This species seems to be quite frequent in the North Sea during the summer months. At any rate, I found it in the vicinity of Scheveningen as well as in den Helder in July, in centrifugal plankton. A volume of 10cm^3 sea water contained one individual.

The shell is very long stretched, with a sharp point, and a mouth which is not flared at all. But the mouth is characterised by many fine striped bands which indicate later addition. A pulsating vacuole is found at the rear end of the long cell; I was able to observe two macro- 370
nuclei.

16. Cyttarocylis cassis (Haeckel) Fol.

Two species of Cyttarocylis occurred fairly infrequently in the Gulf of Naples in the spring of 1930. A few individuals were caught on only few occasions, specially in the morning of March, 14. At any rate, they seem to be rare there. Other authors also mention the two species in the Gulf of Naples, for instance Entz jr. (1907, p.199).

The shell with its typical uniform structure is already known from many descriptions. A double wall can be clearly differentiated, with the two lamellae connected by large alveolar walls. These alveoli appear as thin

ridges on the surface of the lorica (Fig. 50).

There were 18 or 20 macronuclei which showed no desmose in the investigated specimens (Fig. 49).

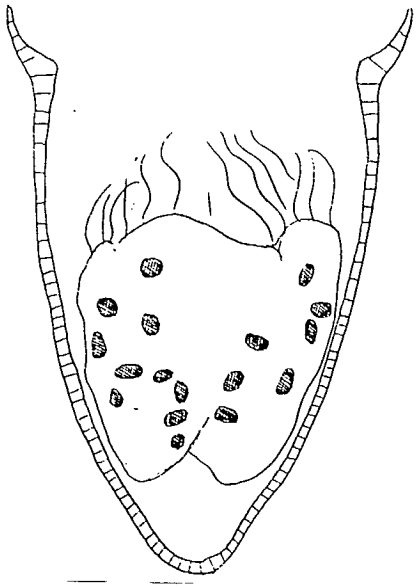


Fig. 49: Cyttarocylis cassis (Haeckel) Fol
Longitudinal optical section through an animal.
Gulf of Naples. Magnification 325:1.

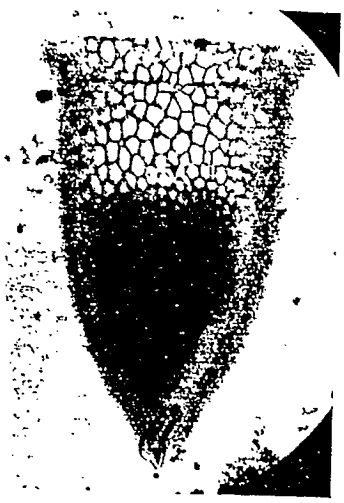


Fig. 50: Cyttarocylis cassis (Haeckel) Fol
Structure of the shell. Photograph.

17. Cyttarocylis plagiostoma (v. Daday) Brandt emend.

This species has only become somewhat better known since I got hold of a fairly large quantity. It always seems to occur in the Gulf of Naples together with the species just described. But the lorica is slightly smaller and more compact; the alveoli are also somewhat finer (Fig. 51). 371

When swimming, the only part of the body which projects from the lorica are the organelles. The cell forms a thin cone at the bottom, but then suddenly broadens and rests on the outward-bent rim of the mouth of the lorica.

The organelles are wide plates without covering lamellae or other formations; there are 18 of them (Fig. 52). They are so wide that they always overlap at the edges. The protoplasm of these wonderful Tintinnoidea is fairly uniformly vacuolised and exhibits a very large number of macronuclei which are small, almost globular, and frequently hard to stain. They penetrate as far as the peristomial rim and often lie so densely that they squeeze each other flat. Their number is approximately 80 (Fig. 53). I have already considered whether these 'nuclei' might be zoöxanthellae but have not found any indications for this. I do not know the number of micronuclei. 372

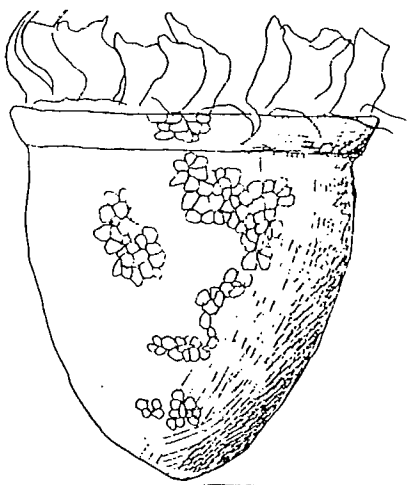


Fig. 51: Cyttarocylis plagiostoma (v.Daday)
Shell with extended cell; structure of the shell partially shown. Gulf of Naples. Magnified 325:1. 371

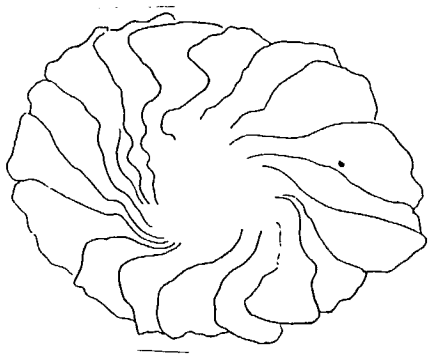


Fig. 52: Cyttarocylis plagiostoma (v. Daday)
Animal seen from above, showing the arrangement of the organelles. Drawn from a specimen fixed in Canada balsam. Technique: trichloracetic acid. Magnification 325:1.

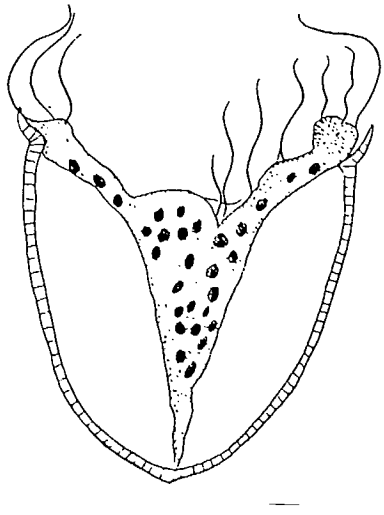


Fig. 53: Cyttarocylis plagiostoma (v. Daday)
Longitudinal section showing lorica, cell, and some of the nuclei. Technique: trichloracetic acid, iron hematoxylin. Magnification 325:1.

18. Favella ehrenbergii (Clap. et Lachm.) Jörgensen emend.

This species was described in my monograph on the Zuider Zee (1922, p. 177, Fig. 87) under the name Cyttarocylis ehrenbergii nov. var. (Fig. 54). It occurs in the North Sea (den Helder, Scheveningen) very frequently in late summer, and often constitutes a major component of the plankton during that period.

The lorica is elongate and cylindrical, drawn a point at the bottom. This point is not hollow and shows very little compartmentation. Usually one ring is observable at the mouth, sometimes also two rings. Below these rings the lorica widens slightly, resulting in a ring-shaped bulge. Just at this point the secondary mesh structure has a number of fairly large elliptical, often very densely crowded windows. Such windows, although of somewhat smaller size can also be observed scattered over the entire lorica. The loricae from the northern part of the Zuider Zee show these windows often very clearly, unlike the loricae from the North Sea.

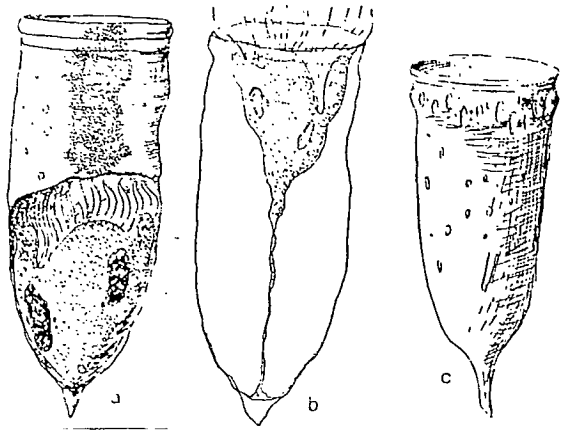


Fig. 54: Favella ehrenbergii (Claparede et Lachmann) Variant from the Zuider Zee. a) partially opened; the alveolar structure is shown exaggerated. b) animal which is not withdrawn; c) lorica with clearly visible collar. Magnification 330:1.

The cell is attached to the posterior end of the lorica. When the animal is swimming, the cell exactly fills the opening of the shell. I was able to count 18 organelles. 373
The front half of the body usually contains the two macronuclei which frequently have a desmose. Length of the lorica is 149 to 200µm, width at the mouth 60 to 69µm.

A very detailed bibliography is found in the Conspectus of Kofoid and Campbell, pp. 152, 153. But missing there is my work cited earlier. A very detailed description of the species is given in the work by Campbell (1927): Studies on the marine Ciliate Favella (Jörgensen) etc.; Univ. Calif. Public. in Zoology, Vol. 29. But I can add something to this here.
I have made numerous experiments with the species, using mostly Feulgen's staining method. It is strange that the micronuclei are almost never tinged with this method, suggesting that tney seem to lack particularly nucleic acids. This agrees with the information of Entz. jr. (1909, p. 162) who observed micronuclei only rarely. But the macronuclei become visible very beautifully with this method while the protoplasm remains almost untinged.

I was able to detect a number of important differences in the structure of the nuclei with this method, differences which are very probably partly due to the method itself. But they occur very regularly at the different stages, and are thus nevertheless characteristic for these stages.

As mentioned earlier, the absolute vegetative state is characterised by the absence of a desmose. With Feulgen's method, the nuclei at this stage have a vacuolized structure (Figs. 55 and 56) which has also already been described by Laackmann.

But as soon as this inactive stage is past the internal structure of the nuclei changes completely. The vacuolation blurs and the structure turns fibrous (Fig. 59)[1].

1) Geza Entz jr. (1909, p.162) also shows such a 'striped structure'. I quote:' The two nuclei in conjugation have a striped structure'. Did he perhaps mean the fusion of the macronuclei at the onset of fission?

Shortly after the desmose appears at the center; the anterior part of the nuclei (the part which is turned toward the peristome) tinges darkly and has a coarse structure, while the other part tinges only little, and shows a very homogenous structure. Then the desmose drifts slowly towards the side which points away from the peristome until that side contains only a small round body of a rather strongly tingeable substance (Fig. 57). (This is the condition which led Geza Entz jr. (1909, p.164) to 374
believe that the micronuclei have their origin in the macronuclei). A desmose is never found without there also being the formation of a new peristome.

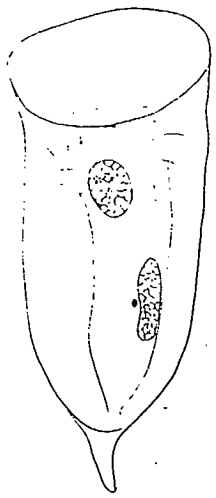


Fig. 55: Favella ehrenbergii (Clap. et Lachm.) Animal from Helder (coast of Holland). The structure of the macronuclei is alveolar. Technique: trichloracetic acid, Feulgen's staining method. Magnification 325:1.

The subsequent conjugation (sic) of the macronuclei was described in detail by Geza Entz jr. (1909, p.172-173) and by Laackmann (1909, p.140). I should mention here only that the two nuclei approach each other with the end containing the darkly stained objects which appear to become sharp points. This was also described by Entz.

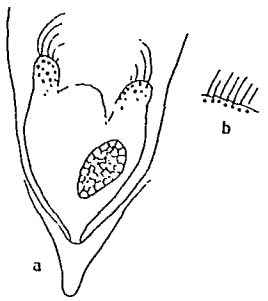


Fig. 56: Favella ehrenbergii (Clap. et Lachm.) From Helder a) section; trichloracetic acid, Feulgen's staining, macronuclei with alveolar structure; b) tangential section showing the basal bodies of the organelles. Magnification 325:1.

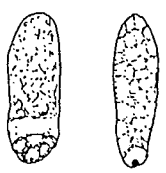


Fig. 57: Favella ehrenbergii (Clap. et Lachm.) Two stages of the nucleic phase change. Highly magnified. Feulgen's staining.

But other things are also stained with Feulgen's method. First, there are almost always very fine grains to be found in the posterior end of the animal (Fig. 58). Secondly, accretions of fine grains in the peristomial rim are made very clearly visible: they are somewhat larger just under the surface of this organ where they probably constitute the basal grains of the organelles. 375

The lorica tinges a fine reddish color with this method, while the protoplasmatic structures have a definite blue tinge (Fig. 60). The alveolar structure in particular frequently stands out sharply. Here I noticed that in the

pointed end of the shell, just where the soma is attached, a reddish accumulation of more darkly staining substance occurs in the shell wall which also contains some fine grains; there the alveoli are small and blurred.

A few times I observed the parasitic dinoflagellates which were described as microspores in the past. I frequently saw typical cell fissions, with a spireme and nucleic coil, while these nuclei also have the characteristic dinoflagellate structure when at rest. This parasite was named Dubosequella tintinnicola (Lohmann) by Chatton (1919, Archive de zoologie experimentale et generale (Archive of experimental and general zoology), Volume 59, pp.322-335). (See also Figs. 61 and 62)

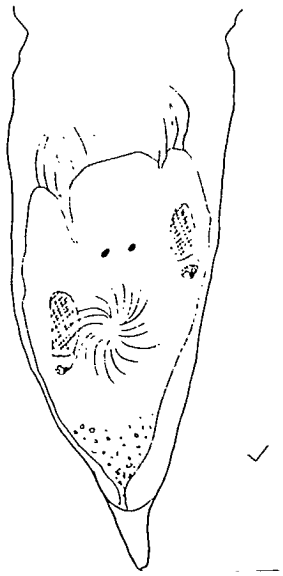


Fig. 58: Favella ehrenbergii (Clap. et Lachm.) Individual ready to divide. At the rear of the animal, the pellicle contains small bodies which can be stained with Feulgen's method and with Ehrlich's hematoxylin. Helder, Holland. Magnification 375:1.

374

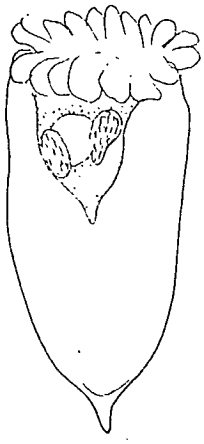


Fig. 59: Favella ehrenbergii (Clap. et Lachm.)
Animal engage in the formation of the collar of the Lorica. The structure of the nucleus (fibrous) is very noticeable. Technique: Trichloracetic acid. Feulgen's reagent. Magnification 325:1. 375

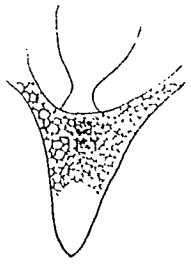


Fig. 60: Favella ehrenbergii (Clap. et Lachm.)
Bottom part and pointed end of the shell. The specimen was stained with Borrel's method. The shell appeared reddish, with dark red-tinged grains just where the animal (tinged blue) is attached. Magnification 500:1.

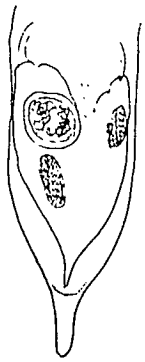


Fig. 61: Favella ehrenbergii (Clap. et Lachm.)
Animal with parasitic object which has a twofold spireme and a double wall. Technique: trichloracetic acid, Ehrlich's hematoxylin. Magnification 250:1.

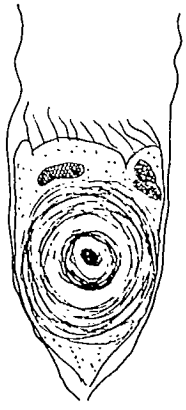


Fig. 62: Favella ehrenbergii (Clap. et Lachm.)
Animal with an enormous parasitic enclosure which has a shelled structure. Magnification: 325:1.

19. Favella helgolandica (Brandt) emend. Jörgensen

I observed a very small number of individuals in Naples in the spring of 1930. It is very probable that they belonged to this species. But they frequently exhibited strong degeneration of the cell, in conjunction with the presence of the parasite Dubosequella (Fig. 65). I was able to study a few nucleic structures and came to the conclusion here as well that they are dinoflagellates. Two macronuclei, often with desmose, could be observed in the oval part of the cell of normal animals. When observing living animals, one can see rows of tiny cilia covering the entire ventral part of the body. One of these rows extends along the animal down to its stalk, and forms a kind of undulating membrane. It extends close to the side of the animal which is nearest to the mouth. The number of organelles is 20 (Figs. 63,64). 376 377

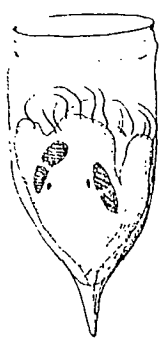


Fig. 63: Favella helgolandica (Brandt)
Individual stained with Ehrlich's hematoxylin; Gulf of Naples. Magnification 250:1. 376

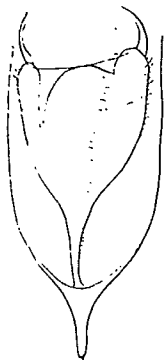


Fig. 64: Favella helgolandica (Brandt)
Living animal, showing distribution of cilia on the body. Magnification 250:1.

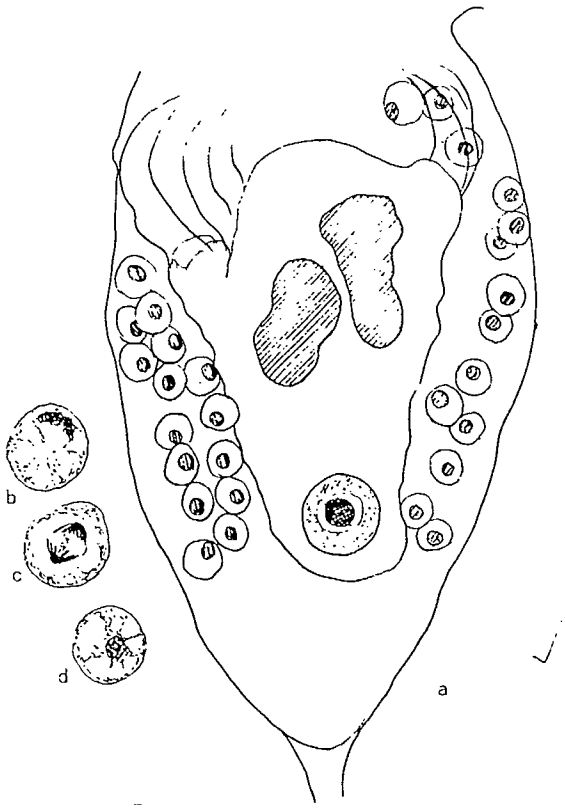


Fig. 65: Favella helgolandica (Brandt)
a) Animal, heavily infected with Dubosequella; Magnification 625:1
b,c, and d) Dubosequella tintinnicola at various stages of division. Magnification 1200:1.

20. Epiplocylis reticulata (Ost. et Schm.) Jörgensen

This species is apparently rare in Naples where I could observe only two specimens, one on February 8, 1930 and the other on March 27, 1930. The habitus of the lorica is bell shaped, with a fairly pronounced point and a slightly constricted oral rim. The wall consists of two undistinguished lamellae, and thickens particularly in the vicinity of the posterior point although this point is not solid as in Favella. The outlines of the rather coarse alveoli clearly stand out as fine ridges on the shell surface. On the oral rim they degenerate into short lines running parallel with the mouth. One of the shells I stained according to Borrel's method. It turned completely red. A circular piece in the center of each alveolus was tinged only light pink, gradually getting darker towards the edge of the alveolus, while the ridges appeared dark red.

The internal and external structures appear to be those of Tintinnopsis. The number of Macronuclei is two. I was unfortunately not able to observe clearly the micronuclei.

20a. Petalotricha ampulla (Fol) Kent. (Fig. 66)

I was able to observe this species in Naples in only a few individuals. But Geza Entz jr. has described it in exact detail. He published various important data on this interesting species already earlier (1909), and later dedicated a paper to the organelles (1929). They are 16 in number and have a fairly complex structure; the number of nuclei is very large (1909, p.164), something this species has in common with Cyttarocylis (I was only able to count twelve nuclei in one specimen, in addition to a probable micronucleus) which has however somewhat more organelles (18).

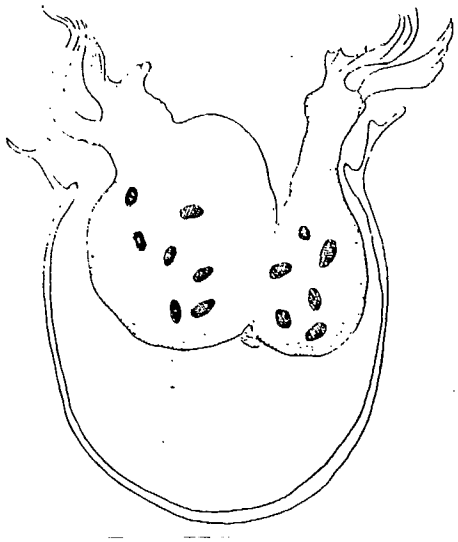


Fig. 66: Petalotricha ampulla (Fol) Kent
Longitudinal optical section. Technique:
Trichloracetic acid, iron hematoxylin.
Magnification 325:1.

21. Rhabdonella spiralis (Fol) Brandt emend.

This species which is abundant in the Gulf of Naples was 378
first described by Fol (1881). It has been repeatedly
investigated, especially its shell, by various authors.
The very long lorica has a slightly flared mouth: the
living compartment is long and cylindrical, and the
hollow spike is almost as long as the living compartment
(Fig. 67). Very characteristic is the fine spiral striping
on the lorica, especially on the spike, and which has
given the species its name. When observed in sea water, the
wall of the lorica clearly exhibits a thickening at the
oral rim. There the two lamellae which form the external
and internal surfaces of the shell are joined but form a
sharp ridge (Fig. 68b) at the inside of the rounded (on
longitudinal sections) oral rim. The cavity between the

two lamellae is filled with clearly visible primary alveoli which can also be observed from the outside of the lorica. The longitudinal stripes appear as the ribs joining the two lamellae, and also stain a somewhat darker red with Borrel's method than the intervening sections. There are also small oval windows located at regular intervals in the center of the primary alveoli. But the windows did not appear to me to be open (Fig. 68). 379

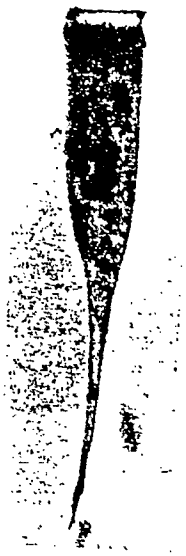


Fig. 67: Rhabdonella spiralis (Fol)
Naples, photograph. Magnification 200:1.

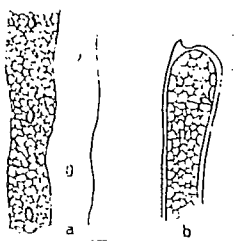


Fig. 68: Rhabdonella spiralis (Fol)
Structure of the wall of the lorica.
a) outside view, on the left, shown with alveolar structure, on the right without this structure but only showing the windows.
b) optical longitudinal section through the rim of the lorica. Both illustrations very much enlarged, and stained with Borrel's method.

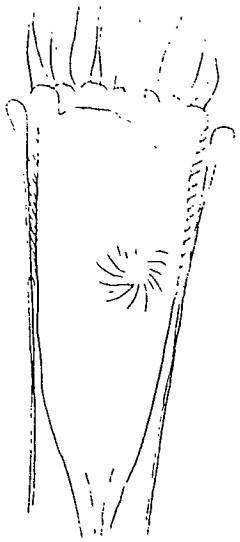


Fig. 69: Rhabdonella spiralis (Fol)
Optical section through a living specimen, with organelles, new peristome, somatic cilia, and folds on the stalk. Magnification 387 1/2:1.

The formation of the shell was described in one of my earlier papers (1931, Tijdschrift der Nederlands Dierkundige Vereeniging (Journal of the Dutch Zoological Society), Series 3, Volume II, p. 145). After division the free individual surrounds itself with a ring secreted by the pellicle, but which remains open at the aboral end for a fairly long time until it is gradually completed into a spike by the animal. The spike is thus formed later than the mouth section of the shell (Fig. 73).

The cell is, at least in its upper third, covered with many rows of cilia which are clearly observed in the living individuum but only rarely remain visible in dead specimens (Fig. 69). The peristomial rim is rounded at the top and not very pronounced but clearly exhibits socalled 'associated combs' (Begleitkämme). No row of lateral cilia is found. The organelles are not very stout; they number 18.

In the vegetative state there are always two macronuclei in the upper part of the oblong body (which is attached to the side of the wall in the spike). These nuclei

frequently show a clearly visible desmose (Fig. 70) and exhibit all the metamorphoses already described for Favella Ehrenbergii. Staining almost always makes two micronuclei visible in the vicinity of the macronuclei. I once saw an animal which had only a single macronucleus with two micronuclei beside it. This was probably an 380
animal which was getting ready for division, especially since a second peristome was forming on one side. I clearly saw a number of fairly large basal grains in the vicinity of this peristome but also a second row of small bodies in the vicinity of one of the micronuclei (Fig. 71A). Phases of division are quite rare in day plankton. Geza Entz jr. (1907, p.163) also observed once such an animal with a single nucleus, but he also saw one which had four nuclei. Of course it is possible that he confounded it with Favella franknoii which can easily happen with fixed material since the clear outline of the shell disappears in Canada balsam.

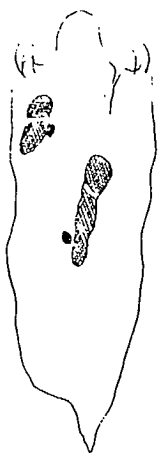


Fig. 70: Rhabdonella spiralis (Fol)
Normal animal with desmose. Technique: Trichloracetic acid, Ehrlich's hematoxylin. Magnification 325:1.

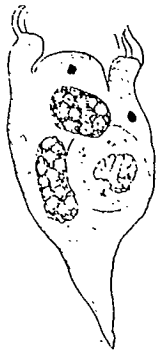


Fig. 71: Rhabdonella spiralis (Fol)
Animal engaged in the digestion of a voluminous feeding vacuole. The macronuclei lie close to the vacuole, and are themselves strongly vacuolised. Technique: as Fig. 70. Magnification 325:1.

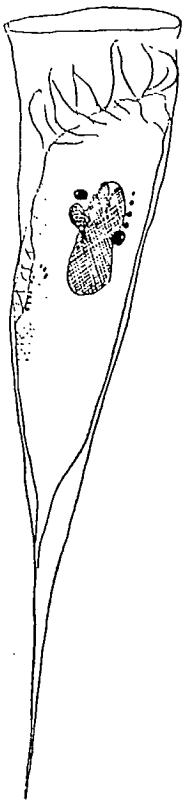


Fig. 71A: Rhabdonella spiralis (Fol)
Animal which is about to divide, with one macronucleus, two micronuclei, and a row of grains in their vicinity. Technique: Trichloracetic acid, Ehrlich's hematoxylin. Magnification 325:1.

Fig. 72: Rhabdonella spiralis Fol
Digesting animal. The macronucleus closest to the feeding vacuole is heavily deformed, and does not show a desmose while the other macronucleus has a normal aspect. Technique: as in Fig. 70. Magnification 325:1.

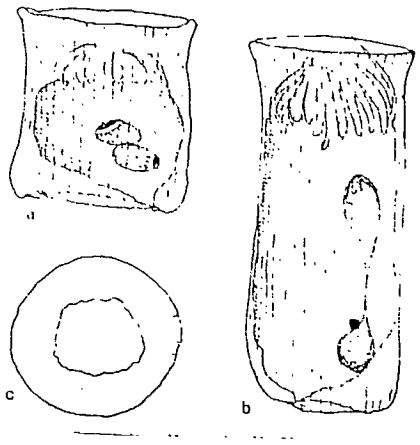


Fig. 73: Rhabdonella spiralis Fol
Formation of the shell.
In a) the shell is still completely open at the bottom, in b) it is already closed around the edge; c) shows this shell from the bottom. Magnification 325:1.

22. Hystonella treforti v. Daday Laackmann

I observed this species alive just once in the Gulf of Naples (February 22, 1930). The lorica has fairly large alveoli located in a single layer between the two lamellae.

23. Proplectella fastigata (Jörgensen)

The plankton of Naples contained a fair number of Undella-like tintinnids which had a perfectly hyaline double wall in which the lamellae were not joined to each other by primary alveoli. The two lamellae do not even come in contact at the aboral end of the shell. This is a characteristic which Jörgensen describes in his Undella claparedei forma fastigata which was newly described as a species in its own right by Kofoid-Campbell (p.278). I observed two macronuclei.

24. Dictyocysta mitra Haeckel

This species was not rare during my sojourn in Naples (spring of 1930), and it is probably identical with Dictyocysta elegans Ehrenberg as Kofoid and Campbell (1929, p.296) have argued. The slender lorica was adorned with relatively large windows (which in my opinion are not real windows) a number of which formed the collar part (Fig. 74). The cell is large and, when withdrawn, fits precisely inside the living compartment. The eight macronuclei often have a desmose and lie distributed throughout the body; two micronuclei lie between them. With Borrel's staining method, the lorica and the protoplasm is tinged a beautiful blue while the macronuclei become deep red (Fig. 75). 382

Geza Entz jr. (1907, p. 163) reports having observed six nuclei. But I have always observed eight. I have also not observed the structure of the nuclei (Dictyocysta elegans) described by Entz. The nuclei are moreover always of the same shape and size, and I believe that Entz may have interpreted other objects as nuclei as well.

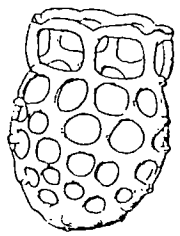


Fig. 74: Dictyocysta mitra Haeckel
Shell from the Gulf of Naples. Magnification 325:1.

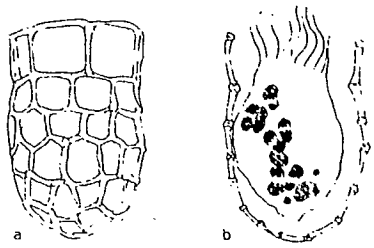


Fig. 75: Dictyocysta mitra Haeckel
a) slightly differently shaped shell
b) optical longitudinal section, showing the animal with its eight macronuclei and two micronuclei. Technique: Trichloracetic acid, stained according to Borrel. Gulf of Naples. Magnified 325:1.

25. Dictyocysta lepida Ehrenberg

This species which is identical with Distyocysta templum Haeckel is one of the most common of the dictyocystae in the Gulf of Naples. But it never occurs in large numbers in the plankton samples. The lorica has a number of large 'windows' at the center of the living compartment, and the collar part also contains a number of large rectangular

windows (Fig. 76b). There are often hundreds of coccolites attached to this shell on the outside which suggests that the food seems to consist primarily of coccolitophores Fig. 77). A 'Schliessapparat' (interlocking set of membranelles) which is attached at the base of the collar can be easily observed in the living animal (Fig. 78). This 'Schliessapparat' consists of the oral part of a pouch which, closely nestled along the shell wall, surrounds the entire 383
body of the animal, as can be readily seen in preserved specimens. Here we also have eight macronuclei and two micronuclei in the protoplasm (Fig. 76a).

With Borrel's method the loricae and the protoplasm are stained blueish violet, and the larger windows seem to be really quite open here after all, since they are not stained in any way. The nuclei are stained red.

Geza Entz jr. (1907, p. 162) reports to have observed eleven specimens in Naples, 'one with seven, one with six, four with five, and five specimens with four nuclei; in one case (he) saw the nuclei of this species joined into a spiral thread, similar to what Haeckel describes for Dictyocysta templum'. The latter case is probably a phase of division. With Borrel's method I was able to detect eight macronuclei in each of the observed specimens. The other staining methods always yield less clear pictures. This may be the reason for the different numbers observed by Entz. v. Daday also reports eight nuclei but 20 ciliate lamellae (Brandt, 1907, p. 48).

The shell of the dictyocystae, less any foreign particles attached to it, seems to consist entirely of a substance which stains like the protoplasm, and is probably of lenticular nature. The number of membranelles of the 'Schliessapparat' corresponds to that of the cilia (18), but the number of windows in the collar of Dictyocysta lepida is always less (6), so that there are three membranelles for each window. The same is probably true for Dictyocysta mitra as well.

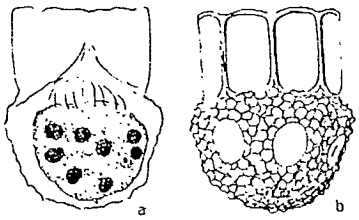


Fig. 76: Dictyocysta lepida Ehrbg. 382
a) animal with 'Schliessapparat', eight macronuclei and one micronucleus. Technique: Trichloracetic acid, Ehrlich's hematoxylin.
b) shell of the same animal. Gulf of Naples. Magnification 325:1.

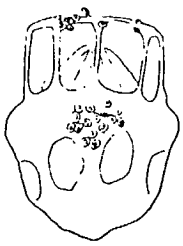


Fig. 77: Dictyocysta lepida Ehrbg. 383
Shell with 'Schliessapparat' and attached coccolites. Drawn to life. Gulf of Naples. February 19, 1930. Magnification 325:1.

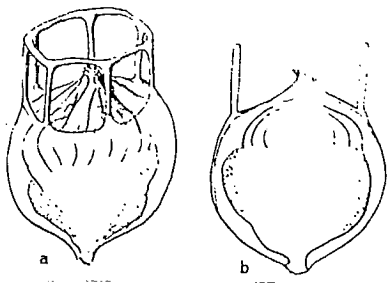


Fig. 78: Dictyocysta lepida Ehrbg.
Drawn to life. a) complete shell with 'Schliessapparat'. b) optical section through the shell with animal and 'Schliessapparat'. Magnification 325:1.

Most of the literature on the genus Dictyocysta is already referenced in Brandt (1907, p. 48-73), who gives a precise 384
analysis of the various species and forms. An almost exhaustive bibliography can further be found in the Conspectus of Kofoid and Campbell (1929, p. 285-302). But these authors list all of Brandt's variants as species in their own right, thus creating 14 new 'species'. But these are only based on differences of the shell, and they frequently appear to be very trivial differences one need only compare for instance Dictyocysta lata, Dictyocysta mexicana, and Dictyocysta nidulus with each other and with Dictyocysta reticulata) which therefore do not have any real value. This new taxonomy can thus only confuse.

26. Amphorella ganymedes v. Daday (Fig. 79)

I found this species only rarely (February 21, 1930) in the plankton of the Gulf of Naples. The very hyaline lorica has a flared mouth, fine longitudinal pleats at the mouth part, and a button shaped broadening at the posterior end. The living animal shows no unusual characteristics. I was able to observe two macronuclei and two micronuclei.

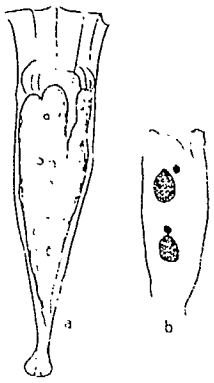


Fig. 79: Amphorella ganymedes v. Daday
a) complete animal, drawn to life (Gulf of Naples).
b) fixed and stained animal.
Magnification 387 1/2:1.

27. Amphorella quadrilineata (Clap. et Lachm.) v. Daday

I found a small number of these animals in the plankton of Naples, in the morning of March 9, 1930. In the large cell I found eight macronuclei and (most likely) two micronuclei. I did not observe any structuration of the lorica except the longitudinal creases. It will be immediately clear that at least these two species, Amphorella ganymedes and Amphorella quadrilineata are distinct since the number of macronuclei is very constant in the different species of tintinnids.

Amphorella quadrilineata was investigated in detail by Faure-Fremiet (1924, pp. 110-112). Unfortunately he did not count the nuclei, and mentions only v. Daday's find who detected four macronuclei. The number of macronuclei 385
is thus not yet established with certainty. But Faure-Fremiet describes the peristome as clearly being at an angle, having much in common with that of Salpingella. I myself have not been able to notice this but then I have only been able to observe few specimens. But it is very well possible that quite different species exist which have the same shape of lorica. The description by Faure-Fremiet at any rate cannot be questioned.

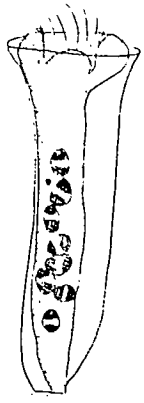


Fig. 80: Amphorella quadrilineata (Clap. et Lachm.) Fixed animal, stained with iron hematoxylin. Magnification 430:1.

28. Tintinnus frakenoii v. Daday

This species is often quite frequent in the plankton samples of the Gulf of Naples. The lorica is often very long: but I believe that the length of the lorica is not a typical species character. The long cell is attached to the lorica in the center, and extends its organelles just barely past the collar section when the animal is swimming (Fig. 81a).

The cell always contains four macronuclei which sometimes exhibit a desmose. The number of micronuclei is two or four. In one instance I saw more than that. The strucutre of the nuclei, when fixed, is highly vacuolised (Figs. 81b,c).

The authors which have taken note of the number of nuclei have always determined that there were four of them.

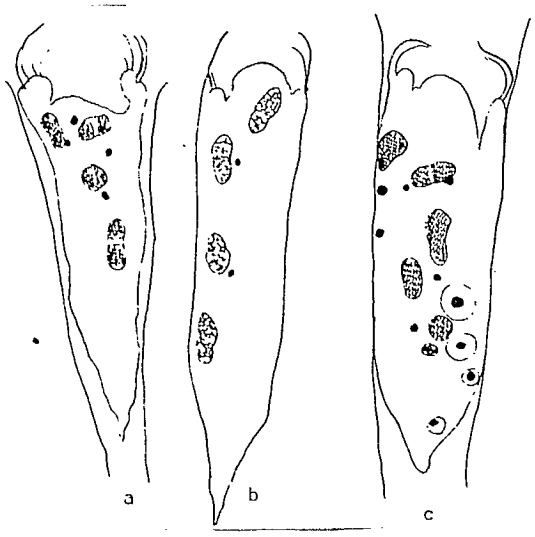


Fig. 81: Tintinnus frakenoii v. Daday
a) Individual with four micronuclei and four macronuclei, b) animal with two micronuclei and four macronuclei; c) abnormal animal, probably with parasitic inclusions. Technique: trichloracetic acid, Ehrlich's hematoxylin. Magnification 325:1.

Faure-Fremiet (1924, pp.98-102) has detected clavicular 386
associate combs and rather well developed somatic ciliation. I have looked for the associative combs in my specimens in vain although such formations were well visible in Tintinnopsis campanula, even in Canada balsam preparations. It is strange that Faure-Fremiet found more fully developed rows of cilia also on the side opposite the mouth. This is very important since such lateral rows of cilia were otherwise found only in the agglutinated forms. The species has been described in detail by Faure-Fremiet, where the more important literature is also listed.

20. Tintinnus inquilinus O.Fr. Müller

This species which lives in symbiosis with the diatome Chaetoceras was frequently found by me in the plankton of Naples (Fig. 82). The shell is slightly constricted at the bottom and where the animal is attached with a broad pedicle. The Chaetoceras consists of three cells and probably constitutes a species in its own right. The number of cilia is 18, there are four macronuclei (with desmoses) and two micronuclei.

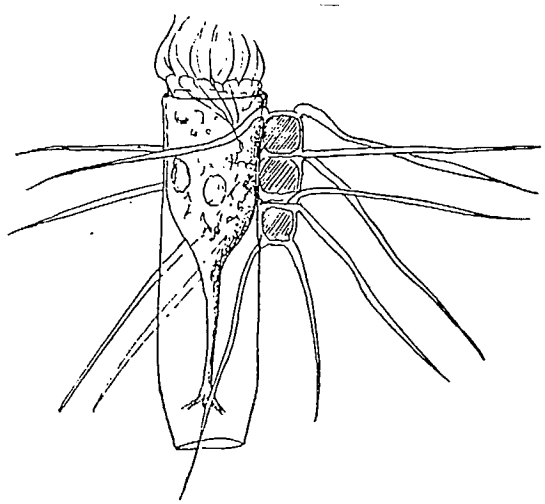


Fig. 82: Tintinnus inquilinus O.F. Müller
Living from the Gulf of Naples, swimming together with Chaetoceras.
Magnification 400:1.

Fig. 83: Tintinnus inquilinus O.F. Müller
Fixed animal, schematized.
Magnification 325:1.

Geza Entz jr. (1909, p.161) and Laackmann also found four macronuclei, so that this number is probably constant (Fig. 83).

30. Tintinnus lusus-undae Entz

The lorica is frequently found in the North Sea, and during the summer also in the Zuider Zee; it is completely hyaline and lacks all structure; it is open at both ends, slightly flared at the anterior end, slightly narrower at the posterior with a pronounced transition one quarter from the end of the shell. The animal has two macronuclei and is attached at the posterior end of the lorica. Length of the lorica 105 to 120µm, width at the anterior opening 22 to 24µm, at the posterior opening 12 to 14µm. 387

This species was found in Naples by Geza Entz jr. (1885, p. 527, Plate 28, Figs. 3,14) but I did not find it there again. Entz possibly confused it with Tintinnus inquilinus. But it differs from it not only in the symbiosis with Chaetoceras but also in the number of nuclei. It is more than probable that Tintinnus lusus-undae is not a Tintinnus at all if we consider Tintinnus frakenoii to be the typus of this genus. It becomes more difficult when Tintinnus lusus-undae is considered as the Typus, as is done by Kofoid

and Campbell (1929, p. 329). But I must add right away that Entz jr. (1909, p. 162) describes four macronuclei in the body of Tintinnus lusus-undae.

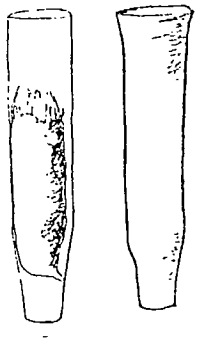


Fig. 84: Tintinnus lusus-undae Entz
Probably the variant tubulosa Ostenfeld .
North Sea and Zuinder Zee. Magnification 375:1.

31. Salpingella acuminata (Clap. et Lachm.) Jörgensen

I found a few individuals of this species in the deep plankton (approximately 300m) in the Gulf of Naples. The extremely long lorica opens like a trumpet at one end while the only moderately pointed posterior side carries a few wings, parallel to the longitudinal axis of the shell. The structure of the peristome is totally different from that of the other tintinnids. It consists of an oblique ring of short, stout cilia which have only few characteristics in common with the proper tintinnids. I saw two macronuclei with desmose[1] and two micronuclei. The number of cilia is 20, the overall length of the lorica is 350µm, the width at the mouth 36µm, the width of the rest of the lorica 30µm. It is possible that this species

388

1) Geza Entz (1909, p.161) has also observed two macronuclei, as have v. Daday, Laackmann and Brandt. Laackmann found two micronuclei as well.

is identical with Salpingella attenuata Jörgensen which has been described by Kofoid and Campbell (1929, p.351).

General Part

After this brief enumeration of the various species which I have studied, I will now proceed to the more general discussion. But first we should summarize the particularities found in the various Tintinnoideae in order to have a more coherent picture of the entire group.

We have found then, that the cell of the Tintinnoidea is bell-shaped, rather elongated when swimming, and attached to the wall of the lorica with a short, thin stalk. A cytostome is located excentrically on the upper part. The cytostome is confined by a pistil on one side which is often motile, and occupies the center of the peristomial field. The peristomial field is surrounded by a wreath of stout organelles which only seem to form a closed circle in as much as they start in the mouth but end outside of the mouth on the other side. The broad organelles are actually rows of cilia cemented together, which stand on torose bulges of the peristome. Many Tintinnoidea also have a somatic ciliature which consists of a longitudinal row of stout cilia in those species which cover their lorica with foreign particles; in the other species, this somatic ciliature consists of more or less developed rows of fine cilia which nevertheless frequently grow quite long outside of the wreath of organelles, and which form several wreaths of circumperistomial cilia. These latter cilia also seem to occur in the species which build shells from foreign particles.

The cells in most cases contain a pulsating vacuole in the posterior part of the body. Several authors mention a neuromotoric centre. The number of micronuclei is two in most of the species. The number of macronuclei is rarely one, usually two, and not so frequently four, eight or even more. (It is evident that I do not concur with Geza Entz's jr. opinion (1909, p.170) that a number of macronuclei in excess

of four occurs only in connection with reproduction). 389

Normal bilateral fission occurs very characteristically and not, as some authors propose, exactly in the same way as in Stentor (these animals have only a vague similarity to tintinnids). The onset of fission becomes noticeable in changes in the structure of the macronuclei. A desmose appears in the centre of each macronucleus and subsequently drifts towards one of the poles. Finally a grain of chromatic substance is found at this pole. This grain stains rather strongly. In the following phase the nuclei merge and become one long sausage-like nucleus.

While this was going on a new peristome, consisting of a spiral of organelles, has formed on one side of the animal. In all species of Tintinnoidea, this new peristome develops on the same side where the macronucleus (or the two macronuclei) was lying. The new peristome appears directly on the front of the dividing animal if it is placed upright, with the mouth on the left.

The structure of the loricae varies widely. I should point out in particular that after division the loricae develop first as ring-shaped formations, and have their posterior end finished later. It seems to me that loricae which are open at the rear must be either primitive, or they are the result of secondary involution. But I also found that newly developed individuals (from permanent cysts?) or animals which had left their lorica behind, formed the (new) lorica on the entire lateral body surface. This suggests that loricae open at the back are in a state of involution.

All tintinnids which carry foreign particles on their lorica (including those foreign particles which are of organic origin) cement these foreign particles onto the shell surface by means of the lateral and circumoral cilia. The material is obtained from the excrement, and it is therefore evident that these foreign particles, their frequency, and their position can never be used as systematic characteristics.

But since the lorica also is actively formed by the animal and furthermore is the result of a solidification of the pellicular layers, it is probably very likely that the shape of the lorica is influenced by internal and external environmental conditions. Many of the established 'species' probably derive from environmental differences. Here we should also point to the different modes of forming the lorica. 390

If we keep in mind that permanent cysts have already been described for several species we may conjecture that the sudden temporary occurrence in massive quantities, so characteristic for Tintinnoidea, is the result of the germination of these cysts. The first of these animals so created, of course form their loricae according to the environmental conditions prevailing during the germination of the cysts. When the animals multiply by normal fission, one of the daughter individuals always retains the old lorica. In this way loricae formed during different environmental conditions will remain together in the plankton samples. This perhaps explains the many 'varieties' (I am thinking for instance, of Tintinnopsis campanula, Tintinnopsis cincta, Tintinnopsis bütschlii, etc.). We must further consider that the tintinnids can leave their lorica behind for a period, swim around freely, and then form new loricae. These loricae also are formed in new environmental circumstances, in as much as the protoplasm finds itself in a different condition than at the moment of fission. The loricae never yield sufficiently sharp characteristics to be able to base the definition of species on them.

Let us now turn to the question of the position of Tintinnoidea as a group of infusorians. Only very little has been published regarding their relationships. This group of infusorians has usually, and for practical reasons, been treated separately; for example in the collection 'Nordisches Plankton' (northern plankton) they are completely divorced from the remaining ciliates as a separate group.

Delage and Herouard (Traite de Zoologie concrete(Definitive zoology), part 1, 1896) follow Bütschlii (Bronn's Classen und Ordnungen des Thierreichs (Classes and Orders of the Animal Kingdom), I., Protozoa, 1883-1887) and include Tintinnoidea under Oligotrichida which in turn are considered to be an aberrant group of Heterotrichida. (Geza Entz jr. (1909, p. 203) comes to the conclusion: ' Summarizing everything said sofar, we can say the following about the systematic position of the tintinnids: they are pelagic heterotrichs which live in shellsand exhibit so many particular characteristics that they may, with justification, be considered to be a separate family, that they are closely allied to the families of strombidians and ophryoscolecides, and may be inserted between these and the stentors. Their newly acquired special properties may be viewed as adaptations of the pelagic mode of living.') This classification is frequently found 391
again in the modern text books, e.g. Calkins Biology of Protozoa (1926, p.383).

Apart from the parasitic , and thus significantly changed Ophryoscolecidae, Oligotrichida is deemed to include the Halteriidae of which the most widely known genera are Laboea, Strombidium, and Halteria.

The work of Faure-Fremiet (1924) in particular has advanced our knowledge of this group considerably. He also considers a close relationship between these forms and the tintinnids to be probable, and divides the 'serie' (sic) of the Tintinnoidea into three families: Strombidinopsinae, Tintinnoinae, Strombidinae.

I have attempted to learn more about these ciliates which are closest to the Tintinnoidea.
In Naples I was able to investigate more closely three species, Strombidium sulcatum Clap. et Lachm., Laboea conica Lohm., and Laboea strobila Lohm. The knowledge regarding the nuclear conditions of these species is still very insufficient. Strombidium sulcatum (Fig. 85) posesses a wreath of twelve rather stout organelles but which have little similarity with the organelles of tintinnids. They surround an excentric

mouth, and also a kind of pistil. The macronucleus is a flattened, concave, somewhat irregular disk. The micronucleus is rather small and lies close to this disk. The nuclear equipment thus has a totally different aspect from that of the tintinnids; the adoral organelles are also not comparable.

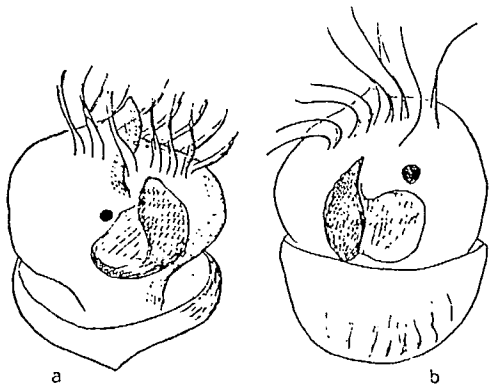


Fig. 85: Strombidium sulcatum Clap. et Lachm.
From the Gulf of Naples
a) obliquely from above b) side view. Technique: trichloracetic acid, iron hematoxylin.
Magnification 575:1.

Strombilidium gyrans (adherens) however, according to investigations by Enriques, seems to exhibit the same nuclear phenomena during fission as we have described for 392
tintinnids. The two macronuclei also are completely equal to those in most tintinnids (Tintinnopsis). It is not at all impossible that we have here an aberrant Tintinnopsis-species, or one swimming around without lorica. Also its tendency to attach itself with posterior end to objects is very characteristic for tintinnids. Tintinnids in their shells also have this tendency, and I have frequently observed it on Tintinnopsis campanula and Favella helgolandica. When these species are kept alive in small containers over extended periods (e.g. 24 hours), most individuals will be found attached to the bottom or on detritus, with the tip

of their shell; they continue to whirl lively with their ciliatures, and so bend right and left but without becoming detached from the substrate.

In Laboea conica (Figs. 86 and 87) the oral cilia actually stand on a collar which is always the case in tintinnids. They are also flat (flame-like) and their number is 16 or 18, also matching that of tintinnids.

The totally organic lorica is hardly distinct from the protoplasm: it is very hyaline and closed at the bottom. The nuclear equipment consists of several micronuclei (4?) and generally twelve macronuclei (in the vegetative state) which frequently have a desmose. This also then fully agrees with my observations made on higher Tintinnoidea.

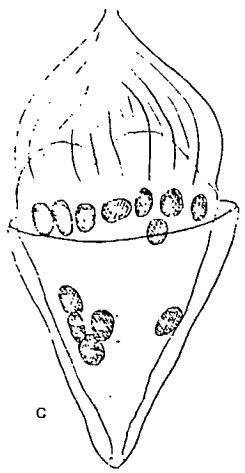


Fig. 86: Laboea conica Lohm.
From the Gulf of Naples. Complete animal, stained with iron hematoxylin. The animal is slightly shrunk, and the hyaline lorica is visible. Magnification 575:1.

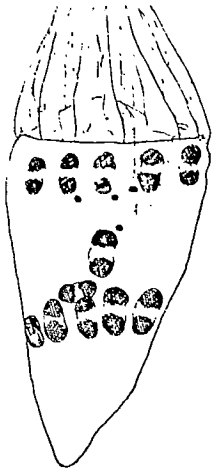


Fig. 87: Laboea conica Lohmann
Animal with desmose and four micronuclei.
Technique: trichloracetic acid, iron hematoxylin.
Magnification 575:1.

To complete this list, let me finally mention Laboea 393
strobila (Fig. 88). The typical ciliature characteristic of the tintinnids also applies to this species with triangular, plate-like organelles, arranged in a wreath around the mouth. The mouth is here also excentric, with a clearly discernible pistil. The cilia are also arranged in an interrupted spiral here, and their number is 20, a number which is also characteristic for many Tintinnoidea. The body has a small number of constrictions, four or five, which are perhaps some kind of inhibited division, in the same sense as is found in Polykrikos. In agreement with this hypothesis, the number of macronuclei is quite large, up to 28[1]. Several micronuclei also seem to be present. The sides of the entire body are covered with a pellicular covering which also follows the constrictions.

We thus come to the conclusion that the Halteriidae probably do not constitute a uniform group (they have also

1) Meunier (1910, p.147) describes a single macronucleus (but in unstained material). This data cannot be correct in my opinion, or perhaps the identification of Meunier's Conocyclis and Laboea (see Faure-Fremiet, 1924, p.79) is incorrect.

been divided into several sub-groups by Faure-Fremiet), but that Genus Laboea seems to be closest to the higher tintinnids without actually exhibiting signs of true primitivity. Genus Laboea is probably a shell-less (or almost shell-less) tribe of Tintinnoidea, and does not belong to the group of Halteridae. 394

But let us now ask ourselves which other family (or order) of Ciliata shows an affinity with Tintinnoidea, and we immediately think of Hypotrichida which are also always considered near Oligotrichida in the systematic handbooks. One family of Hypotrichida in particular, that of the Urostylidae, seems to have to be considered here.

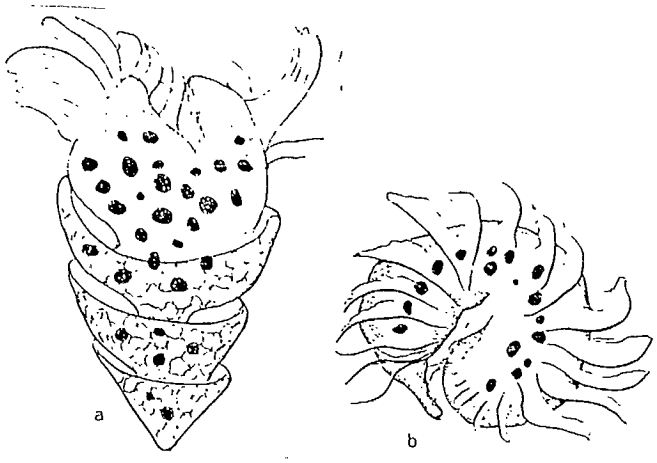


Fig. 88: Laboea strobila Lohmann
a) complete animal, side view.
b) top view of animal. Technique: trichloracetic acid, Ehrlich's hematoxylin.
Magnification 475:1. 393

I had several opportunities to investigate species of this family. All these species are characterized by several macronuclei which have a desmose during the largest part of their existence. In many cases there are only two macronuclei but in the elongated forms a larger number of these nuclei is usually found: the number of micronuclei may also be increased in such cases. I investigated Amphisia gibba O.F.Müller in some detail in Naples, and shall base my discourse on this species in particular (Fig. 89).

Fig. 89: Amphisia gibba O.F. Müller
From the Gulf of Naples. Technique: trichloracetic acid, iron hematoxylin. Drawn from the dorsal side. Magnification 450:1.

A detailed analysis of the somatic cilia reveals the following: The mouth, a longitudinal slit in the anterior third of the body, is accompanied by a row of large, plate-shaped organelles which clearly exhibit 'associative combs' and are oriented sideways. These organelles are located to the right of the mouth, looking at the ventral side of the animal. The front of the animal is marked by an oblique row of stout cilia whose basal bodies are clearly differentiated

from the ectoplasm. This row of cilia starts just at the end of the row of oral organelles, then bends to the left, and ends in a fine row of cilia which runs close to the left edge of the body, towards the posterior end of the animal where it joins the posterior organelles. The anterior part of this row of cilia consists of 15 cilia.

Several longitudinal rows of fine cilia are found everywhere 395
on the body, two of these on the ventral side.

The nuclear equipment usually consists of 16 macronuclei which often clearly exhibit a desmose. The desmose contains one or several dark bodies, especially on specimens stained with iron hematoxylin. This has also been observed by Calkins. Division of the hypotrichous infusorians and the associated changes in the nuclear equipment are strikingly similar to those in tintinnids (as Weyer's investigations (1930, p.160-165) on Gastrotyla show). Micronuclei are usually in the majority. I frequently counted six of them. When a desmose is present, division states of the micronuclei are also frequent. The macronuclei join and merge during fission.

This brief exposition makes it clear that the nuclear aspects (of Amphisia gibba) are completely equal to those of the Tintinnoidea: desmose, single macronucleus during fission, several micronuclei. (In the stentors we also have a merging of the macronuclei during fission, but never in conjunction with the formation of a desmose.) In the hypotrichous infusorians a new cytostome is also developed in the posterior half of the body during division, just as it is the case in Tintinnoidea. The peristome of the tintinnids does not start in the form of a spiral but (according to the description of Geza Entz, 1909, p.177) in the form of a curved line. In the heterotrichous infusorians (Stentor!) the new peristome also develops from a linear configuration but which seems to have a connection to the old peristome (Johnson, 1893).

Secondly, there are several Urostylidae which form casings (e.g. Stichotricha secunda). These loricae are usually open at both ends.

Thirdly, I must mention Salpingella, a genus which has a tilted wreath of peristomial organelles and which is possibly a transitional form.

I come to the conclusion then that it is best to consider the Tintinnoidea as having evolved from Urostylidae-like ancestors, and should probably be included under the hypotrichous infusorians. In connection with the formation of the lorica, the mouth has moved more towards the end of the body, became more rounded, but still continued to be excentric. The organelles laid themselves in a spiral around the mouth. Because of the rearrangement of these components, the anterior row of cilia moved away laterally, and now forms the lateral row of organelles which reach down as far as the cytopyge. The remaining lateral rows of 396
cilia can still be found in many species where they constitute the fine cilia which cover the body. The posterior organelles which anyway frequently tend to metamorphosis in Urostylidae have become the pedicle with which the animal attaches itself to the shell wall. The anterior part of the body of the Urostylidae, to the left of the mouth, probably became simply transformed in the pistil.
In any case, Tintinnoidea and the genus Laboea should no longer be described as Oligotrichida or Heterotrichida but should be accepted as true hypotrichous ciliates: their characteristics can without artificiality be interpreted as typically hypotrichous.

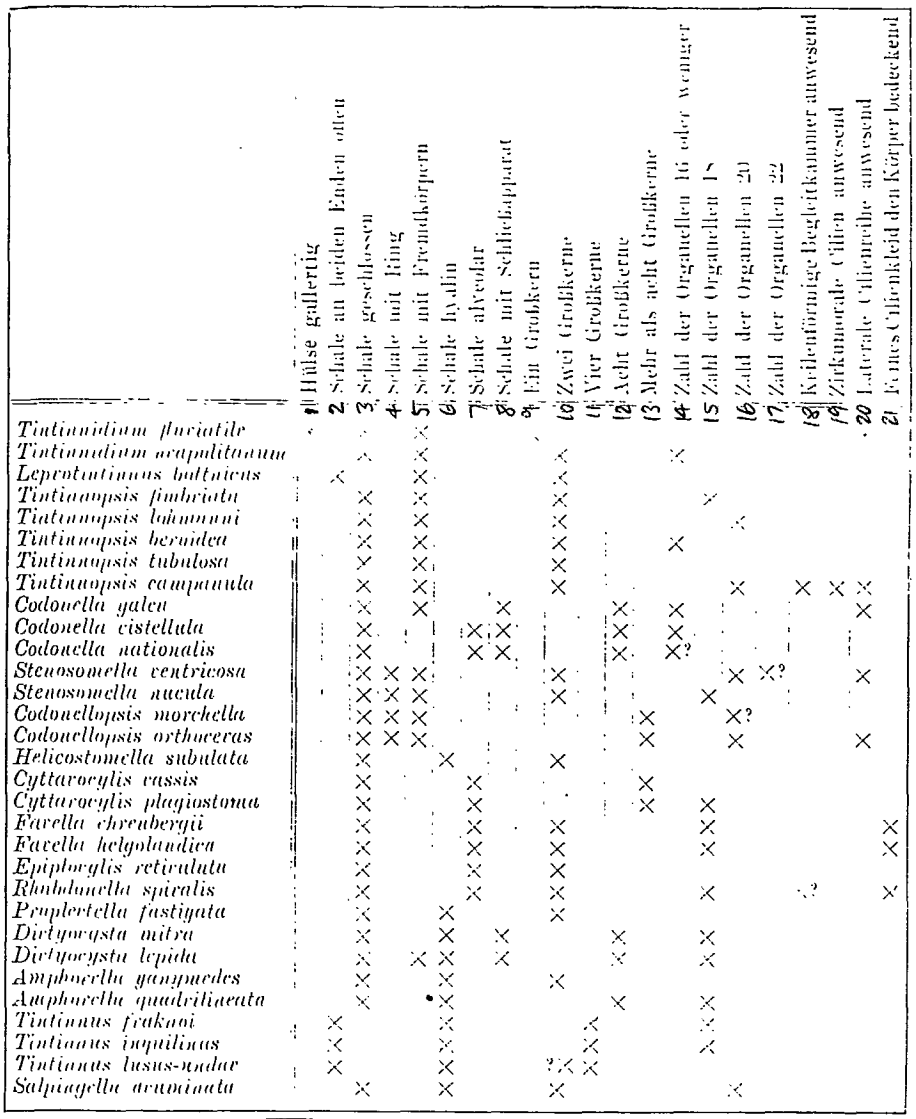
Now that we have thus analysed the position of the entire group more precisely, let us reconcile the taxonomy of the Tintinnoidea with the new knowledge of the cell body. But this is a much more difficult undertaking since it requires us to break with the assumption that the lorica constitutes an important characteristic. The shape of the body can be taken into account only for a few species since it is usually claviform and only rarely assumes a different form. Only Salpingella (and partially(?) Amphorella) deviate as was already mentioned, and so are closer to Urostylidae than any other.

The lorica in its lack of structure (I ignore the primary alveoli of Brandt and Biedermann since I cannot associate any taxonomic value with such structures) approaches that of Laboea, and I would like to conclude from this that this genus should be differentiated from the remaining typical tintinnids, and be considered an aberrant form of this genus.

If we now no longer consider the characteristics of the loricae as the primary principle of classification[1] we arrive at the following classification based on the number of macronuclei in the vegetative state, as foremost characteristic:

1. One macronucleus	Tintinnidium fluviatile
Several macronuclei	2
2. Two macronuclei	3
More than two macronuclei	4
3. Number of organelles = 18	5
Number of organelles = 20	6
Number of organelles less than 18	7
4. Four macronuclei	Tintinnus
Eight macronuclei	8
More than eight macronuclei	9
5. Lorica always without foreign particles, with pointed end	Favella-Rhabdonella
Lorica with foreign particles	10
6. Cell with clavicles	Tintinnopsis campanula
Cell without clavicles	11
7. Lorica soft, gelatinous	Tintinnidium neapolitanum
Lorica solid, with foreign particles	Tintinnopsis beroidea
8. Number of organelles = 16	Codonella
Number of organelles = 18, lorica with window structure	Dictyocysta
Shell without fine structure, hyaline	Amphorella
9. Shell with foreign particles and with ring, lateral wreath of cilia	Codonellopsis
Shell without foreign particles, alveolar	Cyttarocylis
10. Shell fringed, without ring	Tintinnopsis fimbriata
Shell with ring	Stenosomella
11. Shell with foreign particles	Tintinnopsis lohmanni
Shell without foreign particles	Salpingella

1) Brandt also devised a system which always first considers cell characteristics (1907, p.43-47). The more recent systematic researchers (Jörgensen, Kofoid-Campbell) more and more ignored this principle, and emphasized the characteristics of the shell more and more: as a result, the system has more and more lost its values as a natural system. Brandt also



1 Lorica gelatinous
2 Shell open at both ends
3 Shell closed
4 Shell with ring
5 Shell with foreign particles
6 Shell hyaline
7 Shell alveolar
8 Shell with 'Schliessapparat' (interlocking set of membranellae)
9 One macronucleus
10 Two macronuclei
11 Four macronuclei
12 Eight macronuclei
13 More than eight macronuclei
14 Number of organelles = 16 or less
15 Number of organelles = 18
16 Number of organelles = 20
17 Number of organelles = 22

---

attributed particular value to the typical number of macronuclei.

18 Wedgeshaped associative comb present
19 Circumoral cilia present
20 Lateral row of cilia present
21 Fine coat of cilia covering the body

Since the number of macronuclei is always very constant (much more constant than had previously been assumed) I think it can be used as an important genus characteristic; and it is a much better one than the shape of the shell. We consequently automatically reach the conclusion that the currently common classification leads to systematic errors.
Because, to begin with, the genus Tintinnopsis does not seem to be a consistent genus: Tintinnopsis campanula at any rate has an important peculiarity: the associative combs. The genera Favella and Rhabdonella form a unit. Tintinnopsis neapolitanum and Tintinnopsis beroidea are very closely related, as are Tintinnopsis fimbriata and Stenosomella genus.

The genera Dictyocysta and Codonella are probably very closely related, they differ in only a single characteristic - which with closer analysis might even prove to be wrong - : The number of organelles. But both have a 'Schliessapparat'.

It is also not impossible at all that future investigations will show that a difference in the number of organelles for instance may only have the power of a species character, 399
and that the number of macronuclei is the more important characteristic[1]. We must then bring together in a single genus, e.g. the genera Tintinnidium (with the exception of T. fluviatile), Leprotintinnus, Tintinnopsis, Stenosomella, Helicostomella, Favella, Epiplocylis, Rhabdonella, Amphorella, Ganymedes, and similarly Codonella, Dictyocysta, Amphorella quadrilineata, and also Codonellopsis and Cyttarocylis.

1) I am obviously opposed to Geza Entz's jr. opinion who claims (1909, p.160) that the number of nuclei is not a constant characteristic. But we have seen already that during the vegetative stage of life the number of nuclei is certainly very characteristic, but that their number

Of course we are not yet ready to provide a definite solution for the systematic classification of the Tintinnoidea. Too many data are still missing. But it is evident that the shell taxonomy becomes untenable as our knowledge of the cell body increases. A good taxonomy, based on natural relationships, is the only one worth striving for; consequently, tintinnid researchers must do everything to increase their knowledge of the cells of tintinnids, and no longer be led astray with the shell question. This is even more desirable in view of the fact that the great and, in bibliographic respect immensely important work of Kofoid and Campbell (Conspectus, 1929) bases a completely new classification only on the shells, and so, as a systematic experiment, must be considered to have miscarried, as I have been able to show repeatedly. How much better would it have been if these two authors had made the last words of the great work of Geza Entz jr. (1909, p. 204-205) their own: 'If the tintinnids had been studied under consideration of all these variations, correspondences could certainly be found which would allow a clearer assessment of relational circumstances: but as long as the morphological circumstances of almost 150 species and 300 varieties are only known for a few of them, hardly anything definite can be said in this matter'.

'This is also the reason why I do not undertake to give a classification of the family of tintinnids. The one very problematic merit of such an undertaking would probably only be this: to have increased the number of known systems by one.'

I can only emphasize one result of my investigations: the number of macronuclei is very constant for different genera which would also be classified together on the basis of the lorica. Most other characteristics, especially also pectinelle and associative combs, lateral rows of cilia etc. have only general value together. The shells have a specific value 400

1) may vary during reproduction. I believe, however, that it is always possible to exclude from systematic studies such animals which are engaged in reproduction.

only when small differences are abstracted. These latter differences probably have no hereditary value in most cases since they depend on the age of the individual, their life history, and various circumstances. Only in cases where somatic characteristics are always associated with characteristics of the lorica can the loricae also be considered as systematic objects.

Postscript

After this manuscript was ready for publication the new work of Kofoid came to my knowledge (C.A. Kofoid, Factors in the Evolution of the pelagic ciliate, the Tintinnoinea; Contrib. to marine biology, Stanford Univ. Press, 1930). Two views are put forward in this work which are important with respect to my own work. The first is Kofoid's statement that 'the physical nature of the substance of the lorica appears to be a generic or family character,in some instances at least' (p.9). Our present knowledge, however, cannot be reconciled with this statement, all the more since I have been able to point out repeatedly that the species collected into the same families often seem to belong to entirely different families. But it is especially these families which were established on the basis of the loricae; if one now concludes that these properties are characteristic for a particular family then this is obviously true.

The second point is that Kofoid feels he has to set up the theory that the new loricae are formed only after division (p.6), and that the posterior part of the lorica of the daughter animal which keeps the old peristome, is manufactured by the other animal, or at least modelled by it. But Kofoid offers no proof whatever for this theory and, although it is very attractive, it contradicts my results reported in the present essay. Because, firstly a new lorica is formed also at times other than during division, and secondly the actual fission very probably takes only very little time (More advanced stages of division are found only very rarely); I have repeatedly pointed out the fact that the one daughter animal forms its own shell, without

assistance from the other daughter. Conclusions based on this (Kofoid's) theory are therefore not admissible in my judgement. The reasons for his theory which Kofoid lists on p. 14 can be perfectly explained even if one assumes that the daughter animal forms the entire shell. We have also seen already that the animal is quite capable of reaching the posterior end of its shell after the separation. 401

With respect to this latest work of Kofoid's I must again make the point that, although Kofoid and Campbell have done much important work for the group of the tintinnids, the systematic conclusion of their thoughts goes much too far, especially since it is based on unproved hypotheses and exclusively on characteristics of the lorica.

Literaturverzeichnis.

1 Biedermann, R. (1893): Über die Struktur der Tintinnengehäuse. Diss. Kiel.
2 Brandt, K. (1907): Die Tintinnodeen der Planktonexpedition. Ergebn. Bd. 3 L. a. Systematischer Teil (mit Atlas 1906).
3 van Breemen, P. J. (1905): Plankton van Noordzee en Zuiderzee. Diss. Amsterdam.
4 Bresslau, E. (1906): Eine Anzahl Tintinnen aus dem Plancton der Bucht von Rio de Janeiro. Verhandl. deutsch. zool. Ges. Bd. 16.
5 Busch, W. (1925): Beitrag zur Kenntnis der Gehäusebildung bei den Tintinnidae. Arch. f. Protistenk. Bd. 53.
6 Calkins, G. N. (1926): The biology of the Protozoa.
7 Campbell, A. S. (1926): The cytology of Tintinnopsis nucula (Fol) Laackmann. Univ. California Bull. Zool. Vol. 29.
8 — (1927): Studies on the marine ciliate Favella (Jörgensen). Ibid. Vol. 29.
9 Chatton, E. (1920): Les Péridiens parasites. Arch. de zool. Expér. et Gén. T. 59.
10 v. Daday, E. (1887): Monographie der Familie der Tintinnodeen. Mitt. d. zool. Stat. Bd. 7. Neapel.
11 Delage, G. et Hérouard, E. (1896): Traité de Zoologie concrète. I. La cellule et les Protozoaires. Paris.
12 Entz sen., G. (1885): Zur näheren Kenntnis der Tintinnodeen. Mitt. d. zool. Stat. Bd. 6. Neapel.
13 — jr. (1909): Studien über Organisation und Biologie der Tintinniden. Arch. f. Protistenk. Bd. 15.
14 — (1929): Über Struktur und Funktion der Membrannlae der Tintinniden, speziell von Petalotricha ampulla. Xe Congrès International de Zoologie, Section V, Evertébrés p. 887—895.
15 Fauré-Fremiet, E. (1924): Contribution à la connaissance des infusoires planctoniques. Bull. Biol. de France et de Belgique Suppl. 6.

16 Fol, H. 1884): Sur la Famille des Tintinnodea. Recueil Zool. Suisse T. 1.
17 van Gloor, A. C. J. (1923): Beiträge zur Kenntnis des Nannoplanktons der südlichen Nordsee. Verh. Rijksinst. Visscherijond. Dl. 1 Afl. 2.
18 Hofker, J. (1924): Over Hulsvorming en „microsporen" der Tintinnodea. Tijdschr. Ned. Dierk. Vereen. Ser. 2 Bd. 18.
19 — (1924): Die Trichloressigsäure als Fixierungsmittel. Zeitsch. f. wiss. Mikrosk. Bd. 38 p. 130—137.
20 — (1922): Protozoa. in Flora en Fauna der Zuiderzee. Helder.
21 — (1930): Besprechung des Conspectus von Kofoid und Campbell. Die Naturw. Bd. 18 p. 395.
22 — 1930): The study of plancton by means of Canadabalsam preparations. Pubbl. Staz. Zool. Napoli Vol. 10 p. 279—280.
23 — (1931): Die Bildung der Tintinnengehäuse. Tijdsch. Ned. Dierk. Vereen. Ser. 3 Bd. 2.
24 Jorgensen, E. (1899): Über die Tintinnodeen der norwegischen Westküste. Bergens Museum Aarborg 1899.
25 — 1924): Mediterranean Tintinnidae. Rept. Danish. Oceanograph. Exp. 1908—1910 Bd 2 (Biol.).
26 — (1927): Tintinnidae. Grimpe u. Wagler's Die Tierwelt der Nord- und Ostsee. Lief. 8.
27 Kofoid, C. A. (1915): Notes on Tintinnoina. Univ. Calif. Publ. Zool. Bd. 16.
28 Kofoid, C. A. und Campbell, A. S. (1929): A conspectus of the Marine and Fresh-Water Ciliata belonging to the suborder Tintinnoinea. Univ. Calif. Publ. Zool. Bd. 34.
29 Laackmann, H. (1906): Ungeschlechtliche und geschlechtliche Fortpflanzung der Tintinnen. Wiss. Meeresunters. Abt. Kiel Bd. 10.
30 Merckle, H. (1909): Untersuchungen an Tintinnodeen der Nord- und Ostsee. Diss. Kiel.
31 Meunier, A. (1919): Microplancton de la Mer Flamande. Vol. 4. Mém. Mus. Roy. Hist. Nat. Belgique T. 8.
32 Schuurmans Stekhoven jr., J. H. (1931): Ökologische und morphologische Notizen über Zuiderseenematoden. 1. Die westliche Hälfte der Zuidersee. Zeitschr. f. Morph. u. Ökol. d. Tiere Bd. 20 H. 4.
33 Schweyer, A. W. (1909): Zur Kenntnis des Tintinnodeenweichkörpers. Arch. f. Protistenk. Bd. 18.
34 Weyer, G. (1930): Untersuchungen über die Morphologie und Physiologie des Formwechsels der Gastrostyla steinii Engelmann. Arch. f. Protistenk. Bd. 71.

Bibliography

1. On the structure of the shells of tintinnids.

2. The Tintinnoidea of the Plankton Expedition. Result, Volume 3,L a. Systematic part (with atlas, 1906).

3. Plankton of the North Sea and the Zuider Zee.

4. A number of tintinnids in the plankton from the Bay of Rio de Janeiro. Proceedings of the German Zoological Society. Volume 16.

5. Contribution to the knowledge of the formation of shells in the tintinnids. Archive for protistology. Volume 53.

9. The parasitic peridinians. Archive of experimental and general zoology. Volume 59.

10. Monograph on the family of Tintinnoidea. Reports from the zoological station, volume 7, Naples.

11. Definitive zoology. I. The cell and the protozea.

12. Advances in the knowledge of the Tintinnoidea. Reports from the zoological station, volume 6, Naples.

13. Studies of the organisation and biology of the tintinnids. Archive, for protistilogy. Volume 15.

14. On the structure and function of the membranelles of the tintinnids, particularly of Petalotricha ampulla. Tenth International Congress of Zoology, Section V, Invertebrates.

15. Contribution to the knowledge of the planktonic infusorians. Biology report of France and Belgium.

16. On the family of Tintinnoidea. Swiss zoological review, Volume 1.

17. Contributions to the knowledge of the Nannoplankton of the southern part of the North Sea. Proceedings of the Imperial Institute of Fisheries (Holland).

18. On the formation of loricae and 'microspores' in Tintinnoidea. Journal of the Dutch Zoological Society, Series 2, Volume 18.

19. Trichloracetic acid as a fixative. Journal for scientific microscopy. Volume 38.

20. Protozoa in flora and fauna of the Zuider Zee.

21. Review of the Conspectus of Kofoid and Campbell. Natural Science, Volume 18.

22. ———————— (Publication of the zoological station, Naples).

23. The formation of the shells of tintinnids. Journal of the Dutch zoological society, Series 3, Volume 2.

24. On the Tintinnoidea at the westcoast of Norway.

26. Tintinnidae in: Grimpe and Wagler, The fauna of North Sea and Baltic Sea.

29. Asexual and sexual reproduction of the tintinnids. Scientific Oceanography.

30. Investigations on the Tintinnodea of North Sea and Baltic Sea. Dissertation.

31. Microplankton of the Flemish Sea, Report of the Royal Museum of Natural History in Belgium, Volume 8.

32. Ecological and morphological notes on nematodes of the Zuider Zee. 1. The western part of the Zuider Zee. Journal for morphology and ecology of animals, Volume 20, issue 4.

33. Contribution to the knowledge of the cell of Tintinnoidea. Archive for protistology, Volume 18.

34. Investigations on the morphology and physiology of the metamorphosis of Gastrotyla steinii Engelmann. Archive for protistology, Volume 71.