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by Hans Laackmann

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ASEXUAL AND SEXUAL REPRODUCTION IN THE TINTINNUS GROUP

By Hans Laackmann

(Ungeschlechtliche und geschlechtliche Fortpflanzung der Tintinnen. Wissenschaftliche Meeresuntersuchungen, Vol. 10, pp. 15-38, 1906.)

Introduction

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Historical summary of research into the reproduction of the Tintinnus group.** Asexual reproduction, the transverse fission or budding in the sense of earlier investigators, has been observed by all investigators who have dealt with this interesting group of heterotrichous Ciliata. O. Fr. Müller figured an advanced fission stage of Tintinnus inquilinus (1776, Pl. 9, Fig. 2), two animals immediately after completed constriction. Claparede and Lachmann observed in Ptychocylis urnula Cl. & L. (Brandt) the insertion of the new aboral wreath of cilia (1859, Pl. 8, Fig. 14). Codonella lagenula Cl. & L. is represented by

* Figures in the margin give page numbers in the original. -- TRANSL.

** The term "Tintinnus group" is an attempt to reproduce the general sense of the German plural "Tintinnen," which does not clearly refer to any specific taxonomic category. -- TRANSL.

an illustration of two animalcules (Pl. 8, Fig. 11). They do not, however, provide an exact description of the fission process.

Detailed information on the fission, especially as relates to the inception of a new peristome, has been provided by Entz in respect of Tintinnidium fluviatile Stein (1885, p. 193). But neither he nor Daday provided details concerning the behavior of the nuclei. Subsequent data on the Tintinnus group are confined almost entirely to the shell, or they are of a faunistic-taxonomic nature. A budding stage in Tintinnus gracilis Brdt. was still figured by Vanhöffen (1897, Pl. V, Fig. 30).

The fact that, in addition to fission, the Tintinnus group also reproduces by other means can already be established from an illustration in Claparede and Lachmann. In Pl. 8, Fig. 3, we find within the shell of Tintinnus amphora a stalked animalcule, which lacks the adoral wreath of cilia. Claparede and Lachmann believe it to be a cyst of unknown provenance, but they suggest that it may represent a stage in the development of Tintinnus. Kent shares the latter view, but his assumption is based merely on the observation of Claparede and Lachmann.

The first detailed information on the sexual development of the Tintinnus group is found in Häckel. In Pl. XXVII, Fig. 1, he provides an illustration of Cyttarocylis cassis, where the animalcule is filled with numerous spores. Häckel also figures spores of Codonella campanella as well as ciliate embryos (Figs. 11, 13, 14).

Later investigators doubted these data. Entz and von Daday regard the presumed spores and holotrichous embryos as embryos of parasitic Acineta. Von Daday believes that this assertion is the more justified as he found numerous pelagic, freely floating Acineta in

association with the Tintinnus group.

Hensen believes that the Tintinnus group may very well reproduce by means of spores. In the Baltic Sea and in Kiel Bay he found in the shells of Tintinnus subulatus, Tintinnus acuminatus, Tintinnus fistularis* (Möbius) (= Cyttarocylis helix Cl. & L.) and Tintinnus (Cyttarocylis) denticulatus spores and cysts, which he assumed were development stages of the abovenamed species.

Following a suggestion by Prof. Dr. Brandt, I have investigated Hensen's discoveries in greater detail, and the present paper is the result.

Material and methods of investigation 16

The specimens for my investigations were caught by me in the Bay of Kiel, either in the inner harbor from the Seeburg Bridge or in the outer part of the bay at Laboe. During periods when the development stages of the Tintinnus group were common in the plankton, I made two to three plankton catches per week; otherwise I collected at least once a week.

My investigations were favored by the fact that thanks to the kindness of Prof. Dr. Lohmann I had the opportunity of obtaining plankton from the outer bay. I should hereby like to express my deep gratitude to Prof. Lohmann for enabling me to participate in the expeditions which he undertook in behalf of the Committee for the Scientific Investigation of German Seas.

On the other hand, the surface catches made by me in the inner harbor were at certain times more suitable for my studies than the vertical catches from a depth of 15 m at Laboe, since I found in the

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* Spelling doubtful because of poor xerox. -- TRANSL.

inner harbor a much purer assemblage of Tintinnus, which had particularly abundant development stages.

A part of the specimens was killed immediately, another part was kept alive for investigation. The investigation of living specimens was undertaken immediately after the catch. The animals are very delicate and exhibit lively movement only on the first day. Many have died on the second day. The movement of the living animals is slow, they soon withdraw into the housing. I was never able to keep Tintinnus specimens alive for more than half a week, even if the container in which they were kept was fairly large.

It was found to be practical in the study of living specimens to transport the plankton catch in only a small quantity of seawater (one vertical catch per $\frac{1}{2}$ to 1 liter of water). This increases the chances that development stages will be found. Once these have been isolated they can be observed separately in suspended droplets. Even though this results in an earlier death of the plankton mass, the saving in time is considerable. No damage to the Tinntinus specimens occurs even in this little diluted plankton, as the animalcules react to disturbances by immediately withdrawing into the housing, and only later to they extend again.

To kill the catches I used Flemming's solution (chromosmium-acetic acid), chromosmium acid, picric sulfuric acid, picric acid (concentrated) with a few drops of chromic acid, formol and sublimate. All of these reagents produced good results, with the exception of sublimate, which never produced a distinct differentiation of the nuclei.

The plankton mass was subjected for a short time (3-5 minutes) to the fixing liquid, after which it was washed thoroughly and conserved

in 60-70 per cent alcohol.

Beautiful colorings were achieved with hemalum, boric carmine, and picric carmine; the first was used especially for bringing out the micronuclei. For the study of the shells* we prepared mounts with glycerin. Such mounts of Tintinnopsis species are not suitable for studies of the soft body of the animal, as the shells, which are closely covered with foreign bodies, are nearly opaque. For this purpose I dyed the entire fixed catch or a part thereof, after obtaining a fairly pure Tintinnus material by pouring off the lighter diatoms and Ceratia; the dyed mass as then placed in Canada balsam. This lightens the color of the shells to such an extent that they no longer present any impediment to the investigation of the dyed nuclei.

Systematic description of the Tintinnus group occurring in Kiel Bay

Genus Tintinniudium Kent.

Tintinnidium mucicola Cl. & L.

(Tintinnus mucicola. Cl. & L., Pl. 8, Fig. 12.) Brandt, 1906, Pl. 70, Figs. 8, 9, 10.

The jelly-like shell is brownish in color, often closely covered with diatoms; the shape is often rounded off cylindrically at the aboral end. The length of the shell varies from 100 to 240 microns, the width from 45 to 63 microns. The very delicate animal has two round nuclei and two small micronuclei measuring 1 micron. Occurrence in the plankton is irregular, never abundant.

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* Literal translation of "Hülse." -- TRANSL.

Genus Tintinnus Schrank.

(Amphorella v. Daday.)

Tintinnus subulatus Ehrenberg

(Möbius: Systematic description of animals, etc. Pl. VIII, Fig. 34. Brandt, 1906, Pl. 65, Figs. 1, 2.)

The transparent shell made it possible to observe the living animal in detail. The slim body terminates in a long stalk, which is attached at different points, usually in the centre, to the shell.* If the animal is swimming and moving the stalk is stretched out tautly. If the animal is stretched but does not move, one notes in the stalk one or several spherical dilations. Such swellings were already observed by Fol in Tintinnus spiralis Fol and by von Daday in Tintinnus inquilinus and angustatus (1884, Pl. 4, Fig. 4; 1887, Pl. 18, Figs. 10, 15). Von Daday notes that the swellings do not occur in all individuals of the same species. In Tintinnus subulatus I observed the following: During a sudden withdrawal of the stretched animal into the shell, which can easily be provoked by vibration, the body slides away over the stalk. The latter forms loops that adhere closely to the body. The stalk then becomes detached from the shell wall; at the same time, 2 or 3 nodules form in the loops and become gradually larger. When the first dilation on the body has reached a certain size the plasm suddenly flows into the body. This process is repeated with the other nodules, so that a jerking movement results during the contraction of the stalk. A small portion of the stalk is not withdrawn. When the danger has passed the end of the short portion of the stalk that was not withdrawn and that hardly

* Literally: "housing." The context indicates that the term is synonymous with "shell." -- TRANSL.

changed position in the shell, adheres to the shell wall; the body stretches by means of a vigorous oscillation of the cilia. If the animal pauses during its locomotion, the body withdraws slightly into the shell, and the stalk forms nodules. Such phenomena can be observed only in animals with a long stalk; I have also observed them in Tintinnidium mucicula.

This observation induces me to explain the contractibility of the Tintinnus group by a tension in the cuticula. The stalk is attached to the shell wall by means of an attachment apparatus such as has been demonstrated by Entz in Tintinnus amphora and Tintinnidium fluviatile. By locomotion the expansible cuticula becomes tensed and, at the same time, the protoplasm is caused to flow into the stalk. As soon as locomotion ceases the cuticula contracts. In long, thin stalks such as that of Tint. subulatus the viscous plasm prevents the membrane from immediately resuming its quiescent state. In such a case, nodules form in the stalk; the plasm is being forced in spurts through the cuticula, which has tensed like a membrane, into the body. If the contraction occurs slowly the plasm flows gradually into the body, and nodules do not form in the stalk.

Tintinnus subulatus has 2 elongated, nearly round nuclei and 2 very small micronuclei not hitherto observed. Its occurrence in the plankton falls in the period from August to November.

Tintinnus subulatus var. kiliensis n. v.

(Pl. I, Figs. 1 and 3)

The shape of the shell is cylindrical, the posterior part terminates abruptly in a short point. The anterior end exhibits spiral rings similar to those of Tintinnus subulatus, but they are much more delicate. This variety differs from Tintinnus subulatus both in the length and the shape of the shell. Whereas the T. subulatus caught by me exhibit a shallow indentation in the centre and terminate gradually in a point that is often curved irregularly, T. s. var. kiliensis has a strictly cylindrical living chamber, which terminates abruptly in a short, straight point.

This form resembles the unnamed species figured by Fol (1884, Fig. 15), which v. Daday regards as Tintinnus inquilinus. However, the specimen in that figure lacks the spiral rings. The size of the shells agrees with that of the form described by v. Daday as Amphorella subulata.

Tintinnus subulatus var. kiliensis has the same width as T. subulatus. Its length, on average, is considerably less. Shells that are longer than those of T. subulatus are rare.

In this instance, var. kiliensis had many spiral rings (up to 30), 18
whereas T. subulatus had few or none.

If we compare the living chambers, i.e., the shells without the ornamental spiral rings, we find that they are invariably much shorter than in T. subulatus. In the table on p. 9 we are giving the measurements for a number of shells of the two forms, in microns.

The animal has two rounded nuclei with a fine nuclear framework and 2 round micronuclei measuring 1-2 microns, larger and more easily

	Length of shell	Pointed part	Living chamber	Length of rings	Number of rings	Width, aperture	Width, centre
Tintinnus subulatus var. *kiliensis*	97	31	87	10	4	21	21
	114	32	100	14	4	21	21
	124	37	104	20	5	21	21
	146	50	125	21	5	22	22
	156	54	138	18	6	21	21
	176	40	135	41	11	22	22
	190	67	134	46	12	22	22
	240	67	140	100	30	22	22
Tintinnus subulatus	200	87	200	0	0	21	14
	282	125	267	15	4	23	19
	303	108	244	59	15	24	17
	334	162	309	25	6	24	14
	445	189	310	135	38	24	19
	516	195	305	211	60	24	20

distinguishable than in T. subulatus.

I caught this variety in July and August, earlier than T. subulatus. On 9 August, a vertical catch contained abundant numbers of both forms. By its sharp point and its lesser length, the variety was easily distinguishable from T. subulatus. On 14 August, this form attained is maximum abundance in the inner harbor.

Tintinnus acuminatus Cl. & L.

(Brandt, 1906, Pl. 66, Figs. 3 and 4)

The animal is attached to the posterior part of the shell by the stalk. It has two spherical nuclei with a distinct, coarse nuclear

frame. The nuclei are close together in the posterior part of the body. We also observed two micronuclei.

This species occurs in winter, from November to January.

Genus Tintinnopsis Stein.

Tintinnopsis ventricosa Cl. & L.

(Brandt, 1906, Pl. 17, Fig. 2; Pl. 18, Figs. 1, 2.)

(Pl. I, Fig. 3.)

Two Tintinnopsis species are particularly abundant in Kiel Bay; either may be a candidate for Tintinnopsis ventricosa. Both species possess a jelly-like, flexible dilation*. Otherwise they differ considerably in size as well as in shape. In 1905, van Breemen in his study Plankton van Noordzee en Zuiderzee used this feature to divide Tintinnopsis ventricosa into a large and a small form, which was pointed out to me by Prof. Brandt even before the publication of the study. The length of his large form is 70-99 microns, the width is 64-80 microns. The measurements of the small form are: Length 35-64 microns; width 28-45 microns. Fol describes from Villafranca the large form under the name Codonella ventricosa (1884, Fig. 12). He uses the name Codonella nucula (Fig. 13) for a smaller Tintinnopsis form with a flexible dilation.

Jørgensen found only the large form at Bergen, with a length of 19
86-88 microns; its dimensions, as he notes, differ considerably from those of the specimens caught by Entz and von Daday at Naples. A smaller form, whose dilation resembles that of T. ventricosa, is figured by him as Tintinnopsis nitida Brdt. var. ovalis.

Claparede and Lachmann do not provide any measurements of

* "Aufsatz." The term is open to many interpretations. -- TRANSL.

Tintinnopsis ventricosa. As their description is based on Norwegian specimens, the shells with the larger dimensions ought to be considered T. ventricosa.

I did not find Tintinnopsis ventricosa with its typical shape and size in the plankton of Kiel Bay. The larger shells that are found here are distinguished by a dilated aperture rim. In his atlas on the Tintinnodea of the Plankton Expedition, Brandt provides a rather exact illustration of this species. In the lines that follow I shall, in agreement with Brandt, describe this species as Tintinnopsis ventricosa. It may be appropriate to designate the form with a dilated aperture rim as a variety of T. ventricosa.

The length of the Kiel specimens is 64-94 microns, the width is 54-81 microns. The great majority of the shells measures 80-87 microns in length and 67-75 microns in width.

The jelly-like, flexible dilation was always found in living animals. Its height is usually 10 microns. Sometimes it is so heavily encrusted with foreign bodies that it reaches a height of 45 microns.

The animal has two elongated-oval nuclei and two micronuclei that are closely contiguous to the former; the micronuclei have a diameter of 2 microns. Crevices in the nuclei were observed frequently.

T. ventricosa occurs in winter, a time when the smaller form, which we shall term Tintinnopsis nucula Fol, is only sparse.

Tintinnopsis nucula Fol.

(Figs. 4, 5)

The second Tintinnopsis form with flexible dilation which is most common in the Bay of Kiel, is easily distinguished from the preceding one in its smaller size and in the absence of a dilated aperture rim. In Pl. I, Figs. 4, 5, I have figured two shells, one of them almost spherical and the other elongated; the former (Fig. 4) is by far the most common. I found it in nearly every catch, while the elongated form (Fig. 5) was found only in a few catches during November.

Following a suggestion by Prof. Brandt, I have named this form Tintinnopsis nucula Fol, so as not to introduce a new name. At the same time I should like to refer the reader who may be interested in a more detailed interpretation to the soon to be published text to Brandt's atlas on the Tintinnodea of the plankton expedition. I should also like to note that in separating the two forms with flexible dilations but with different sizes I was also motivated by the difference in spore formation, which will be dealt with in greater detail.

The length of the shells is 44-58 microns, the width is 40-50 microns. The jelly-like dilation which was never lacking in living specimens, has a height of about 9 microns. As in T. ventricosa, it may be heavily encrusted with foreign bodies, in which case it has a height of 20 microns.

The animal has two nuclei, which are usually elongated. The nuclear framework is very fine, and only rarely did I observe a coarser structure.

A striking feature, which is particularly distinct in this

small species, is the nuclear slit or crevice,* which occurred fairly frequently among the Tintinnus group caught by me. It is present among all of the species occurring in the Bay of Kiel.

Von Daday attributes this crevice only to certain species (Amphorella punctatostriata v. Dad., Pl. 18, Fig. 19. Tintinnopsis nucula Fol, Pl. 19, Fig. 30). Entz observed it in Tintinnidium fluviatile. Both investigators describe the crevice as a fusiform cavity. In the Tintinnus specimens observed by me the crevice had the same thickness throughout, like some sort of colorless wall dividing the nucleus into two unequal, rarely equal, parts (Fig. 24). When fixed, the nucleus is slightly constricted at the crevice.

In addition to the two elongated meganuclei, I was always able 20
to observe in Tintinnopsis nucula two micronuclei; they were fairly large, having a diameter of 2 microns. Their position in relation to the meganuclei is fairly constant. Most commonly they are located on the narrow side of the meganuclei.

Tintinnopsis beroidea Stein.

(Brandt, 1896, Fig. 4; 1906, Pl. 16, Figs. 5, 6, 7.)

(Pl. I, Figs. 6, 7, 8.)

The shell of the form that occurs in the Bay of Kiel consists of a living chamber with an elongated point and a cylindrical dilation, which, like the living chamber, is encrusted with foreign bodies. The dilation may occasionally be lacking (Fig. 6). This, I suspect, is the

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* "Kernsperult," a term not found in any of the available dictionaries, subsequently termed "Kernspalt." "Spalt" may mean fissure, crevice, slit, crack, etc. -- TRANSL.

case with young, immature shells. On the other hand, I also caught shells where the dilation was longer than the living chamber. In this case the total length was 90 microns, of which the living chamber accounted for 37.5 microns (Fig. 8).

In the table that follows I have provided the measurements of five shells with dilations of different heights:

Total length of shell . .	46	47,5	52,5	60	70	90
Length of living chamber . .	46	40	45	40	50	37,5
Width . .	32	27,5	25	27,5	35	27,5
Length of dilation . .	0	7,5	7,5	20	20	52,5
Width . .	0	25	20	20	25	20

The animal has two round or elongated nuclei, often with a crevice, and two small micronuclei measuring 1 micron.

Tintinnopsis baltica Brandt

(Brandt, 1906, Pl. 15, Figs. 6, 8, 9, 15.)

In the shells caught in Kiel Bay I was usually able to distinguish clearly two parts: a rounded living chamber terminating in a point, and a cylindrical part, expanding into a wide brim. The cylindrical part often bears bulge-like spiral rings.

This species may also have additional dilations with a considerable height (50 microns). The latter forms occur frequently in September and October. (Brandt, 1906, Pl. 16, Fig. 4.) I observed two nuclei and two micronuclei.

Tintinnopsis baltica var. rotundata n. v.

(Pl. I, Fig. 9.)

This variety differs from Tintinnopsis baltica Brdt. in that the living chamber, the cylindrical dilation and the brim merge through gradual transitions ["in einander übergehen"], the point on the posterior end is rounded, so that the shape of the shell is that of a goblet. It resembles the shape of Tintinnopsis cyathus var. annulata v. Daday, but differs considerably in size. The measurements of T. cyathus var. annulata are: length 135-140 microns, aperture 63-81 microns; those of T. baltica var. rotundata are: length 65-81 microns, aperture 50-52 microns.

The nuclear relationships are as in Tintinnopsis baltica.

Tintinnopsis lohmanni n. sp.

(Brandt, 1906, Pl. 17, Figs. 1 and 3)

(Pl. I, Figs. 10, 11.)

The shell is composed of a round, spacious living chamber, with a blunt point at the posterior end, and a somewhat narrower, cylindrical dilation with bulge-like spiral rings.

This form is probably identical with that figured by Brandt on Pl. 17, Figs. 1 and 3, and designated as Tint. sp.?.

Tintinnopsis lohmanni differs from T. baltica in its larger size and the complete absence of the brim-like expansion of the aperture.

Length of shell 75-110 microns; length of living chamber 21
57-63 microns; width of living chamber 58-70 microns; length of dilation 15-50 microns; width of dilation 50-57 microns.

The two meganuclei are spherical, in older animals they are elongated and often split. The two micronuclei have a diameter of 2-4 microns. (Pl. II, Fig. 23.) Occurrence: September to March.

Tintinnopsis subacuta Jørg.

(Jørgensen: Tintinnodea from the west coast of Norway, Fig. 6.)

I found a few specimens of this species in two catches at the end of May. The shape and size of the shell agree with Jørgensen's figure.

The animal has two round, often elongated nuclei with a crevice, and with a framework varying in delicateness. The micronuclei measure 2 microns.

Tintinnopsis karajacensis Brandt

(Brandt: The Tinntinus group from the Greenland Expedition, Fig. 5. Levander: Fall and winter plankton from the Gulf of Finland, p. 18, Fig. 4. Pl. I, Figs. 12, 13, 14.)

More frequent than the preceding species was a cylindrical Tintinnopsis form, which I regard as Tintinnopsis karajacensis. The shell is cylindrical, with a shallow indentation in the centre; the posterior is rounded. I frequently observed shells with a distinctly differentiated dilation. This latter type of shell agreed both in size and in shape with those described by Levander as Tintinnopsis tubulosa forma a (p. 18, Fig. 4).

Total length of shell . . .	90	113	127	145
Length of living chamber .	90	113	113	95
Length of dilation . . .	0	0	14	50
Greatest diameter . . .	42	45	47	48
Smallest diameter . . .	38	40	40	41

I observed two rounded nuclei and two micronuclei.

Tintinnopsis campanula Ehrbg.

(Pl. I, Figs. 15, 16.)

The shells of this species, which occurs abundantly during summer, were found to have widely varying shapes. Sometimes the brim is lacking altogether, and sometimes it is strongly developed. An interesting feature which has not been described before, is the presence of a dilation on the brim. The latter type was fairly common (Pl. I, Fig. 16); a form with a double dilation was less common. On the other hand, the shell lacked a point. (Tintinnopsis Bütschlii v. Daday, Tint. camp. var. Bütschlii Jørgensen.) I was not able to distinguish Tintinnopsis cincta Cl. & L. in its really typical shape.

In addition to two elongated nuclei, frequently with a crevice, I always observed two micronuclei with a diameter of 2-3 microns. In the latter I was often able to observe a nuclear framework similar to that of the meganuclei (Pl. II, Fig. 1 [sic]).

Genus Cyttarocylis Fol.

Cyttarocylis helix Cl. & L.

(Tintinnus fistularis Möbius, Pl. VIII, Fig. 38.)

The size of the shells fluctuates greatly. The measured width varies from 45 and 55 microns; the length varies from 150 to 350 microns. In some catches made during August I often found shells without point. 22
(Cyttarocylis helix var. cochleata Brandt, 1906, Pl. 33, Figs. 1 and 6.) Sometimes the posterior portion had expanded into a bulge. The animal has 2 spherical nuclei with a coarse framework and 2 small, round micronuclei that are hard to make visible. Occurrence July to October.

Summary

All Tintinnodea having two nuclei also have two round micronuclei, whose position is constant near the meganucleus [sic] . In the older specimens, the latter has a crevice.

Conjugation and multiplication of nuclei during fission

The first precise data on fission phenomena in the Tintinnus group were provided by Entz, who based himself on his observations of Tintinnidium fluviatile. However, his detailed description is confined to the new formation of the vacuoles and the peristome appearing in the centre of the animal. There is almost no information as to the behavior of the nuclei. Here is what Entz has to say about this process:

"During the fission process, the nucleus appears to remain entirely passive for some considerable time. The formation of the new peristome may have advanced to a considerable degree, and the new contractile vacuole may also have formed, without any observable change in the nucleus, with the possible exception of an elongation. The subtler changes in the nucleus and the micronucleus during fission remain unknown to me. I can only state that I did not observe a finely striate structure either on the nucleus or the micronucleus, and that juvenile nuclei lack the transverse, crevice-like aperture." (Entz, 1885, pp. 193-194.)

Von Daday adds the following observation, which he noted in Tintinnus inquilinus: "Later during fission the nucleus becomes elongated in the direction of the longitudinal axis, its two ends become dilated

while the centre becomes thinner. In connection with this, the substance of the nucleus changes: its granules become concentrated in the two ends. Its centre becomes homogeneous, and after a short period, fine, long striae make their appearance." (1887, p. 509, Pl. 18, Fig. 12.)

These complementary remarks by von Daday are the result of an erroneous interpretation of his observations. He refers to only one nucleus, whereas, according to his systematic description, Tintinnus inquilinus has four nuclei, which can also be seen from his figures (Pl. 18, Figs. 2, 10). Entz' observation also relate to only one of the nuclei.

My own investigations covered binuclear members of the Tintinnus group. I observed fission and the same nuclear changes in all of the species caught by me.

The description that follows is based primarily on observations of Tintinnopsis campanula and Cyttarocylis helix. Investigations with living animals were largely unsuccessful, as the shells make it impossible to recognize the nuclei. I often found animals that had left their shells; strikingly enough, it was often these animals that exhibited budding features, recognizable in the newly formed peristome. These animals, however, were too restless and they soon died.

In my studies of changes in the nuclei I was compelled to confined myself to preserved specimens. With the use of numerous dyed mounts I have compiled the following description.

Normally, the members of the Tintinnus group observed by me have two spherical or elongated meganuclei and two micronuclei that are always round and adhere closely to the meganuclei.

The first indications of fission are external; they consist of the new formation of the peristome in the centre of the animal, as may be gathered from Entz' data. Initially, the position and shape of the nuclei as well as the micronuclei remain unchanged. When the adoral wreath of cilia is fully developed, the meganuclei become elongated in the direction of the longitudinal axis. Both nuclei elongate simultaneously. In Cyattarocylis helix, where the elongation of the nuclei can be seen to best advantage, I have occasionally observed that one nucleus still retained its spherical shape while the other had already become elongated.

The elongated nuclei become pointed on the sides where they face one another, and merge (Pl. II, Fig. 25). The resultant body is at first fusiform and heavily dilated at the ends. The nuclear substance exhibits a finely striate structure at the place of fusion (Figs. 26, 27). 23

The conjugation of the nuclei continues; the dilated ends move towards one another, the centre becomes wider, so that the fused nucleus assumes a sausage-like shape (Fig. 28), as was figured by von Daday in Pl. 18, Fig. 12. The slightly dilated ends exhibit a denser nuclear framework, in the centre there is a pale striation, which fades gradually. Most often I observed such sausage-shaped fusion stages without any striation but with a uniformly granular structure.

After this, the fused nuclear body dilates in the centre, at the same time striae become visible on either side of the dilation, and the striate portions constrict (Fig. 29). Finally, constriction becomes complete and the body divides into three nuclei, all exactly

spherical and without crevices (Fig. 30). The latter, however, does not seem to be true in all cases, as there was one instance when I observed during a fission stage one spherical nucleus and two elongated-oval nuclei with crevices.

The micronuclei become active during fission later than the meganuclei, but their fission proceeds more rapidly, so that it is completed before that of the meganuclei.

The latter may long have fused, without any change in the shape and position of the micronuclei. They are located at the dilated ends of the sausage-shaped fusion product of the meganuclei (Figs. 25, 26). The micronuclei then enact a conjugation similar to that of the meganuclei. However, I did not succeed in observing a fusion. I observed at the inflated ends of the fused meganuclei elongated, pointed micronuclei (Fig. 27), or three micronuclei in the centre (Figs. 28, 29). I therefore conclude that the fusion and fission of the micronuclei proceeds in the same manner as that of the meganuclei, but that the process is more rapid.

After the fusion product has separated into three nuclei, each of these is associated with a micronucleus (Fig. 30).

I was not able to observe the fission process in the daughter nucleus. I believe, however, that fission proceeds in a transverse diagonal direction.

Among my preserved specimens I very often found animals with one round nucleus without crevice and one micronucleus (Fig. 32). I therefore assume that, after fission, the daughter animalcule contains one round nucleus and one micronucleus. This is supported by the fact

that I observed in one animal, shortly before the separation of the daughter animal, different types of nuclei: two were elongated-oval with a crevice, and one was round, and had no crevice. The following description of sexual reproduction will also show that juvenile animals lack the crevice, a fact already observed by Entz in Tintinnidium fluviatile.

I have not been able to observe with certainty when the fission of the meganucleus takes place in the daughter animal. According to my observations, the start of fission appears to vary even in the same species. In Tintinnopsis campanula I found animals where the fission of the nucleus had started before constriction; the animal undergoing fission had four nuclei, of which two were elongated (Fig. 31).

In one case I found in Tintinnopsis baltica with dilation (Brandt, 1906, Pl. 16, Fig. 4) two separated animals in one shell, both of them had two meganuclei and two micronuclei. I regarded the lower animal as the offspring, firstly because of the round nuclei, and secondly because the peristome was much more delicate than in the upper animal. It therefore appears that the lower offspring would continue to live in the old housing and that the parent would undertake the new construction of the shell.

The fission of the nucleus in the daughter animal usually takes place after separation. In catches of Tintinnopsis campanula frequently exhibiting fission processes I found many animals of that species which had only one nucleus and one micronucleus (Fig. 30). I also observed animals where the nucleus was in the process of fission.

Summary

During the fission of binuclear members of the Tintinnus group, the nuclei conjugate after the completed formation of the adoral wreath of cilia. The fusion results in the daughter nucleus, which separates from the parent animal after, and occasionally before, the separation of the daughter animal. The activity of the micronuclei starts later, after the meganuclei have already fused; but the process is more rapid. The fission of the micronuclei is already complete when the meganuclei are still joined.

Sexual reproduction of the Tintinnus group

As we already noted in the introduction, Hensen was the first to observe spores and cysts in the Baltic Sea and in Kiel Bay. In Pl. IV, Fig. 21, he figured a cyst of Tintinnus subulatus, and in Fig. 22 he figured spores of Tintinnus acuminatus. He also remarked that he observed similar features in Cyttarocylis helix (= Tintinnus fistularis Möb.) and Cyttarocylis (Tintinnus) denticulatus. He considered the possibility that he might have observed parasites, but regarded it as more likely that these were development stages of the Tintinnus group, since the features begin to appear when the animal begins to disappear, and they increase relatively until the animal has disappeared entirely. He also remarked: "It is probably excluded that we are witnessing a periodic disease; also, the forms (Fig. 22) are highly typical of the supposition that the animal itself separates into these cysts, and since such forms were observed only in Tintinnus acuminatus, I believe I have

grounds for assuming spore formation in the Tintinnus group, even though I am unable to provide any data as to the future fate of these bodies. I assume that these spores, after they fall from the housing or after the housing has dissolved, come to rest on the bottom, where they pass through a latent stage. In Tintinnus acuminatus spore formation is connected with an increase in the number of individuals; should this not be the case in all instances (or: everywhere), a procreative act would first have to take place with the aid of the spores, for even here we must surely postulate sexual procreation." (Page 68.)

I investigated this phenomenon in greater detail in both living and preserved specimens, and I have concluded that sexual reproduction does indeed take place in the Tintinnus group by means of mega- and microspores.

As regards the observations of Häckel, I consider it quite possible that Cyttarocylis cassis may indeed form spores such as illustrated by him (Pl. XXVII, Fig. 1). I observed similar features in Tintinnopsis beroidea and T. ventricosa. I have not observed ciliate embryos, such as those illustrated by Häckel in respect of Tintinnopsis campanella (Fig. 13).

I should also like to note that I observed on the shells of Tintinnopsis species numerous small, elongated Infusoria, especially if the catch was left one day at room temperature.

The sporocysts

Like Rhumbler, I understand under "sporocysts" those rounded animals that form spores through fission. Rhumbler describes this type of cyst formation in respect of the holotrichal Infusoria genus Colpoda.

However, the sporocysts of these ciliates, which were very much doubted later on by Bütschli, exhibit little agreement with those occurring in the Tintinnus group, so that I shall refer to them only briefly.

The sporocysts differ from the fissions cyst and the permanent cysts ("Dauercysten"), also described by Rhumbler in respect of Colpoda, in the absence of a differentiated nucleus. As no expulsion of the latter was observed, Rhumbler explains its disappearance by stating that its substance had completely dissolved in the plasm of the sporocyst. The cyst is surrounded by several coarse shells. In the interior of the cyst the spores develop in the "sporoblast"; in the smaller cysts there are 8-10 spores, in the larger, 20-30.

Growing steadily, the spores become transformed into amoebas. 25
They put forth pseudopodia, and they may even form a very long, flagellum-like pseudopodium, thus entering the flagellate state.

The larvae of Colpoda have initially 2-4 nuclei in the interior, during a subsequent stage there is only one nucleus. The manner in which the nucleus forms is not clear.

After the larva has become mononucleate, it retracts the pseudopodia, forms fine cilia on the surface, and thus grows into a Colpoda.

Even though spore formation in the Tintinnus group -- which will be dealt with in greater detail in this section -- exhibits little similarity with this procreative process in the Colpoda spores, it is highly significant that a development by means of spores occurs not only in the Infusoria genus Colpoda but also in the Tintinnus group.

I very often found sporocysts in the shells of Tintinnopsis

campanula and Cyttarocylis helix, less often in Tintinnopsis nucula, baltica, lohmanni and karajacensis, and in one instance in Tintinnus acuminatus.

They always occupy the lower part of the shell, are pale yellow in the interior and are surrounded by a narrow, colorless rim (Figs. 17, 18). In some live cysts one may observe striation the form of concentric circles. Their shape is somewhat elongated (Fig. 35), during a subsequent stage it is spherical (Fig. 36).

The size of the cyst is governed by the size of the shell. The average diameters are as follows:

Cyttarocylis helix . .	32—50 μ	*Tintinnopsis lohmanni* . .	30—35 μ
Tintinnopsis campanula	32—50 „	„ *karajacensis* .	27—30 „
„ *baltica* . .	25—30 „	„ *nucula* . . .	13—16 „

The description that follows is based on observations of Tintinnopsis campanula and Cyttarocylis helix. The cysts of both these species, which during summer occur in masses in the plankton, were placed on an object support, which was suspended above a small bowl with water in order to prevent desiccation of the specimen.

The cysts that were briefly described above were newly formed, a fact established by subsequent investigations concerning their origin. During cultivation in a suspended droplet I was able to observe the following changes.

The somewhat elongated cyst gradually assumes a spherical shape, losing some of its volume. Meanwhile, the plasm has been distributed evenly, the colorless rim has disappeared (Fig. 19). Its color is pale gray, and its structure is granular. In the interior a sharply delimited, deeply yellow spot has emerged whose diameter decreases gradually (even during fission). The spot usually occupies an eccentric

position in the cyst, and is also differentiated from the plasm by its finer structure.

This differentiation is more distinct in dyed specimens. If boric or picric carmine was used, one can observe in the interior of this "yellow spot" a number of small, unstructured, elongated, rarely round granules, which are arranged in concentric circles (Figs. 36, 37). If treated with hemalum, they are not colored. The "yellow spot" has retained its yellow appearance or is pale blue. It stands out from the plasm because of its finer structure. In elongated cysts, i.e., those that are newly formed, the granules dyed by boric or picric carmine are distributed throughout the interior of the cyst (Fig. 35).

These granules produce the yellow color in living cysts. The cyst is pale yellow when the granules, during the initial stage, are distributed throughout the cyst (Fig. 18). If they have become concentrated, which takes place after approximately 15 hours, the "yellow spot" arises (Fig. 19).

I believed at first that I was dealing with a disintegration of the nucleus. However, the unstructured nature of the granules as well as the fact that they are not dyed in the slightest by hemalum soon caused me to drop that theory. The origin of these granules remains a puzzle.

The nucleus of the cyst is located directly at the rim at the opposite end from the "yellow spot" (Figs. 34, 36, 37). It has a distinct, fine structure and, in lateral view, is shaped like a crescent. Viewed from above it is elongated-oval (Fig. 35). In this case it can easily be overlooked, because it is located directly along the periphery

of the cyst. In some cysts I could not detect any nucleus. I am unable 26
to determine whether the nucleus, in such cases, was actually lacking or whether it could not be recognized due to poor coloring or because of unfavorable position.

Formation of sporocysts

During the investigation of living cysts I was struck by the fact that above them there were large, rounded or very small, entirely shapeless lumps of plasm (Figs. 18, 19, 20). I found shells where this mass was very large, and the cyst associated with it was very small (Fig. 34). During cultivation in a suspended droplet I discovered that the small, spherical cyst increased in size, while the lump became smaller. Gradually, the link between the two parts was dissolved. The separated cyst is elongated, it has a colorless rim and the appearance described previously. While the "yellow spot" develops in the interior, the lump located above it disappears gradually. It is filled with numerous yellow food vacuoles.* Its round shape gradually disappears, the mass becomes shapeless, until finally only a diffuse yellow mass can be discerned, which disappears entirely after about 15 hours.

This phenomenon, which was observed frequently in Tintinnopsis campanula and Cyttarocylis helix, suggested to me that it might represent the formation of the sporocysts. This assumption was supported by observations made on dyed specimens.

In a surface catch made on 6 July from the Seeburg bridge I found numerous individuals of Tintinnopsis campanula with normal development,

* Literally: "food bodies." -- TRANSL.

having the adoral wreath of cilia, two nuclei and two micronuclei, whose lower part was dyed dark by the boric carmine. Under strong magnification it was possible to observe in this elongated-oval part a number of heavily colored, homogeneous granules, arranged in a circle (Fig. 33). The latter phenomenon immediately pointed to a relationship with the cyst.

Later on I found in the shells animals which had no ciliate wreath at all, and which did not exhibit mouth or forehead.* At the posterior part or somewhat to one side, a small cyst was separated by a constriction, still connected to the animal that was already in a process of dissolution; the cyst exhibited in its interior the homogeneous colored granules, arranged in a circle. The typical, crescental nucleus was located at the periphery (Fig. 34). Since the non-ciliate animal clearly exhibited two meganuclei but no micronuclei, the conclusion suggests itself that the micronuclei fuse and migrate into the separated cyst. The meganuclei are in process of dissolution, along with the plasm lump. I observed such nuclei in the process of dissolution where the chromatin was bunched in the centre. Around it one could recognize a less strongly colored framework as well as the clearly differentiated, corrugated membrane (Fig. 34).

Spore formation

(a) Macrospores. I was not able to establish exactly the time when the cyst is formed, as I did not know how long before the discovery the formation had started. If the animal has withdrawn the adoral ciliate wreath and has detached in the posterior a small cyst, the formation proceeds rapidly. The connection with the animal is broken 2-3 hours later

* Literal translations. -- TRANSL.

(Fig. 18). After another 15 hours, the "yellow spot" has formed in the interior (Fig. 19). The cyst is ready for fission.

After 8 hours, a slight constriction appears in the centre of the cyst; in Cyttarocylis the constriction usually has an equatorial orientation. The yellow spot is not affected by the fission. This is followed by separation, so that there are two fission cysts in the shell, one of which contains the yellow spot (Figs. 20, 38). The subsequent fission process takes 20 hours and proceeds by means of continuous binary fission. During this process, the "yellow spot" again remains whole, but it grows somewhat smaller. The fission cyst that contains the"yellow spot" is always the largest; its position in relation to the others is changeable. Sometimes it is located in the midst of the other cysts, and sometimes it is in the very posterior of the shell (Figs. 21, 39).

On rare occasions I observed two fission cysts with "yellow spots." However, I do not believe that they arose from the fission of one such spot, but that they originated during the formation of the cyst. Among my dyed specimens I found individuals of Tintinnopsis campanula in whose posterior part the homogeneous colored granules were arranged in two separate circles. I did not observe the fission of a "yellow spot." 27

The fission of those fission cysts that are located in the upper part of the shell proceeds more rapidly than that of the cysts in the lower part. The first end-product, the spore, has formed 6 hours after the start of fission.

These spores, which are macrospores, have an elongated

shape resembling the Gymnodiniales, with a slight constriction in the centre (Fig. 21c). Their length, in Tintinnopsis campanula and Cyttarocylis helix, 17-20 microns, the width 10-12 microns. The posterior part is rounded, hemispherical and has a furrow in the centre, oriented along the longitudinal axis. The anterior part is more elongated. I could not establish with certainty whether this part also has a longitudinal furrow. In one instance this appeared to be true, but I was not certain. The location and nature of the flagellae also remain unclear. The fact that flagellae are present can be deduced with certainty from the locomotion of the spores.

As soon as a spore has formed, one can observe occasional abrupt spasms. This movement usually occurs simultaneously in 2 or 4 spores. The spasms become stronger, more frequent, until finally the spores leaves its place and, after a brief, rapid movement, it comes to rest in a different place of the shell. Shortly therefore, this circulation within the shell resumes, movement becomes calmer, more continuous, until the spore leaves the shell in a straight line. Movement occurs with the elongated part in front, with constant revolutions around the longitudinal axis. The posterior, round part performs a wriggling movement.

In this manner, all spores exit from the shell soon after their formation. Outside the shell I have been able to observe them only for short periods; their movement is so rapid that they easily leave the field of vision. On the other hand, they quickly perish.

After about 14 hours, the last spore has left the shell, so that the total duration of spore formation amounts to 42-43 hours in

Tintinnopsis campanula and Cyttarocylis helix.

When all spores have left the shell one still notices in the lower part a rounded object that is yellow in the interior. It does not develop further, becomes gradually paler and disappears finally. This is the "yellow spot" which did not participate in the fission, as far as could be observed.

All spores are colorless, only in one case did I notice in Cyttarocylis helix that the last spore to leave the shell had a yellow sphere (Figs. 21a, b). No residual body was observed in this case.

(b) Microspores. The number of the macrospores that originate in the manner described above is 12-14. I was not able to establish the exact number.

On the other hand, I found shells in Tintinnopsis campanula that contained a much greater number of spores and [sic] which differed from those described above in being much smaller. I was not able to observe this formation of microspores in more detail. I found some shells of Tintinnopsis campanula that were filled with 25-30 fission cysts; the suspended droplet contained about 50. The process was then disturbed by Infusoria, which entered the shells and displaced the immature fissure cysts. Outside the shell I observed further binary fission, but no fully formed, mobile microspore. In a preserved plankton catch (on 18 July) I found many shells of Tintinnopsis campanula that were filled almost entirely with small spores measuring 5 microns. The number of these microspores, which are spherical when fixed, greatly exceeds 100.

(c) Nuclear fission during spore formation. The fission process of the sporocyst begins with nuclear fission. Externally, no constriction is as yet observable when the nucleus, which is located at the margin, begins to divide. It becomes elongated and constricted in 28
the centre (Fig. 37), until it finally divides (Fig. 38). Further fission is always preceded by nuclear fission. The shape of the nucleus is spherical in the fission cysts; the cysts that are in process of fission have the shape of a dumbbell. The size of the nucleus in Tintinnopsis campanula is 4.5 microns in macrospores, and 2-3 microns in microspores. In fixed, spherical spores the nucleus is located along the margin; the centre is occupied by a vacuole.

Spore formation in Tintinnopsis ventricosa

In Tintinnopsis ventricosa and in a single instance in Tintinnopsis beroidea I noticed a striking phenomenon which I am also inclined to regard as spore formation. It resembles closely the spore formation described and figured by Häckel in respect of Cyttarocylis cassis (Pl. XXVII, Fig. 1). I made these observations only with preserved material. Study of living animals is very difficult, owing to the opacity of the shells.

The presumed manner of spore formation occurs in May. In dyed specimens, I noticed in the centre of the animal a spherical object that was colored darked in the interior. I did not distinctly notice a nucleus in it. The animal itself had two meganuclei and two micronuclei; the adoral ciliate wreath was fully developed. I did not ob-

serve yellow granules such as I had observed in the other species.

In other specimens I saw in the interior of the cyst many nuclei; no external fission had occurred. Finally I encountered animals were fission had already begun. Beside the animal, which had an adoral ciliate wreath, there was a lump of about 20 rounded spores, each of which had a round nucleus. During a more advanced stage of this spore formation I noticed the dissolution of the meganuclei; the chromatin mass had gathered in the centre. I assume that the meganuclei perish with the departure of the spores, as I noticed several animals without nuclei.

I was not able to observe the behavior of the micronuclei.

I found one shell of Tintinnopsis beroidea (with a high dilation) which, in addition to the binucleate animal, contained many separate spores.

I cannot state whether this manner of spore formation is a modification of that described above or whether it has any connection with the development of the Tintinnus group members at all, as I did not observe it in living animals. It is striking, however, that I encountered none of the previously described cysts in Tintinnopsis ventricosa and T. beroidea.

Even though I did not succeed in demonstrating the existence of macro- and microspores in one of the species occurring in Kiel Bay, Tintinnopsis campanula, I do not doubt that they are present in the other Tintinnopsis species, the more so as spores are rare in the plankton. In vertical catches I often found undivided sporocysts as well as others that had begun to divide. In order to obtain developed spores it is necessary to cultivate the cysts. In one plankton catch which was accidentally killed only after it had remained nearly

two days in a glass bowl I found a fairly large number of micro- and macrospores. It follows that the spore formation takes place in the deeper parts of the water column or, in shallow coastal areas, even on the seafloor. After withdrawal of the adoral cilia the animals lose their ability to move and sink to the bottom. It is there that the micro- and macrospores are formed and, as seems certain, conjugate. The embryos then pass through a quiescent stage, and make their appearance in next season's plankton.

Juvenile animals

At their earliest appearance, juvenile members of the Tintinnus group differ from adult individuals in the complete lack of an adoral ciliate wreath. In the plankton catches from the inner harbor, which at first contained Tintinnopsis campanula in large numbers, I found in the shells many juvenile animals without adoral ciliate ring, which had a spherical shape when contracted (Figs. 40, 41, 42). Such juvenile stages of Cyttarocylis helix, Tintinnus subulatus and Tintinnopsis ventricosa, T. nucula, T. baltica, T. lohmanni and T. beroidea were less common.

The contracted, spherical animals resemble sporocysts, but 29
they differ from the latter in lacking the "yellow spot." Their color is pale gray, frequently rendered yellowish-brown owing to the ingestion of numerous food vacuoles. Exact observations reveal short fine cilia on the anterior cusp; these cilia usually adhere closely to the body and only occasionally do they flicker slightly. I became

completely convinced that I was dealing with development stages of the Tintinnus group after I noticed that the spherical animals were able to extend themselves exactly like adult members of the group. The upper cusp of the spherical animals bears a slight depression, which is the excentrically situated oral aperture. It is surrounded by fine, strongly flickering cilia. I also noticed a somewhat heavier row of cilia running downward along the body as far as the centre (Fig. 15). I did not observe four spiralling rows of cilia either in juvenile or in adult members of the Tintinnus group.

When dyed and embedded in Canada balsam, the juvenile members of the Tintinnus group exhibit two round nuclei without crevice and two micronuclei (Fig. 42). I often found animals with only one nucleus and one micronucleus (Fig. 40). I also observed the division of the mega-nucleus (Fig. 41).

At first I believed these non-ciliate animals to be stages the way to encystment. However, study of the sporocysts, which turned up in the plankton only later, revealed very soon that this phenomenon is not related to cyst formation, so that I can describe them without any doubt as juvenile animals, of a type already noticed by Claparede and Lachmann in Tintinnus amphora; they figured it as a stalked cyst (Pl. 8, Fig. 3). Among the numerous juvenile animals I found two with a very delicate ciliate wreath, somewhat as in budding.

Summing up our observations of sexual reproduction, we arrive at the following

Development process in the littoral Tintinnus group

Encystment (in Tintinnopsis campanula and Cyttarocylis helix) starts approximately eight days after their appearance in the plankton. The sporocysts, by means of a repeated binary fission, give rise in different shells to micro- and macrospores, a process that takes 43 hours, after the shells containing the cysts have reached the seafloor. There the spores conjugate and pass through a latent stage. I am unable to determine whether the embryos develop in the same year. A striking feature is the considerable decrease in the numbers of Tintinnopsis campanula during August, followed by a sudden increase toward the end of the month. I suspect that the embryos on the seafloor construct the new shell. They make their reappearence in the plankton as juvenile individuals lacking the typical adoral ciliate wreath. The fine, paroral cilia enable the animals to move even at that stage. Initially the juvenile Tintinnus individuals have only a round nucleus without crevice and one micronucleus. The adoral ciliate wreath begins to grow with the fission of the meganucleus, which is preceded by a fission of the micronucleus.

Permanent cysts

In addition to the sporocysts described above I observed in the housings of Cyttarocylis helix and Tintinnus subulatus, on frequent occasions, and in Tintinnopsis baltica with a high dilation on rare occasions cysts of an entirely different type. Whereas the sporocysts

occupy the lower part of the housing and do not have a strong cyst membrane, the other type of cysts, which I shall call permanent cysts,* is distinguished, firstly, by a solid shell and, secondly, by its position in the upper part of the shell (Fig. 22).

Even though the permanent cysts of Cyttarocylis helix and Tintinnus subulatus are generally the same, they do differ sufficiently to render separate descriptions necessary. The small number of permanent cysts which I found in the shells of Tintinnopsis baltica, are, as far as I could determine, identical with those of Cyttarocylis helix.

Permanent cysts of Cyttarocylis helix 30

The length of the shell of Cyttarocylis helix is subject to wide fluctuations. At a diameter of 45 to 55 microns I measured a length of 150-337 microns. I found sporocysts in shells of any length but most often in shells of lesser length (150-250 microns). Permanent cysts were observed only in shells having a greater length, 272-337 microns. They appear in the plankton about 14 days after the appearance of the sporocysts. On 22 August I found them most frequently in the inner harbor.

The permanent cysts are always located in the upper third of the shell. When alive they have an even brown color (Fig. 22). Sometimes I noticed that the anterior part of the shell had the same color. The permanent cysts usually occupy the entire width of the shell, so

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* "Dauercyste." The word "Dauer" may mean "continuous", "durable," "permanent," "long-lasting," etc. -- TRANSL.

that their transverse diameter is about 40-50 microns. The longitudinal diameter fluctuates among the three different stages observed by me.

The first type is elongated to rounded. The longitudinal diameter is 52-70 microns. The cyst is surrounded by a thick membrane (1 micron), which adheres closely to the shell wall (Fig. 44). The cyst contents have contracted, more so in the centre than along the sides, so that the contents assume the shape of a cylinder that is hollowed out at the bases. Those cysts whose contents filled out the entire cysts I considered to be undeveloped.

Subsequently I quite often found cysts with a spherical shape, which did not fill the width of the shell. The surrounding membrane adhered closely to the plasm (Fig. 45). The diameter was 35-38 microns. The cyst is held in position in the shell by means of strong membranes top and bottom.

Finally I found cysts whose length was less than their width. When alive, these cysts had the appearance of a rectangle, which adhered to the shell with its narrow side. The longitudinal diameter was 25 microns. In glycerin mounts one could observe that the contents were greatly compressed in the centre, so that an optical longitudinal section reveals the shape of a double T. In one case the cyst measured 25 microns along the shell wall and about 5 microns in the centre (Fig. 46).

I cannot say what type of genetic relationship exists between these forms. I never observed a change in living cysts, which I cultivated in the same manner as the sporocysts.

The last-named stage (Fig. 46) appears to be the final stage of encystment. One could visualize it as originating from the form in Fig. 45 through a flattening of the cyst at top and bottom, which would be the result of pressure exerted on the plasm by the shell wall. The shells, stretched like an umbrella or a screen, would presumably close off the cyst at top and bottom.

As regards encystment, I can add that in those catches that contained permanent cysts the animals were often located in the centre of the shell. I made attempts to induce encystment in such animals while they were suspended in a droplet. My efforts were in vain; the animal usually perished within a few hours. I was successful in only one instance. The rounded animal was located in the upper part of the shell. The adoral cilia adhered closely to the body, and only occasionally did a single cilium rise up, returning immediately to its former position. Mouth and forehead could not be distinguished. After 24 hours, no trace could be found of the cilia. Their place had been taken by a firm cover, which on the second day enclosed the entire elongated-oval animal. I did not observe any further changes.

Among the preserved specimens I found a number of animals that were rounded at the posterior, whose cilia were indistinct and covered by a solid membrane (Fig. 43). This indicates that the formation of the cyst cover starts at the anterior end, a feature which I also observed in Tintinnus subulatus.

In studying the nuclei I had to content myself with glycerin and Canada balsam mounts, and here again great problems were encountered in dyeing. Incompletely formed cysts were easy to color. Completed

cysts could be colored only with von Gieson's coloring solution. This, however, yields only poor specimens. This dye gives a strong color to the shell, which makes it difficult to observe the cyst itself. I obtained better results with hemalum, if I applied this dye for longer periods, followed by extraction with hydrochloric alcohol. Even though 31
coloring never occurred, the use of the hydrochloric alcohol did result in a differentiation of the nuclei.

The contents of the permanent cyst exhibit a regular, granular structure, from fine to coarse. I observed granules measuring 3 microns, and in other cases I was able to discern only a dotted structure, in spite of maximum magnification. The centre is occupied by the meganuclei, which initially retain their coarse structure and spherical shape (Fig. 43). I did not observe micronuclei in the cysts. However, it is probable that I overlooked them, as they are hard to discern even in a normal animal with the most favorable coloring. In cysts that have reached the final encystment stage, the shape and structure of the meganuclei undergo a change. The structure becomes finely granular, so that it is distinguishable even without coloring from the always coarser plasm. With the contraction of the plasm, the nuclei also become compressed at top and bottom. Their shape becomes elongated-oval, and the longer diameter is at right angles to the longitudinal axis of the shell (Figs. 45, 46).

I observed two meganuclei in all cysts, and only in a few cysts that had been favorably colored did I find only one round nucleus. It therefore appears that encystment is also accompanied by nuclear fusion.

Permanent cysts of Tintinnus subulatus

These cysts were first discovered by Hensen in the Baltic Sea (Pl. IV, Fig. 21). They occur fairly frequently in Kiel Bay during October and November. On the basis of observations of these cysts I came to the conclusion that the cyst figured by Hensen (Pl. IV, Fig. 21) is an incomplete one. In animals with only an indistinct wreath of adoral cilia I observed the formation of a solid cyst enclosure; formation began at the anterior end and gradually enveloped the rounded body. The posterior end remained irregular at first, as is shown in Hensen's figure. In other cysts -- which I assume to be later, well-developed stages -- the shape of the enclosure was regular, sharply round both at the anterior and posterior. At the posterior end I also noticed a coarse enclosure that connected the cyst with the shell wall like an umbrella or screen (Fig. 47). In a living cyst I discerned on this screen fine lines running from the cyst to the shell wall.

The contents of the cyst are coarsely granular; at the posterior end, or distributed throughout the cyst, there are 4-6 larger spherules that stand out because of their higher light refraction. I observed them only in living cysts and not in each case. The centre is occupied by the two meganuclei, which are nearly spherical and are hard to color. I also observed in the permanent cysts of Tintinnus subulatus a stronger contraction of the plasm in the centre, in a manner similar to Cyttarocylis helix (Fig. 47).

I did not observe micronuclei or nuclear fusion.

I do not know the further fate of these permanent cysts.

The abundance in the plankton decreases gradually. Because of the weight of the shells they probably sink to the bottom, where further development must take place. To judge from the general nature of the cysts I do not regard it as probable that this encystment is followed by procreation. Rather I am of the opinion that it is a device whereby the animals survive a certain period during which the ecological conditions in the ocean are unfavorable.

Among the permanent cysts we shall probably have to count those which van Breemen found in the shells of Cyttarocylis serrata (p. 51, Fig. 14).

Conjugation processes in the Tintinnus group

Conjugation was first observed by Fol in Petalotricha ampulla On Pl. IV, Fig. 3, he figures two intergrown animals. The process itself is described as follows: „*Chez [illegible] la présence de la coquille n'est pas un obstacle à la copulation. Les individus ne quittent pas leur coquille pour se réunir; ils se soudent par le bord du péristom. Le point de soudure est absolument constant; il est placé dans le voisinage de la bouche, mais un peu à gauche de cette dernière en sorte que deux individus en conjugation forment toujours une figure parfaitement symmetrique. La soudure est assez étendue, très intime et dure plusieurs heures.*" (1884, p. 44, Pl. IV, Fig. 3.

As to the behavior of the nuclei, he notes:

Les noyaux des deux individus copulés se soudent aussi et paraissent échanger une partie de leur substance (pag. 43—44).

Apstein observed conjugation in Tintinnopsis (= Codonella) lacustris from Lake Plön in 1893, and figured it in 1896. Vanhöffen (1897) provides an illustration of conjugation in Ptychocylis Drygalskyi. At the end of August, the German Zoological Society published a brief, preliminary

communication from Dr. Bresslau, pp. 260-261, with two figures, on studies of preserved specimens of Tintinnopsis ventricosa (= nucula) in the process of conjugation (Rio de Janeiro). In one of the figures, Bresslau portrays a case of trinary conjuction. Only two of the individuals exhibit changes in the nuclear behavior. One has 8 micronuclei which are embedded in a lighter, spherical plasm zone; the other has 4 elongated nuclei in process of fission, in addition to two meganuclei in each individual. This demonstration in early June 1906 is the first communication since Fol on the behavior of the animal during conjugation in the Tintinnus group.

Position during conjugation

The last-named investigators portray the conjugants so that the apertures of the shell are opposite one another, whereas Fol shows the animals alongside one another. I frequently observed conjugation, and I concluded that the position drawn by Fol is the typical conjugation position. The animals fuse at one place of the peristome. Whether it is always the same place in the vicinity of the cytostome, as Fol states, I was not able to determine. The fused individuals swim alongside each other, so that the longitudinal axes of the shells are parallel. If they are irritated by vibration or touching the animals withdraw into the shell. This has the effect of positioning the shells so that the apertures are opposite one another, as shown by Apstein and Vanhöffen. Withdrawal is slow and spasmodic. The longitudinal axes of the shells first form an acute angle, until they coincide after 3 or 4 spasms. It

follows from this observation that the last-named position is a protective one, assumed by the conjugants in the event of danger. If killed, the animals immediately contract (or: draw together), so that preserved material contains only pairs whose apertures are exactly opposite one another or whose longitudinal axes form an obtuse angle.

After the danger has passed, the conjugants resume a position enabling them to move. When observed under the microscope, conditions for the animals are most unfavorable, so that they soon assume their protective position. Only rarely did I observe in the smallest species, Tintinnopsis beroidea, that the conjugants relinquished the protective position and returned into the natural one.

As to the duration of the conjugation, which Fol states to be several hours, I cannot provide any information. I did not observe a juncture and separation of the conjugants. As soon as a pair assumes a protective position --an event that occurred rather quickly, even under the most favorable circumstances in the shallow bowl -- further observations are precluded by the opacity of the shells. In my investigations of internal processes I was therefore confined to specimens preserved in Canada balsam.

Behavior of micronuclei

The description that follows is based on a small number (about 50) of prepared specimens, mostly of Tintinnopsis nucula and T. beroidea. Less often I observed conjugation in Tintinnopsis baltica, T. lohmanni and T. campanula. In the last-named species I observed two cases of

conjugation, in a plankton catch made on 7 August. In the small Tintinnopsis species conjugation occurs in October, but it is confined to a very short period. Only on two days did I find fairly large numbers of conjugating Tintinnopsis -- on 9 and 12 October. Occasionally I observed conjugation in Tintinnopsis beroidea in May.

After the union of the two animals, the micronuclei increase 33
considerably in size. They become twice as large as in the vegetative state. The finer structural changes, the transformation of the micronucleus into a fusiform shape (according to Maupas, Stage A of the conjugation of Infusoria) I was not able to discern in the small number of specimens. I was, however, able to observe Stage B, the first fission of the micronuclei. Fission need not occur simultaneously in both animals. I found one pair where one animal retained both micronuclei in a spherical shape, while in the other one of the micronuclei had already divided and the other was in process of division. The latter was fusiform; the ends were more heavily colored, and in the centre I noted a fibrous structure (Fig. 48).

Thus we see that in the Tintinnodea, too, conjugation may proceed more rapidly in one animal than in the other.

The result of further fission of the fusiform micronuclei is that there are finally eight micronuclear parts in each animal. The details of the fission remain unknown to me. I assume that it proceeds in the normal way, as described by Hertwig in respect of Paramecium. After two successive divisions, each micronucleus has produced one main spindle [sic] and three reduction spindles. The difference between main and reduction spindles can be seen clearly in Figs. 49 and 50.

According to this observation, the fission of the micronuclei does not proceed in the same manner as in other Infusoria equipped with two micronuclei. For example, Paramecium aurelia has during the vegetative state two micronuclei and, unlike Tintinnopsis, one meganucleus. According to communications by Maupas and R. Hertwig, fission proceeds in such a way that the two micronuclei first produce four others, which are again subject to binary fission, so that each animal has 8 spindles. Of these 8 spindles in Paramecium, seven perish, and the eighth becomes the main spindle. After this the one micronucleus is completely expelled.

In Tintinnopsis the fission process is the same. However, this genus does not form 7 microspindles but only 6. Thus each micronucleus produces one megaspindle and 3 microspindles, parallel to the normal pattern in Infusoria with one micronucleus. In Tintinnopsis this process, so to speak, occurs in a dual form, alongside one another.

After fission is complete, four spindles grow into megaspindles, while the remaining 12 perish. The former are at first spherical and are located along the boundary of the fusion link (Fig. 49). They attain a considerable size -- their diameter may be 5 microns -- and are distinguished by a more intensive coloring. Changing into the spindle shape, they migrate into the narrower plasm band that unites both animals (Fig. 50). Whether this is followed by a fission of the megaspindles -- according to the normal conjugation process among the Infusoria -- could not be established. As far as I could determine, we are faced here with a deviation from the normal course of conjugation, since the megaspindles migrate undivided into the fusion margin, without first dividing into a stationary and a migrant nucleus.

Unfortunately I did not succeed in discovering further conjugation stages. I am therefore compelled, for the time being, to leave the further fate of the megaspindles open.

The microspindles survive for quite some time. In one pair I found all of them, even though some were rather pale (Fig. 49). Fig. 50 still shows four microspindles in each animal.

Behavior of the meganuclei

With the fission of the micronuclei, a profound change begins to affect the meganuclei. They usually retain their external shape. In Tintinnopsis beroidea the nuclei usually become elongated; in T. ventricosa and T. baltica they remain rounded; on rare occasions they become sausage-shaped during a later conjugation stage. More important are the internal processes. As soon as the micronuclei begin to divide, the meganuclei lose their regular framework. One observes in the nucleus small rods which are distributed irregularly and are more strongly colored (Fig. 49). These rods bunch up in the centre of the nucleus, which represents the concentration of a strongly colored 34
mass, chromatin (Figs. 49, 51). All around it one can discern a slightly colored and indistinct framework. After this, I observed several times in Tintinnopsis beroidea and once in T. nucula and T. lohmanni that the chromatin mass had passed from the nucleus into the plasm. There I observed the chromatin either undivided or divided into two parts (Fig. 51). The remainder of the nucleus appeared colorless, as a nearly homogeneous mass. Close by was the removed chromatin lump.

I never observed the passage of the chromatin from the nucleus in the two nuclei at the same time, but I did observe it in two nuclei in different animals.

As I noted earlier, I was not able to observe a more advanced conjugation stage; neither did I observe the separation of the united animals.

However, I should like to mention one phenomenon which I observed repeatedly in Tintinnopsis beroidea. In a surface catch containing conjugating Tintinnopsis I found animals which contained in the interior of the body a large, nearly homogeneous, colorless sphere, which in some instances contained a delicate punctate structure. These spheres bear a close resemblance to the meganuclei of conjugants from which the chromatin has departed (Fig. 50). I also observed such a homogeneous sphere in place of the meganuclei in one instance in Cyttarocylis helix, in a catch made on 28 August.

I believe that we are here dealing with animals that have separated after conjugation is complete, since I observed in one individual of Tintinnopsis beroidea an indistinct plasm process, the remainder of the locus of fusion. The origin of the sphere remains unknown to me. I would assume that it is formed from the fusion of the meganuclei that are low in chromatin, and is expelled later on after the new formation of the vegetative nuclei.

Alongside this remnant of the meganuclei, which occupies the entire central part of the animal, I observed two small, round micronuclei. Throughout the plasm there were the darker spherules or rods of the chromatin substance of the meganuclei that had passed from

the nucleus into the plasm, which made it difficult to discern the micronuclei. The animal often has one or two (less often three) vacuoles (Fig. 52).

Even though this description of conjugation in the Tintinnus group still has many gaps, it does show that the process is analogous to that in other Infusoria. Both in the fission process of the micronuclei (as far as has been observed thus far) and in the dissolution of the meganuclei we are again faced with phenomena that must strike us as normal.

Explanation of figures

1-22 drawn from observations with a Leitz objective, magnification x 400; the remainder (23-52) drawn from observations with a Leitz "Oelicumersion 2 mm," magnification x 560.

1, 2. Tintinnus subulatus Ehrb. var kiliensis n. var.

3. Tintinnopsis ventricosa var.? Cl. & L.

4, 5. Tintinnopsis nucula Fol.?

6, 7, 8. Tintinnopsis beroidea Stein. with various dilations.

9. Tintinnopsis baltica Brdt. var. rotundata n. var.

10, 11. Tintinnopsis lohmanni n. sp. N.K. = food vacuole.

12, 13, 14. Tintinnopsis karajacensis Brdt. with various dilations.

15. Tintinnopsis campanula Ehrb. Juvenile, drawn from life.

16. Tintinnopsis campanula, with dilation.

17. Cyttarocylis helix Cl. & L. Sporocyst in initial stage.

18. Idem, two hours later.

19. Idem, 15 hours later.

20. Idem, 23 hours later.

21. Cyttarocylis helix. Formation of macrospore from the same cyst after six hours. (c) Macrospore. (a) and (b) -- the last departing spore with yellow spot.

22. Cyttarocylis helix Cl. & L. Permanent cyst in upper part of shell.

23. Tintinnopsis lohmanni sp. n.

24. Tintinnopsis campanula Ehrbg. Nuclear fission.

N.K. = food vacuole.

25-28, 30, 31. Tintinnopsis campanula Ehrbg. Various stages of the nucleus during fission.

29. Tintinnus subulatus Ehrbg. var. kiliensis. Fission stage.

32. Tintinnopsis campanula Ehrbg. Mononucleate animal produced by fission.

33-39. Tintinnopsis campanula and Cyttarocylis helix. Spore formation, drawn from prepared specimens.

33. Tintinnopsis campanula. Start of spore formation.

34, 35. Cyttarocylis helix. Sporocyst in initial stage.

36. Tintinnopsis campanula. Sporocyst in initial stage.

37. Cyttarocylis helix. Sporocyst with incipient nuclear fission.

38. Idem, after first fission.

39. Idem, spore formation. (a) and (b) -- macrospore.

40-42. Tintinnopsis campanula Ehrbg. Juvenile animals with nuclear stages.

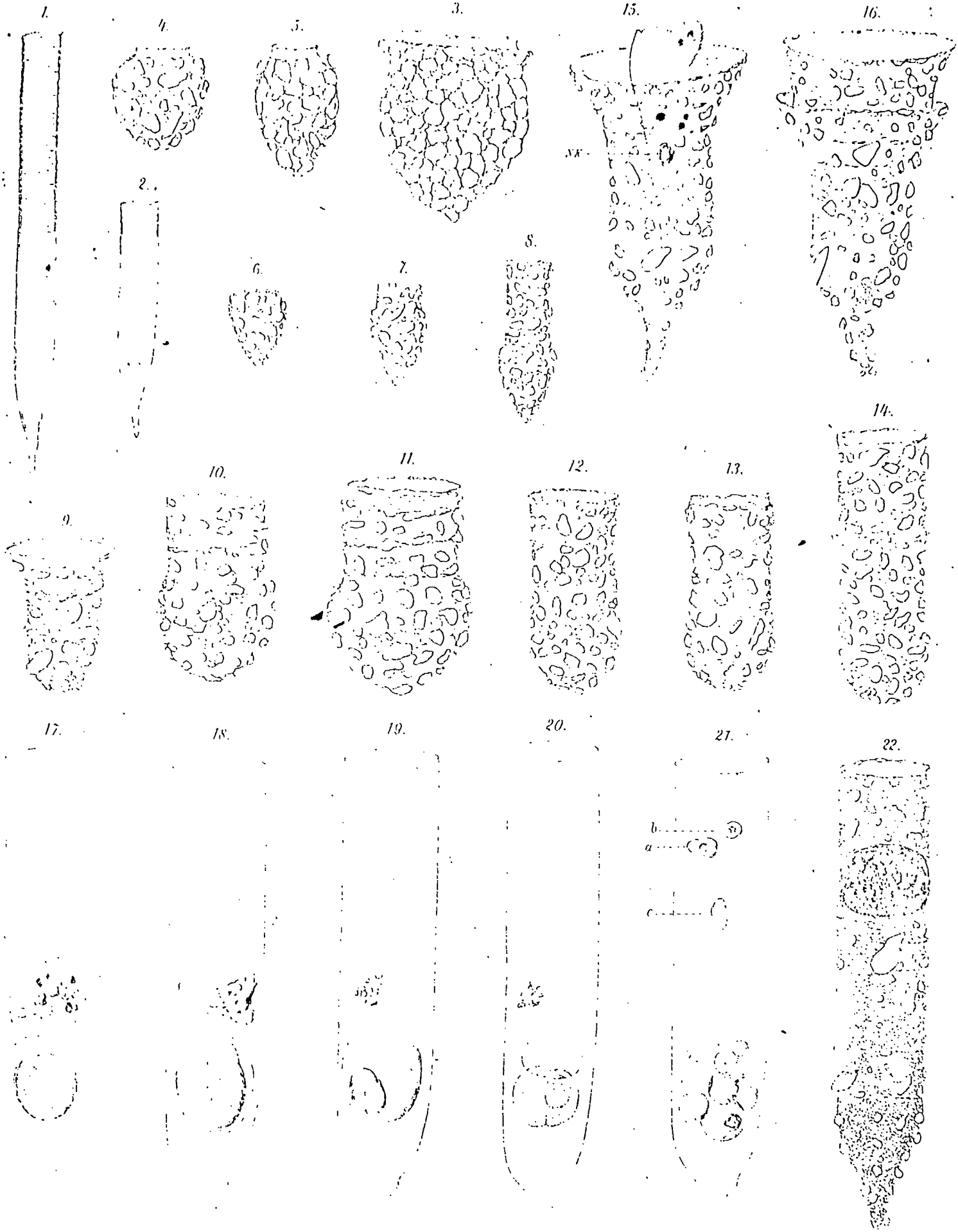
43-46. Cyttarocylis helix Cl. & L. Permanent cysts in various stages.

47. Tintinnus subulatus Ehrbg. Permanent cyst.

48-50. Tintinnopsis nucula Fol.? Various conjugation stages.

51. Tintinnopsis beroidea Stein. (Brdt.) Advanced conjugation.

52. Idem, after conjugation.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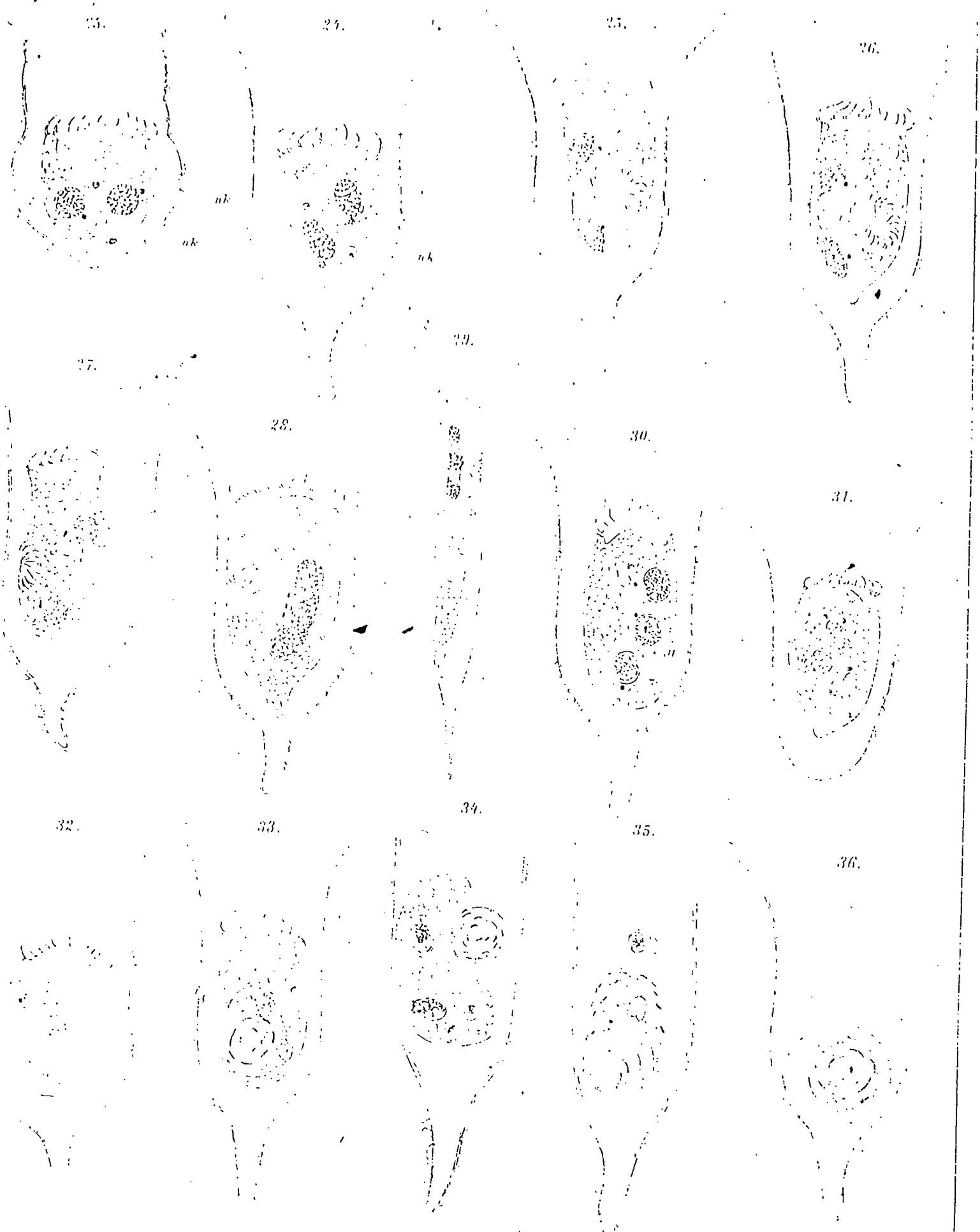
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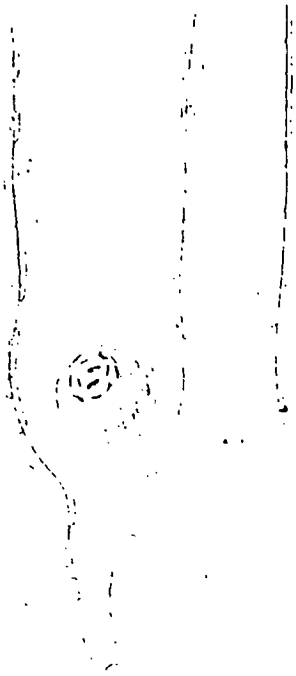

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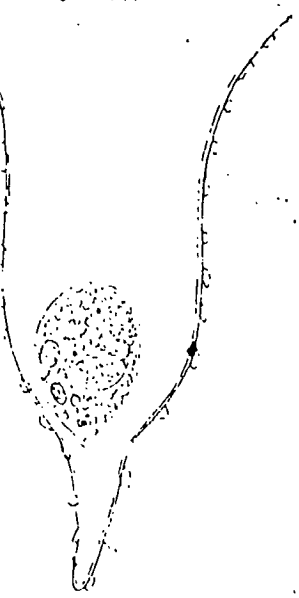

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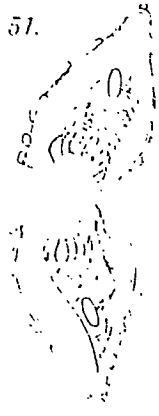

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*) Diese Mitt., die ich im Jahresbericht d. Stat. Neapel angeführt fand, habe ich mir nicht verschaffen können.

Übersicht

über das Auftreten der Entwicklungsstadien der Tintinnen in der Kieler Bucht 1905

August						September							Oktober					
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Tintinnopsis baltica Brdt. .	--	--				—						—			—				—	—	—	—	—	+	+	—	—	-
. Teilungsstadien . .																											
. Sporocysten . . .																				—	—						
. Konjugation . . .																											
Tintinnopsis lohmanni n. sp.															—				—	—	—	—	—	—			
. Teilungsstadien . .																											
. Sporocysten . . .																											
. Konjugation . . .																											

in der Kieler Bucht 1905 06.