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Reproduction and life histories of tintinnid ciliates (Review)

by

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Abstract

General remarks on the reproductive method of tintinnid ciliate, though almost all knowledges are of the neritic tintinnids, are given. Most common method is the binary fission or plasmotomy, which proceeds asexually. After new peristome with developed membranelles is formed on ventral side of the mother cell and after two daughter cytosomes are almost completely developed, the nuclei undergo visible changes. At late stage of the fission, well-grown two daughters which are connected by a thin and short strand of protoplasm still inhabit a mother lorica. When the daughters are freed, in most cases, since the posterior daughter occupies a mother lorica, the anterior daughter must be provided with a newly built lorica. Because morphological characteristics of the tintinnid loricae are extremely diversified, the methods of the lorica building should be also very much diversified. It takes, however, only a short period to complete the fission including the lorica building.

Among the sexual reproductive methods, isogamous conjugation occurs rather frequently but anisogamous conjugation seems to be very few. Cyst formation has been observed for some neritic tintinnids.

From these limited informations, the following life history of the neritic tintinnids could be suggested: Under optimal conditions, the tintinnid populations are rapidly growing at high division rate. As the populations are old, the isogamous conjugation occurs; the growth rate in this period is decreased. The environmental conditions become unsuitable, the tintinnids can survive severe season by forming the cyst. Therefore, except a limited period of the cyst stage and for lorica building in some arenaceous species, the tintinnids live free from the sea bottom. Apart from the neritic species, the life history of the oceanic tintinnids, especially that of tropical oceanic species, may be a very simple one among those of marine zooplankters.

Role of the loricae in planktonic life of the tintinnids is also discussed.

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Introduction

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In recent years, studies have become numerous on the nanno-zooplankton as a group linking the ultraplankton with the macroplankton in the food chain. Particularly, the tintinnid ciliates form an important group from the following points of view: they remain nanno-zooplankton all their life; they appear abundantly (The number of individuals found in 1 litre of seawater is in the order of tens or hundreds.) in any sea area. However, they seem to be rather unfamiliar to both researchers studying the zooplankton and those studying the phytoplankton because they slip from an ordinary zooplankton net and are often caught mixed with the phytoplankton. A brief description of the tintinnids is given therefore in the first section of the present study.

Taxonomically, when the tintinnids are classified, they are often considered to be an order of Ciliata in Protozoa. However, in the ordinary animal classification system, it is not uncommon to classify them as a family of Spirotricha in Ciliata. The classification criteria of the species of the tintinnids are fairly well established. Accordingly, there is less confusion of species names than in any other zooplankton group. As it is not the purpose of the present study to discuss the taxonomy of the tintinnids, please refer, if necessary, to the article by Sano (1975) as well as the bibliography given in it.

The variety of species of the whole marine ciliates is richer in the neritic zone, where the bottom mud plays a comparatively important part, than in the ~~pelagic~~ Oceanic zone. However, as far as the tintinnids are concerned apart from the other ciliates, the variety of species tends to be poorer in the neritic zone than in the ~~pelagic~~ Oceanic zone. The main reason is that the tintinnids, unlike the other ciliates, depend little on the deposit and organisms living in it. They mostly live floating and feed on other minute plankton~~s~~ (Kofoid and Campbell, 1939). Not only the variety of species, but also the relative biomass of the tintinnids to the macrozooplankton is greater in the ~~pelagic~~ oceanic zone than in the neritic zone and in the warm current zone, poor in nutrition than in the cold current zone, rich in nutrition. Furthermore, since the ~~lighter~~ lower the body weight, the higher the growth ~~speed~~ rate and metabolic ~~speed~~ rate per unit weight of animals, the ~~part~~ role of the tintinnids in the ~~reproduction of nutritive salts~~ regeneration of nutrients must be considerably more important than what we can imagine from their biomass (Gold, 1968; Gold and Pollingher, 1971). From the above, ecological knowledge through the life history of the nannozooplankton such as the tintinnids becomes indispensable to study the biological production process especially that in the warm current pelagic zone (Taniguchi, 1975, 1976a). p 124

1. Morphology of the tintinnid ciliates

The tintinnids have, as the name implies, a very characteristic lorica. Their size is in the order of tens or hundreds μ. Smaller species are prominent in the tropical pelagic zone and larger ones in the cold and coastal zones.

1-1 Cell-organ (Figure 1)

Figure 1 shows a rough sketch of the morphology of Favella after Campbell (1927).

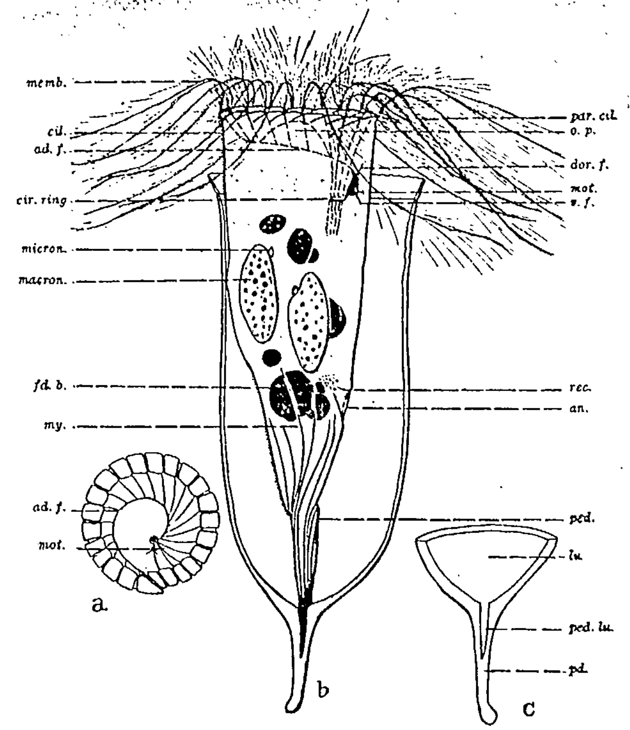

Fig. 1 a-c. Semidiagram of *Favella*. 1 a: Cytosome from above, showing adoral fiber (*ad. f.*), motorium (*mot.*); 1 b: Cytosome, showing adoral fiber (*ad. f.*), anus (*an.*), cilia (*cil.*), circumoesophagel ring (*cir. ring*), dorsal fiber (*dor. f.*), food body (*fd. b.*), macronucleus (*macron.*), membranelles (*memb.*), micronucleus (*micron.*), myonemes (*my.*), paroral cilia (*par. cil.*), peduncle (*ped.*), oral plug (*o. p.*), rectum (*rec.*), ventral fiber (*v. f.*); 1 c: Posterior end of lorica, lumen (*lu.*), pedicel (*pd.*), pedicel lumen (*ped. lu.*), (After CAMPBELL, 1927)

In this figure are shown respectively 2 macronuclei and micronuclei, though, through the whole species of tintinnids, numbers varying from 1 to 300 have been reported for both nuclei. However, the report of respectively 300 nuclei must be an exceptional case in the course of nuclear division or a mistake has been made by counting parasitic organisms. Most species seem to have 2 macro and micro nuclei respectively (Campbell, 1926; Kofoid and Campbell, 1939). It is said that, of the two kinds of nuclei, the macronuclei are found in no organism other than the ciliate, while any ciliate always has macronuclei. Although the macronuclei are more developed in respect of nuclear faculty (Abe, 1972), it is the micronuclei that concern the reproduction directly. p 125

The peristome is situated at the anterior end of the cell. Around it grow the membranellae whose number varies from 12 to 24 according to the species. They are used for swimming and feeding. Food collected by the membranellae goes into the cytosome situated on the ventral side of the peristome and, through the gullet, it is taken in the food vacuole. Indigested food goes in the caecum situated in the posterior part of the cell to be evacuated inside of the lorica from the anus or cytopyge. Some species are known to have tiny feelers at the base of the membranellae.

The cilia covering the entire surface of the cell are poorly developed. The above mentioned membranellae as well as a ciliary membrane are recognized as developed cilia. The ciliary membrane is a line running outside the location of the gullet from the cytosome to the central part of the cellular column. Some species lack ciliary membranes. In fact, the ciliary membrane of the tintinnids is no more than a large number of cilia aligned vertically. It is not exactly membraneous. It must not be identified with the undulating membrane. The movement of the membranellae and ciliary membrane is controlled by the neuromotorium situated adjacent to the gullet and the neuromotor fiber deriving from it. The whole body of plankter is extremely elastic. Its movement is caused by many myonemes running lengthwise in the pellicle and is not directly related to the above mentioned neuromotorium (cf. Campbell, 1926).

The posterior end of the cell extends in a conic and stringlike shape forming a peduncle or attachment to the inside of the lorica, ~~though~~ the cell can get free from the lorica to swim bare when the environmental p 126
conditions become unsuitable. It is said that every tintinnid has a peduncle (Kofoid and Campbell, 1939). However, no peduncle was found in Eutintinnus that the author observed *in vivo* in 1977 in the South China Sea. The plankter of this species has a thick body tightly filling up the interior diameter of the lorica. It migrates freely back and forth sliding inside the lorica. Even a species attached to the lorica can stick the greater part of the body out of the lorica since the body stretches considerably as mentioned earlier.

Hofker (1931a) thought that the ciliary membrane was the principal organ for the formation of lorica. However, some species lack the ciliary membrane while the lateral lobe is observed in the majority of the tintinnids. These facts have led the researchers to conclude that the lateral lobe is the principal organ for the formation of lorica and that the ciliary membrane is an accessory organ (Campbell, 1926; Kofoid and Campbell, 1939).

As mentioned above, the tintinnid, which is a unicellular organism, has a system and organs almost as differentiated as those primitive multicellular organisms.

1-2 Lorica (Figure 2_{a-m})

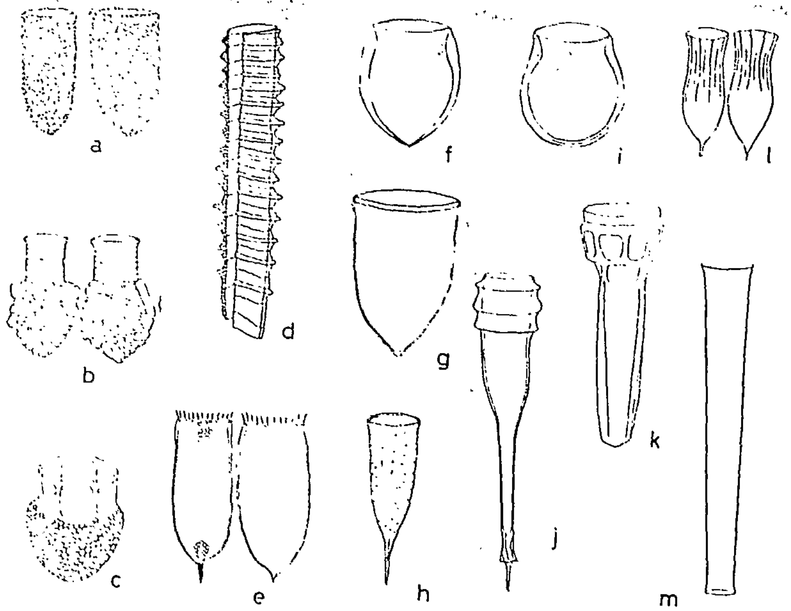

Fig. 2 a-m. Various types of tintinnid loricae. 2 a: *Tintinnopsis beroidea*; 2 b: *Codonellopsis morchella*; 2 c: *Dictyocysta duplex*; 2 d: *Climacocylis scalaroides*; 2 e: *Parafavella longidentata*; 2 f: *Proplectella (Undella) tenuis*; 2 g: *Favella azorica*; 2 h: *Rhabdonella elegans*; 2 i: *Proplectella (Undella) perpusilla*; 2 j: *Xystonellopsis pulchra*; 2 k: *Stelidiella fenestrata*; 2 l: *Dadayiella ganymedes*; 2 m: *Eutintinnus fraknoii*. (2 a-c, 2 g-i, 2 l: after HADA, 1938; 2 e: after HADA, 1937; 2 f, 2 j, 2 k, 2 m: after KOFOID and CAMPBELL, 1929)

The tintinnids are classified according to the morphology of the lorica. The number of tintinnid species is said to be about 1000. We can easily imagine from the fact that the morphological characteristics of their loricae are extremely diversified according to the species. We cannot go into detail here but the tintinnid loricae can roughly be divided into two groups: loricae formed only with materials secreted from the planktonic body itself (Figure 2_{d-m}) and those containing foreign-bodies (Figure 2_{a-c}). The former can be divided once more into two groups: those with a transparent and homogeneous structure (Figure $2_{f,i,m}$) and those with a vesicular or reticular structure, etc., (Figure $2_{d,e,g,h,j}$). Furthermore, the loricae can be divided into those whose posterior end is open (Figure $2_{d,m}$) and those whose posterior end is closed. The latter can be grouped again in those with a pedicel at the posterior end (Figure $2_{e,h,j,l}$) and those without a pedicel.

The loricae can also be divided into the following two groups: those with a collar or denticles at the anterior end (Figure $2_{b,c,e}$), a skirtlike or protuberant structure at the pedicel (Figure 2_{j}) or a ringlike, spiral or vertical line structure on the entire or a part of the lorica (Figure $2_{b,c,d,h,j-l}$) and those without these things. The fact that the morphology of the lorica is diversified as well as the above mentioned various distribution seem to indicate that the reproduction and life histories of the tintinnids vary according to the species (Kofoid, 1939).

Reproduction of the tintinnid ciliates

Most tintinnids distributed in the coastal zone are of the large-sized species. Furthermore, they are prolific and have a comparatively great power of resistance to the environmental conditions. Therefore they are suitable for ecological observation such as reproduction, etc., both in field-work and rearing experiments. As a matter of fact, almost all the tintinnids studied so far are of the neritic* species. On the contrary, very little is known of the oceanic species, especially the tropical oceanic ones, which have a contrasting nature. As a result, all knowledge reviewed in this chapter is of the neritic species.

1. Asexual reproduction (fission, plasmotomy)

In the reproduction process of the tintinnids, the formation of lorica is an event as important as the cell division. In this chapter, the cell division will first be explained then the formation of lorica by daughter cell.

1-1 Cell division

The most common reproductive method in tintinnids is asexual binary fission or binary plasmotomy. Campbell (1926) stated in detail the process of fission of Tintinnopsis nucula collected in the coastal waters of California. In this species, first a groove appears in the pellicle just below the ciliary membrane. Then a new peristome is formed

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* translator's note : literally : "coastal"

there. Membranellae also appear. By this time, the neuromotorium has completed the fission in the mother cell. On the other hand, no serious change has yet taken place in the macro and micro nuclei. Granules are formed on the side of the mother cell surrounding the new peristome. When the entire mother cell appears to be two connected anterior and posterior daughter cells, both nuclei simultaneously start binary fission in the anterior and posterior direction. Of the new 8 nuclei, 2 anterior macro and micro nuclei respectively move in the anterior daughter cell and the 4 posterior nuclei in the posterior daughter cell. During this time, the anterior daughter cell particularly continues growing. Finally, it gets free from the posterior daughter cell to start an independent life with a new lorica.

It is presumed that the greater part of the new lorica is formed by the anterior daughter cell alone but that the posterior end of the lorica is completed with the help of the posterior daughter cell.

According to Campbell (1926), the fission of the tintinnids in the coastal waters of California occurs frequently in the early morning. The first half stage of fission progresses slowly and the latter half rapidly.

Figure 3_{a-d} summarizes the fission process of Favella francisca* observed by Campbell (1927) in the same coastal zone. The mode of fission

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* This species was named F. serrata in the original work (Campbell, 1927) but later it was changed to new species F. francisca (Kofoid and Campbell, 1929).

of this species is almost the same as that of T. nucula mentioned earlier. The figure shows how the lorical materials produced in the mother cell at the early fission stage (small black spots in Figure 3_{a-d}) migrate and are accumulated adjacent to the peristome and gullet of the anterior daughter cell with the progress of fission.

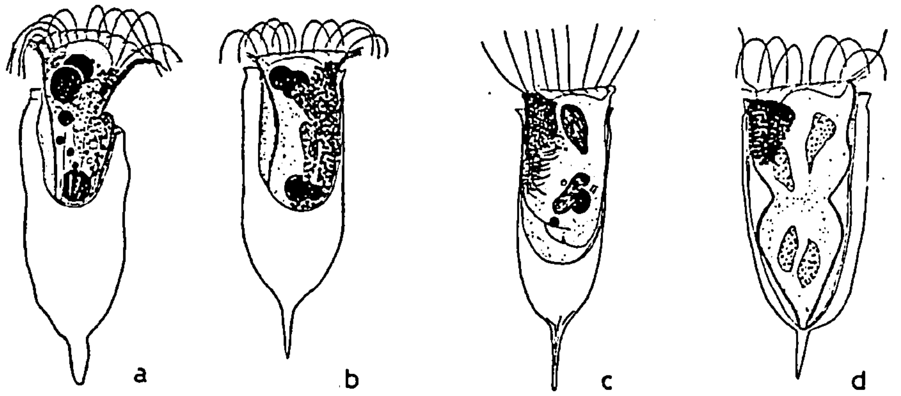

Fig. 3 a-d. Segregation and accumulation of the secreted granules which will give rise to lorical materials (small black spots) to oral region of anterior daughter cell during successive prefission stages in *Favella francisca*: 3 a: secretion of the granules is dispersed at early stage when new daughter peristome is formed; 3 b: the granules are segregated just below the ventral surface where posterior daughter's adoral zone is emerging; 3 c: the granules are massed adjacent to cytosome of anterior daughter at middle stage when macronuclei migrate to two daughters; 3 d: the granules are accumulated in the oral region of anterior daughter at later stage when the macronuclei are dividing within each daughter. (After CAMPBELL, 1927 cited from KOFOID, 1930)

Figure 4_{a-d} shows the fission of Tintinnopsis beroidea observed by Hofker (1931b) in the Bay of Naples. According to the figure, the mode of fission of this species does not in principle differ from those of the two species mentioned earlier. In this species, however, the fission of the macro and micro nuclei may occasionally take place in each daughter cell after the cell division is completed (Figure 4_d). This indicates that under certain circumstances, even in the same species of tintinnids, the reproduction by plasmotomy may take place. Gold and Pollingher (1971) too reported that a mass-reared group of this species collected from p 128 the New York Bight seemed to multiply by plasmotomy.

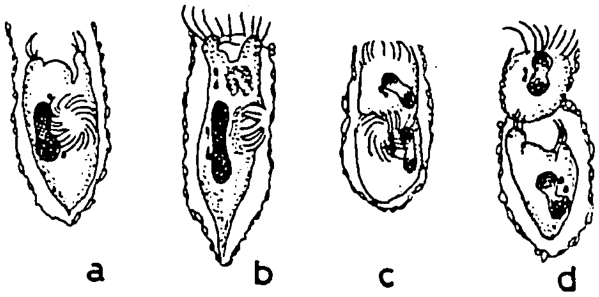

Fig. 4 a-d. Binary fission of *Tintinnopsis beroidea*. 4 a: early fission stage of a cell with single macronucleus; 4 b: fission of micronuclei; 4 c: ligation of mother cytosome; 4 d: anterior daughter sorrounded with a ring-like lorica which is originated from anterior part of mother lorica. (After HOFKER, 1931 b)

In Figure 5, Gold (1971) shows the relationship between the amount of food supply and the growth characteristics of this mass-reared group.

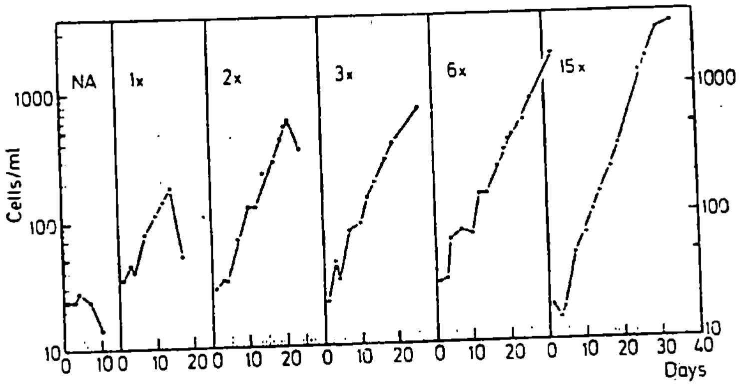

Fig. 5. Growth curves for mass-reared *Tintinnopsis beroidea* supplied with varying concentration of food. NA: no addition of food; 1 x-15 x: relative amount of food added to each flask (After GOLD, 1971)

To sum up, when food is lacking, the number of individuals decreases rapidly without showing a stationary phase (Figure 5 NA, 1x, 2x). That is to say, a stationary phase appears when the food supply is sufficient and when other conditions work as a limiting factor. When the food supply is excessive, a lag phase appears (Fig 5 15x) which lasts longer as the excess of the food supply augments. In this experiment, the doubling time was 2.5 - 6 days. However, according to a later experiment (Gold and Pollingher, 1971), under the optimal conditions, the doubling time was as expected short, that is 0.8 - 1.1 days. This elongation of the doubling time, which is supposed to be short, seems to be related to the fact that T. beroidea started sexual reproduction as the population grew old (cf p. 131).

1-2 Formation of a new lorica

To complete the fission, the building of a new lorica is necessary. As the morphological characteristics of the loricae are diversified, the methods of the lorica building of the daughter cells are not uniform. Briefly, there is a case in which only the posterior daughter cell inherits the lorica of the mother cell as it is, without undergoing any change, while the anterior daughter cell occupies a new lorica. In another case, the mother lorica is divided into two to form a part or the whole of the loricae of the two daughter cells. Furthermore, the following methods of lorica building are observed in the former case:

(1) The anterior daughter cell first secretes a cloud of lorical materials at the anterior peristome. Immediately after that, it completes the lorica in a shape proper to each species (Figure 6_a);

(2) The anterior daughter cell makes a ringlike rudiment first of all around the neck (Figure 6_{b-d});

(3) The total surface of the anterior daughter cell secretes lorical materials at once;

(4) The posterior end of the lorica of the anterior daughter cell is completed first and grows forward gradually.

In the latter case, the following methods are known:

(5) The lorica of the mother cell splits into two just like molting to be inherited by the two daughter cells;

(6) The lorica of the mother cell is fractured at the fission. Then the two daughter cells rebuild new loricae using the fragments;

(7) The lorica of the mother cell, which was enlarged before the fission, is divided into the anterior and posterior parts. Each part is inherited respectively and built up by the anterior and posterior daughters (Figure 4_d, Figure 6_h) (Campbell, 1927; Kofoid and Campbell, 1939; Gold and Morales, 1975a).

Among these theories, the (4) is judged to be doubtful since it is unthinkable that the lorica, which is an external shell, grows by itself (Kofoid and Campbell, 1939). Nevertheless, there is a possibility that the lorical materials are renewed constantly even after the lorica is formed (Gold, 1969a).

Figure 6_{e-j} shows some examples of lorica formation behavior by daughter cells. Some species agglutinate on the surface of the lorica, phytoplankton shells found in feces. After having evacuated the feces excreted inside the lorica using the ciliary membrane, they agglutinate them on the surface of the lorica by means of the membranellae and ciliary membrane (Figure 6_{e-g}). As the ciliary membrane plays an important part especially in the formation of lorica (Figure 6_{i-j}), Hofker thought that this was the principal organ for lorica building. p 129 However, as stated earlier, some species do not have any ciliary membrane.

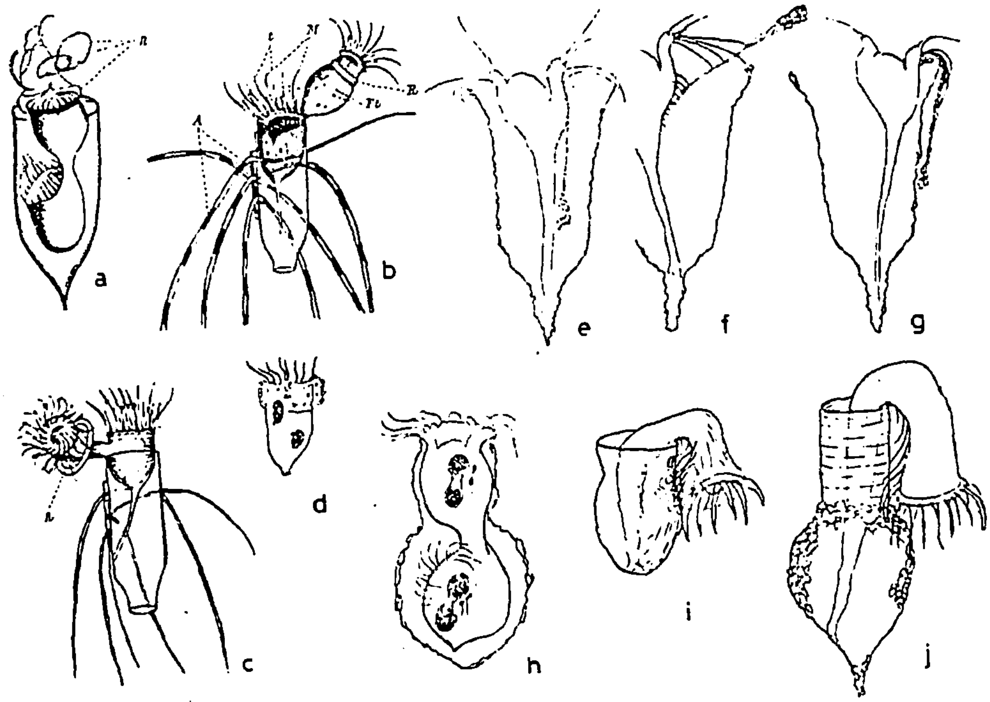

Fig. 6a-j. Formation of lorica. 6a: formation of "the cloud": 6b: formation of "the collar" in *Eutintinnus apertus*; 6c: formation of "the ring" in the same species;' 6d: formation of "the ring" in *Tintinnopsis beraidea*; 6e g: behavior agglutinating feces on outer surface of lorica in *Tintinnopsis campanula*; 6h: enlarged collar of mother lorica enveloping anterior daughter of *Stenosemella ventricosa*; 6i: agglutination of foreign particles on lorica using cilialy membrane in *Codonella galea*: 6j: the same in *Codonellopsis orthoceras*. (6a-c: after SCHWEYER, 1909 cited from KOFOID, 1930; 6d-j: after HOFKER, 1931b)

Figure $7_{a,b}$ shows that the anterior daughter cell may swim without lorica just after the fission. Moreover, it is reported that the bare daughter may continue multiplying by fission (Gold 1968).

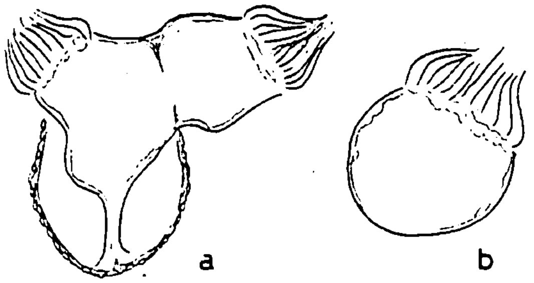

Fig. 7 a-b. Binary fission of *Tintinnopsis* sp. 7 a: ligation of mother cytosome; 7 b: free-swimming daughter without lorica. (Redrawn from microphotographs in GOLD, 1968)

At all events, since individuals on the way of lorica building are rarely collected in natural population, the secretion, consolidation and formation of lorical materials seem to be completed in an extremely p 130 short period.

The difference in organ and behavior of lorica building makes the difference in appearance and structural pattern, etc., of the lorica. For example, as shown in Figure 2, ringlike and spiral structures are generally developed at the anterior end of the lorica, which allows us to presume that they are closely related to the organs in the anterior part of the plankter body. Principal lorica building organs of such species must be the membranellae, ciliary membrane and lateral lobe. Species with a structure developed at the posterior end of the lorica suggest that this part was built by the posterior daughter cell at the moment of fission. Furthermore, the lorica of almost all the species is shaped as if made using a lathe. This makes us think that the tintinnids are constantly rotating in the period of lorica formation. Species with a vertical structure must make not only a simple rotation but also a considerably complex movement (Kofoid, 1930).

Species, which build foreign particles into the lorica or those which agglutinate them on the surface of the lorica, always use the same kind and size of materials according to the species. Species, which use shells of coccolithophore and diatom, pick them up from their own feces. Accordingly, it is possible to infer their main foods from the shells of phytoplankton agglutinated on the surface of the lorica. In an extreme case, some oceanic species belonging to the genus Codonella agglutinate ~~according to heir own particular species the~~ coccoliths of ~~some~~ a given species ~~kind~~ of coccolitho~~fore~~phore only. (Kofoid and Campbell, 1939). Many neritic species agglutinate materials of non-biological origin like sandy particles. Some of them may live in a deposit or just above its surface for a while during the period of lorica formation. These species have a precise preference with regard to quality, size, etc., of sandy particles. It is reported that such species form a transparent lorica if kept in a rearing container without any supply of sandy particles, etc., (Gold and Morales, 1975b, 1976). Furthermore, they have a tendency to agglutinate more materials in polluted areas. It is suggested that the contents and quantity of agglutinated materials can be used as an index of environmental pollution (Gold and Morales, 1976).

The size of a newly built lorica, particularly the length, is known to show an inverse correlation with the environmental water temperature. For example, the length of the lorica of Tintinnopsis tubulosoides tends to be short at the high water temperature season and long at the low water temperature season (Figure 8). On the other hand, the thickness is comparatively invariable. It is a way of adaptation to have a short lorica at the high water temperature season to reduce the sinking rate ~~force~~. The higher the water temperature, the faster the fission rate ~~speed~~. (The number of fissions increases.) As a result, at a higher temperature, the average length of the lorica (Gold, 1969a; Gold and Morales, 1975c) shortens.

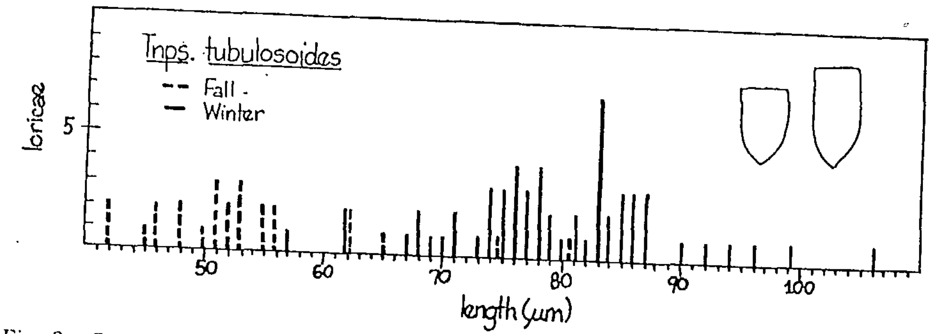

Fig. 8. Seasonal difference in size distribution of lorica Length of *Tintinnopsis tubulosoides*. (After GOLD and MORALES, 1975 c)

The substrate forming the lorica has long been considered to be "a sort of keratin-like derived protein" and not the chitin from the fact that it takes on a colour in the xanthoprotein reaction. The main components of the substrate are evidently protein and carbohydrate but its true nature is unknown. At present it is considered to be the pseudochitin (Kofoid and Campbell, 1939; Gold, 1968; Gold and Morales, 1975a).

1-3 Function of the lorica

The distribution layer of the tintinnids is limited to the photic zone. On the other hand, though the tintinnids have a stock of lipid in the cell (Gold, 1969b), the specific gravity of the body and lorica is slightly greater than that of seawater. In consequence, the tintinnids need to gain ~~floatability~~ buoyancy by the movement of the membranellae. At this moment, the lorica, which has a considerably greater surface area than the body, not only reduces the sinking rate ~~force~~, but also p 131 gives a directivity to the movement ~~owing~~ due to its external shape. In fact, the lorica serves as a rudder for the tintinnids which have a habit of directive movement such as phototaxis and geotaxis (Entz, 1909; Kofoid and Campbell, 1939; Gold, 1973). Small species are prominent in the tropical ocean. Furthermore, the surface of the lorica of large species is not smooth, whether found in a ~~pelagic~~ oceanic or neritic sea or a tropical or cold sea. It is apparently made to increase the friction drag. These facts allow us to think that the function of the light and soft lorica of the tintinnids is related to the floating adaptation and not to the protection against predators. Kofoid (1930) as well as Kofoid and Campbell (1939) examined the morphological evolution of lorica.

The membranellae are the sole active motorial organ for the tintinnids. Accordingly, the movement of the membranellae must be useful not only for floating but also feeding and changing seawater in the lorica. If so, this mode of ~~moving~~ locomotion of three uses is very favorable to the minute zooplankton having little internal energy reserve. It might be a mode of moving common to almost all the floating minute animals (cf. Taniguchi, 1975, 1976b).

2. Sexual reproduction (conjugation and gametogenesis)

The tintinnids rarely reproduce sexually. There are few cases observed. Even more, the evolution of the nuclear phases in the process of sexual reproduction has not been traced with success. This indicates how rare is sexual reproduction.

Figure 9_{a-d} shows the state of conjugation of Favella ehrenbergii* and Stenosemella nivalis*. Figure 9_a is considered to be the beginning position of the conjugation. In this state, the protoplasmic connection between the two cells has not yet occured. The perfect conjugation will be completed with the protoplasmic connection made by joining each other's peristome as shown by the other ciliates (Figure 9b-d).

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* In the original works (Entz, 1909 and Hofker, 1931b), they are called Cyttarocylis ehrenbergii and Stenosomella (= Stenosemella) nucula respectively.

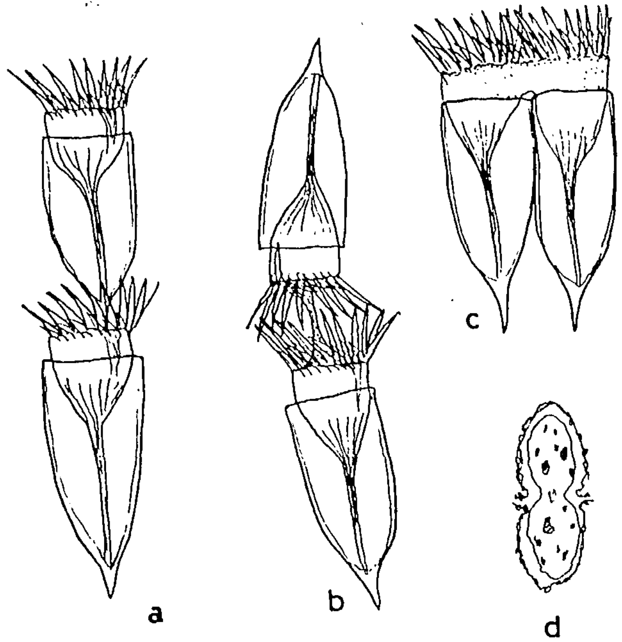

Fig. 9 a-d. Conjugation of tintinnids. 9 a: beginning position of the conjugation of two *Favella ehrenbergii*; 9 b-c: conjugating pair of the same species; 9 d: conjugating pair of *Stenosemella nivalis*. (9 a-c. after ENTZ, 1909; 9 d: after HOFKER, 1931 b)

Gold (1971) thought, from the fact that *Tintinnopsis beroidea* p 132 showed a high multiplication rate still after 1.5 years rearing, that sexual reproduction must have been done during this period for rejuvenation. Nevertheless, he could not actually find a conjugating pair. He could observe only those in the beginning position of the conjugation.

Gold reared and observed *T. beroidea* for a long time. According to his later report (Gold and Pollingher, 1971), the formation of microgamete (anisogamous conjugation) occurs in mass-reared population, which has never been observed in field population. On the contrary, the conjugation (isogamous conjugation) which is sometimes observed in field population does not take place in mass-reared population. The formation of microgamete begins to take place after several months of rearing. Most generally, as in the early stage of the binary fission, the cilia grow on the ventral side of the mother cell (Figure 10_a) where the microgamete develops. The lorica is fractured (Figure 10_b), so that the matured microgamete can get free at any time. However it never starts free-swimming before conjugation. The size of the microgamete remains considerably smaller than that of the mother cell (Figure 10_c). After having reached this stage, at the contact of a macrogamete, it gets free from the mother cell in order to conjugate at the peristome using the cilia as attachment (Figure 10_d). The microgamete has only micronuclei and the existence of macronuclei is rarely confirmed. The nuclear phase of the macrogamete has not been verified. A macrogamete and an ordinary cell are indistinguishable since no apparent difference is observed. Up to the present, the above report (Gold and Pollingher, 1971) is the only example of observation of the gamogomy in tintinnids.

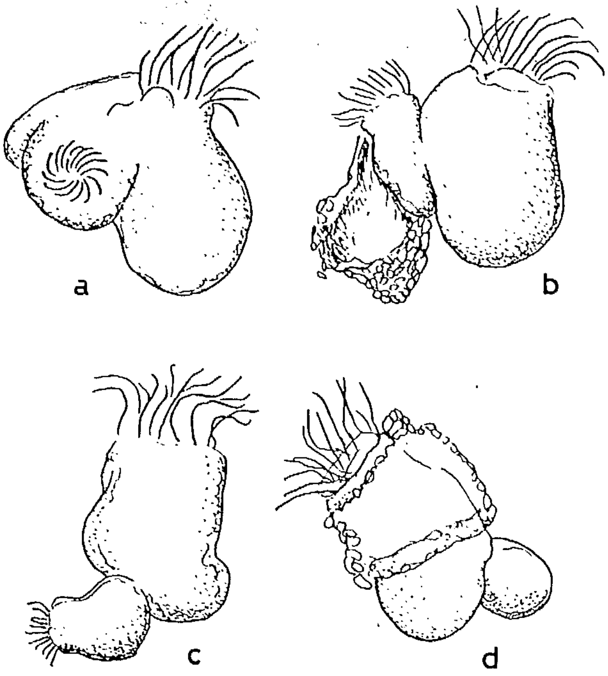

Fig. 10 a-d. Formation and conjugation of microgamete in *Tintinnopsis beroidea*. 10 a: early stage of the microgamete formation on posterior lobe; 10 b: intermediate stage of the formation — the lorica is fractured; 10 c: late stage of the formation — the microgamete is still sticking on mother cell; 10 d: conjugation of gametes. (Redrawn from microphotographs in GOLD and POLLINGHER, 1971)

Like the frequency of conjugation, the frequency of formation of microgamete becomes higher as the reared population grows old. That is to say, sexual reproduction does not seem to take place when the doubling time is as short as 0.8 - 1.1 days. Sexual reproduction seems to occur when the doubling time is as long as 4 - 6 days (Gold, 1971; Gold and Pollingher, 1971).

3. Formation of the cyst p 133

Apart from the oceanic ~~pelagic~~ species which Keep coming and going with oceanic ~~pelagic~~ water, the neritic species, which repeat seasonal increase and decrease in the coastal zone where seasonal changes in the environmental conditions are great, form a cyst at a certain period to survive unsuitable environment. On the contrary, in a rearing experiment where the water temperature and photoperiod are kept constant and only the food condition is variable, the cyst formation does not take place even when the food condition deteriorates and the reared population grows old. The cell dissolves before the formation of the cyst membrane (Gold and Pollingher, 1971). For the time being, information on the formation of the cyst is poor. Further studies are to be made on the cyst formation to throw light upon the life history of the neritic tintinnids.

Conclusion

As remarked earlier, the above information is limited to the neritic species. As the number of the neritic species is only a small part of the whole species of tintinnids, we can go so far as to say that the greater part of the reproduction and life histories of the entire tintinnids is still unknown. Keeping this in mind, the author undertook to sum up the life history of the tintinnids as follows.

The tintinnids ordinarily multiply at a high rate repeating the binary fission (including the plasmotomy). When the population grows old, it rejuvenates by sexual reproduction. The multiplication rate lowers during the period of sexual reproduction. The principal method of sexual reproduction is isogamous conjugation. There is no regular alternation of sexual and asexual generations. Cyst formation is observed in some neritic species at a certain period. However, the cyst formation is not caused only by the deterioration of food conditions. Except for the cyst period in the neritic species and for a certain period during lorica building, the tintinnids live through life as plankton without coming in contact with the bottom of the sea.

Their swimming ability is very poor. Besides, they are not known to make remarkable movement either vertically or horizontally. In consequence, the life history of the oceanic tintinnids must be one of the simplest among marine organisms.

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Addendum

Recently, GOLD and MORALES (1976) report ecology of lorica building of the agglutinated tintinnids. HEDIN (1976) also studies on ecology and cytology of the cold water tintinninds. LAVAL-PEUTO (1977) suggests the possibility that different types of loricae would be built by a single species. These articles and their references should be referred to get better understanding of the up-to-date knowledges about biology of the tintinnids.

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