

STUDIES ON THE MARINE CILIATE FAVELLA
(JÖRGENSEN), WITH SPECIAL REGARD TO
THE NEUROMOTOR APPARATUS AND ITS
RÔLE IN THE FORMATION OF THE LORICA

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ARTHUR SHACKLETON CAMPBELL

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INTRODUCTION

Prominent among the marine plankton collected in a fine silk net are various Tintinnoina. Catches made in San Francisco Bay and at La Jolla during the year 1925 showed, at various times, large numbers of the genus *Favella* (Jörgensen). The technical methods employed in preparing the specimens for study were similar to those described in an earlier paper (Campbell, 1926).

To Dr. C. A. Kofoid, under whose direction this work was undertaken, and to Dr. T. Wayland Vaughan, of the Scripps Institution of Oceanography, I owe thanks for many courtesies.

SYSTEMATIC POSITION

The genus *Favella* has been recently erected to include certain forms of Tintinnoina previously allocated to *Cyttarocydis* and forming a distinct section of the latter. Jörgensen (1924) as a result of his collections in the Mediterranean concluded that these forms formed a homogeneous series and might be profitably distinguished as a genus. He diagnoses *Favella* as having a typical "*Cyttarocydis*

structure," without a collar, save in *F. ehrenbergi* and *F. azorica*, and without coiled structure. For this genus he selects as the type, *Favella serrata* (Möbius). "Here," says Jörgensen, "belong the rest of the old-established genus *Cyttarocyliis*, after the separation of *Xystonella*, *Xystonellopsis*, *Coxiella* and the genus *Cyttarocyliis* proper" (1924, p. 25). In the genus *Favella* belong, according to Jörgensen (1924), not only the type-species, *F. serrata* (Möbius), but in addition *F. ehrenbergi* (Clap. and Lachm.), *F. azorica* (Cleve), *F. adriatica* (Imhof), *F. markusovzkyi* (v. Daday), *F. aciculifera* Jörgensen, and *F. fistulicauda* Jörgensen.

In our investigation *F. serrata* is treated in some detail and unless otherwise stated it is this form that is discussed.

MORPHOLOGY

The form of the *lorica* (pl. 21, fig. 1) is that of a much elongated bell with a short, slender, pointed handle (*pd.*, fig. B, 3). It opens at its widest part to form the oral aperture and narrows somewhat posteriorly at the fundus where the bowl ends. The *pedicel* (fig. A, 1, 2, 4, 7) is seldom straight and generally curves to one side or the other. It is sometimes provided with a slight knob at the tip. The bowl (fig. B, 3) of the *lorica* is usually straight-sided but somewhat below its oral margin it may become locally somewhat distended with the result that the oral margin is slightly narrower than is this widest part of the bowl. In *F. ehrenbergi* the sides are rounded evenly and regularly (fig. A, 6). The *lumen* (*lu.*, fig. B, 3) of the bowl is capacious and the inner surface of the bowl is smooth. The *lumen* extends into the pedicel nearly to its tip, which is closed (*lu. ped.*, fig. B, 3). *F. ehrenbergi* does not have a hollow pedicel (fig. A, 6). The contour of the lumen (fig. A, 3, 6) follows closely that of the bowl except that the wall becomes thinned out orally just below the lip.

The *oral margin* is serrate or denticulate. The *denticles* (pl. 21, fig. 1), arising from broad bases, extend upward in a regularly spaced series in the thin oral margin of the *lorica*. These denticles are acute, short, and erect, and seldom higher than three microns. They are not undulations but rather sharp. There are sixty to seventy-five of them. Their function is difficult to make out. There is some correlation between the number of these denticles and the number of ciliary lines on the cytosome.

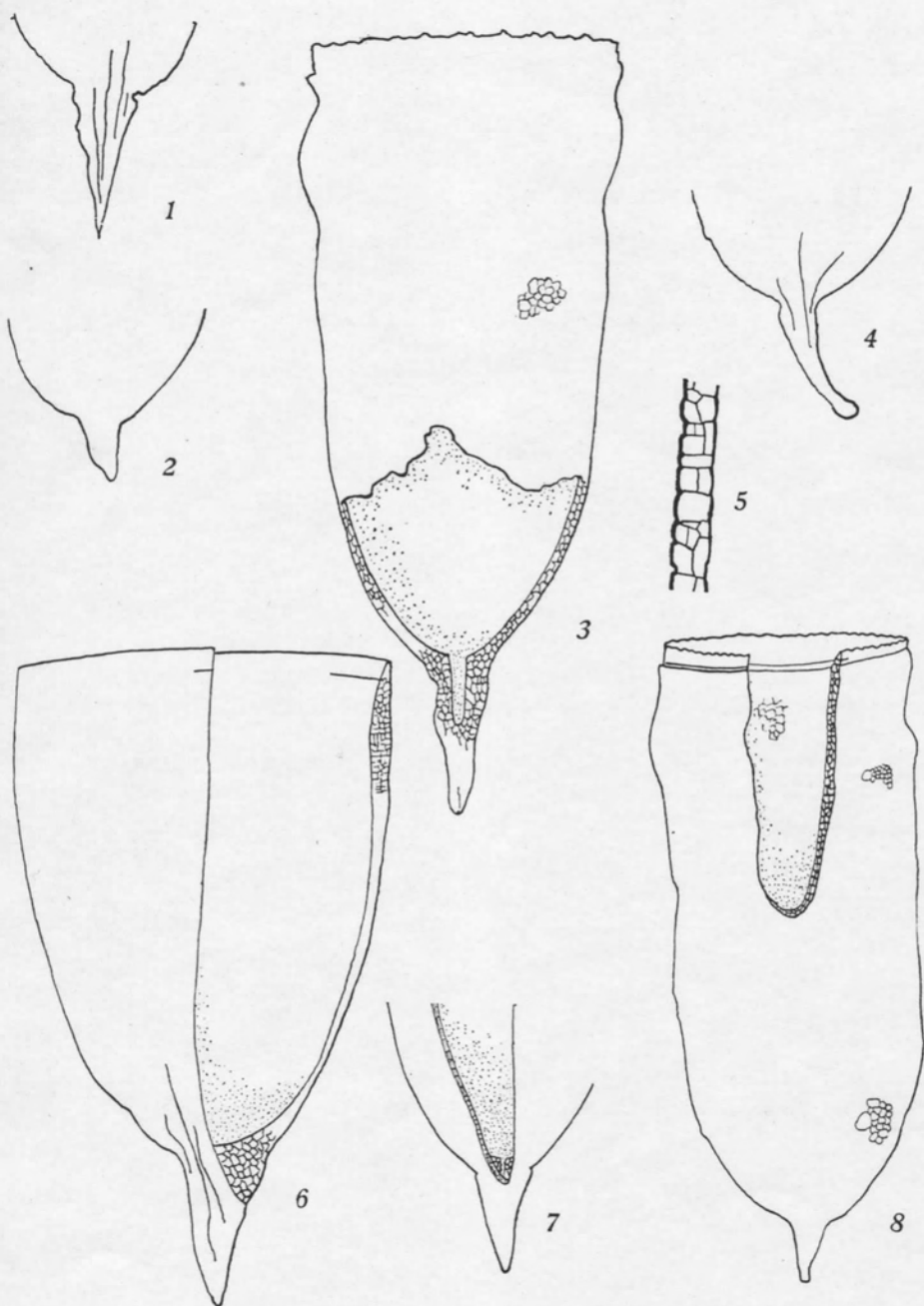


Fig. A. Camera lucida drawings of *Favella*. 1. Pedicel of *F. serrata*. 2. Pedicel of *F. ehrenbergi*. 3. Lorica of *F. serrata*. 4. Pedicel of *F. serrata*. 5. Wall section of *F. serrata* to show structure, greatly enlarged. 6. Lorica of *F. ehrenbergi*. 7. Pedicel of *F. serrata*. 8. Lorica of *F. serrata*. $\times 422$.

The wall of the lorica is distinctively alveolar (fig. C, 2). The alveoles of the wall vary in dimensions from those of about one micron across to larger ones of two or four microns. Often, in the upper part of the lorica near the oral margin, there are large conspicuous, pellucid lacunae. These appear to owe their origin to a differential colloidal aggregation, possibly brought about when the lorica is first formed by some feature of food or excreta. The alveolar structure, which is characteristic of the cyttarocylids and widespread in other Tintinnoina, is formed from layers of secreted colloidal matter of at least two sorts, one possibly forming the wall of the alveole, and the other the contents. The visible walls of the prismatic elements (Kofoid, 1905) are apparently the outer, closely compressed walls of the crowded and crushed substance-filled alveoles described. This is clearly shown by Entz, Jr. (1909, pl. 20, figs. 42-43). The sub-regular prisms (pl. 21, fig. 4) which make up the wall are so placed that their ends form the inner and outer surfaces of the lorica. Their sides form the hexagonal or rounded mesh of alveoles which is designated as the 'secondary structure' (Brandt, 1907). Their ends may form the inner and outer lamelles as suggested by Kofoid (1905). A finer alveolar structure (pl. 21, fig. 4) of 'primary alveoles' may be detected on the inner and outer surfaces, within the coarser secondary ones (fig. C, 2). These two types of alveoles probably owe their origin to differential factors of colloidal aggregation. The outer ends of the peripheral alveoles of the reticulum are hemispherical or irregular and lend a roughened appearance to the wall in addition to the folds or pleats. The whole outer surface of the lorica is unevenly rugose. The short, longitudinal pleats are developed to the greatest extent near the pedicel. The inner face of the wall is smooth and the coarse 'Cyttarocylis-structure' is evident on the outer face only. The alveoles which make up the wall are found between the lamelles, in several layers. *Favella serrata* never shows annulation, although the localized bulging below the rim simulates a tendency to the formation of an annulus.

The alveolar structure is pronounced in the aboral half of the lorica where the alveoles are larger and in many layers and is less apparent above. The alveoles are usually in one to three layers and may be in four or even five layers aborally, especially in *F. ehrenbergi*.

In its measurements *F. serrata* falls into what Brandt (1907) calls the "large tintinnids." My measurements of individuals collected off-shore in California range between 220 and 260 microns in length.

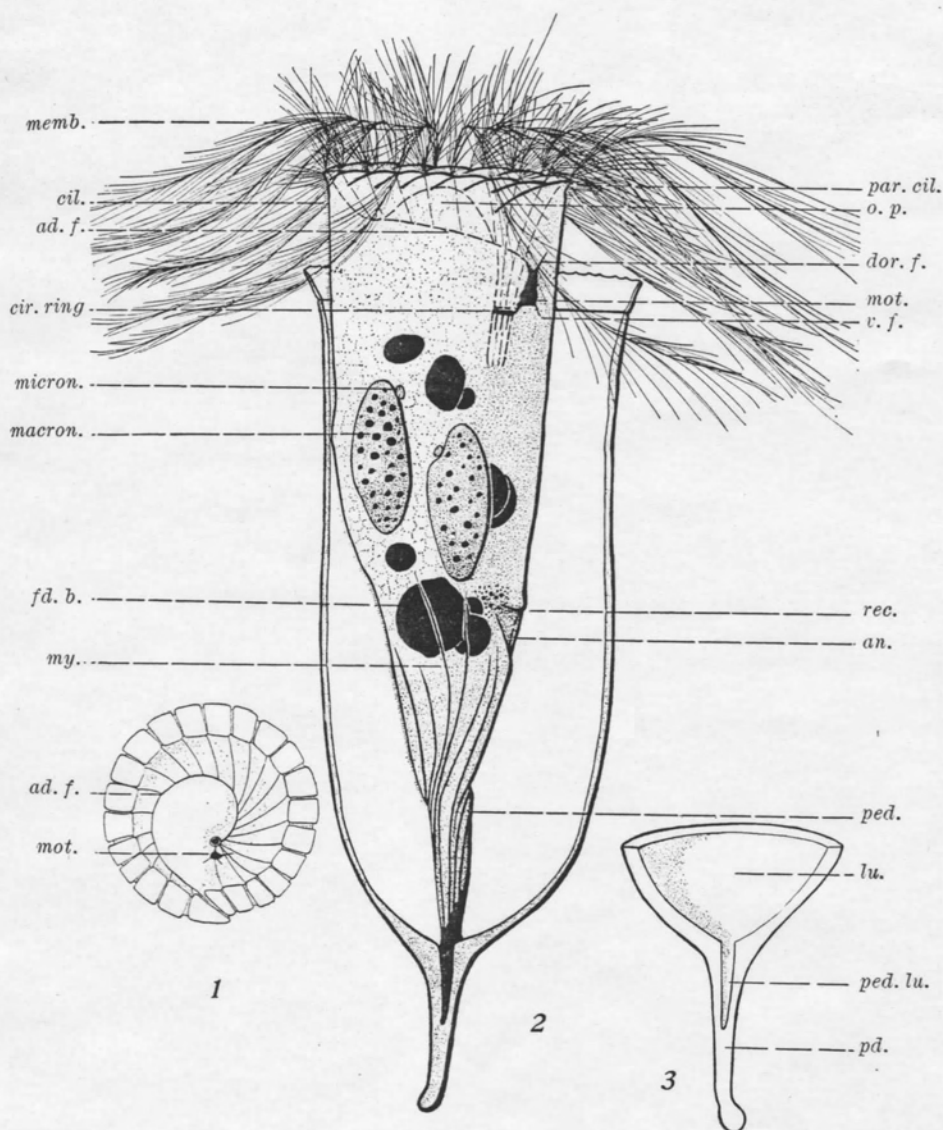


Fig. B. Semidiagram of *Favella*. 1. Cytosome from above, showing adoral fiber, *ad. f.*; motorium, *mot.* 2. Cytosome, showing adoral fiber, *ad. f.*; anus, *an.*; cilia, *cil.*; circumoesophageal ring, *cir. ring*; dorsal fiber, *dor. f.*; food body, *fd. b.*; macronucleus, *macron.*; membranelles, *memb.*; micronucleus, *micron.*; myonemes, *my.*; paroral cilia, *par. cil.*; peduncle, *ped.*; oral plug, *o. p.*; rectum, *rec.*; ventral fiber, *v. f.* 3. Posterior end of lorica, lumen, *lu.*; pedicel, *pd.*; pedicel lumen, *ped. lu.* $\times 525$.

They average about 225 microns in total length. They are 70 to 82 microns across the oral aperture so that they form a length to breadth ratio of 2.5-3.2 oral diameters in length, averaging 2.8. This ratio appears to vary considerably from collection to collection and may be indicative of the widespread possibilities of growth, reproduction, secretion, and flotation factors. The length of the pedicel also varies considerably in any collection (fig. A, 1, 2, 4, 7). Some forms have a short stumpy pedicel of 17 microns in length, while others have one of 50 microns. The pedicel may then vary between 1:1.8 to 1:5.5 the oral diameter, or 1:4.8 to 1:11.8 total length. The pedicel is 14 to 18 microns across at its origin and is usually conical in shape. It is ribbed with longitudinal folds, especially in *F. ehrenbergi* and *F. serrata* (fig. A, 4, 6) and may be knobbed at the tip. This pleating and knobbing may be a structural evidence of the manner of formation of the lorica through building activities.

In the *cytosome* of *Favella serrata* several major regions may be distinguished. These are the peduncle, body, nuclear system, and finally the neuromotor system. These will be treated in order. The animals are somewhat trumpet-shaped, roughly resembling the shape of the lorica in which they dwell. There is a flattened oral end surmounted by a spiral crown of membranelles.

The *peduncle* (*ped.*, fig. B, 2) is the narrow conical part which extends posteriorly from the main part and fastens the animal to the lorica. At the point of junction with the lorica it expands slightly and ends in the canal of the pedicel. In *F. ehrenbergi* there is no canal so that the peduncle is fastened in the fundus. The peduncle is sometimes parted into lateral branches, which may freely anastomose with each other, and form attachments to the wall. The peduncle is not homogeneous in make-up. Within the living animal tiny granules are visible, which upon fixation and staining are often deeply colored, as though this might be a region of secretory activity. The animal may attach itself to the lorica either by secretion or by suction; possibly both are involved.

In the somewhat thickened granular periphery of the peduncle are pronounced fiber-like *myonemes* (*my.*, fig. B, 2) which ascend vertically about halfway up the length of the body. These myonemes are stouter aborally and thin out orally. They are granular in the fixed and stained animal and thread-like in the living organism. They are unlike those of *Tintinnopsis* (Campbell, 1926) in that they do not seem to extend up to the margin of the frontal field. That

they continue along the ciliary lines and join with the adoral motor apparatus is, however, probable, although difficult to trace. The myonemes are similar in number to the membranelles, that is, there are about twenty-four. The peduncle is ciliated only on its upper two-thirds.

The trumpet-shaped body, or *cytosome* proper, surmounts the narrow and rather distinct peduncle already described. It constitutes the greater volume of the organism; in it lie the trophic mass and the nuclei. The motor and feeding organs crown its flattened oral frontal field. As is the peduncle, so also the body is colorless, except as colored food-bodies occupy large vacuoles within it. The body is 50 to 70 microns in diameter and 200 to 265 microns in length, when fully extended.

There is no thick peristome collar enclosing the frontal field as in *Tintinnopsis* (Campbell, 1926); instead the cytosome continues and narrows somewhat as it turns inward to surround the margin of the frontal field, forming, as it does so, a *suboral constriction*. The margin of the frontal field is lobate or undulating, without tentaculoids.

An examination of the *frontal field* from above (fig. B, 1) reveals the most complex and integrated portion of the whole organism. This frontal field is subcircular, concave, except for the projecting oral plug, and occupies the whole oral end of the animal. It spirals ventrally downward toward the deepest part where the excentrically located *infundibulum* leads to the mouth below. Its surface is striated, regularly alternating bands of clear and darker substance forming a spiral which enters the infundibulum. Dorsolaterally arises a highly mobile prominence, or *oral plug* (*o. p.*, fig. B, 2) like that of *Tintinnopsis* (Campbell, 1926) and characteristic of the tintinnids as a whole. While the frontal field may be said to be subcircular and has been so regarded for a long time, a more careful examination demonstrates that it forms a spiral like that of *Stentor* (Johnson, 1893) and other heterotrichous ciliates. The direction of the spiral is left-handed or leiotropic viewed from below. Between the distal and proximal ends of the spiral there is a thin, scarcely marked, but distinctly evident cleft upon the margin of the frontal field. The distal end of the spiral tapers as it ends at the cleft and overlaps the proximal part for a little distance. Thus the frontal field becomes a distinct series of organs of the animal and is not to be regarded as a hypostome. The frontal field is always transverse to

the main axis of the organism unlike *Tintinnopsis* (Campbell, 1926) or *Amphorella* (Fauré-Fremiet, 1924), in which its face is usually at a considerable angle to that axis.

A prominent anus or *cytopyge* (an., fig. B, 2) is located in the lower part of the body, below the mouth and on the same side, at a point just above the oral origin of the peduncle. There is a raised slit in the cuticle which marks its position. When fully open the *rectum* (rec., fig. B, 2) extends as a short canal into the endoplasm. There are no *contractile vacuoles* in these forms and indeed I have been unable to find any in the marine Tintinnoida I have examined. Brandt (1907) lists a series of marine forms with contractile vacuoles.

The *infundibulum* descends from the peristomal field, plunging into the slightly spirally disposed gullet, after leaving the mouth. There are no structural changes associated with this deep funnel-shaped depression as it leaves the peristome and descends the gullet. The *infundibulum* may occupy one-fourth to three-eighths of the breadth of the peristome. Its walls are partly lined by several regularly spaced membranelles.

The *gullet* leads posteriorly from the *infundibulum* after leaving the mouth. It forms a curved tube, the convex side of which is directed toward the outer ectoplasm and the concave side toward the oral plug. It is one-fourth the length of the body and when fully expanded it may be fifteen microns in diameter at the entrance. It is lined by pellicle. Extending down its length are three rows of short cilia which arise from the membranelles which enter the *infundibulum*. At the anterior end of the gullet is the *cytostome* or mouth.

The surface of the body and the peduncle is covered with a *pellicle* slightly more than a micron across where it is widest. That part of the pellicle which covers the frontal field and bears the first shock of surrounding influences, is somewhat thicker, as is the part about the slit-like *cytopyge*. Its surface is unmarked. It is flexible, retentive, and protective in function, and assists in the rapid and extreme changes in form which take place in this very mobile organism.

A distinctly differentiated and sharply limited *ectoplasm* does not distinguish any tintinnid (Entz, Jr., 1909) and no line of structural demarcation is found in *F. serrata*. The large alveoles of the endoplasm merge insensibly with the smaller, denser granules of the periphery.

The *endoplasm* makes up the greater part of the organism. In it digestion and other metabolic processes proceed. The cytoplasm which makes up the central core of the body is highly vacuolated, while that of the oral plug is denser. The endoplasm is crowded with food vacuoles. Most of these are found just above the peduncle which suggests that this region, near the cytopyge, is a food-storing one. The whole endoplasm is highly fluid and readily responds to changes which deform the body; there is little evidence of active streaming in it.

There are two *macronuclei* (*macron.*, fig. B, 2) and two *micronuclei* (*micron.*, fig. B, 2), one of the latter associated with each of the former, and set deeply in the endoplasm, one macronucleus behind the other, behind the gullet and somewhat lower. In the living animal the macronuclei appear as large gray masses and are clearly brought out by aceto-carmin and methyl-green. They readily shift in position, especially at the onset of division and may then occupy a position near the ventral side below the gullet, one macronucleus on either side of the anlage of the new frontal field. In form the macronuclei are somewhat like short sausages. The ends may be strung out irregularly and become ragged in some individuals. The finer structure of the macronuclei is much like that of *Tintinnopsis* (Campbell, 1926). The micronuclei are globular and generally located in depressions in the macronuclei, moving out into the endoplasm only during division. The macronucleus is 8 to 15 microns in width, 35 to 55 microns in length. The micronucleus is 2 to 3 microns across. Fauré-Fremiet (1924) claims that there is but a single micronucleus located about halfway between the two macronuclei in *F. serrata*. Two are uniformly present in my material.

NEUROMOTOR APPARATUS

The neuromotor apparatus includes all the motor elements of the organism and a connected fiber system which centers in the neuromotorium. It makes up a remarkable receptor-effector system which is concerned with the activities of the organism.

There are about twenty-four *adoral membranelles* (*memb.*, fig. B, 2). I have counted as few as twenty and as many as twenty-six in some cases. Each of the membranelles is about forty-five microns in length from the distal tip to the origin below. They form a leiotropic spiral crown which follows the course of the margin of the

frontal field. At the base they connect with each other and with the neuromotorium by a fiber. Three of the proximal membranelles enter the infundibulum and become modified to form the oral membranes, which are made up of short cilia. The membranelles are blade-like and flat. The outermost row of cilia is thick and stiff. Against these the distal ends of the remainder of the cilia may beat rather freely. At the base of the membranelle are three large basal bodies. The cilia which compose the membranelles are long. The function of the membranelles is not only to serve the animal in feeding and in locomotion but also to function in the building of the lorica during periods of division.

The *cilia* which make up the somatic coating are differentiated into longer *paroral cilia* (*par. cil.*, fig. B, 2) which occupy the suboral margin of the frontal field, and the short, barely visible *somatic cilia* which cover the surface of the cytosome (*cil.*, fig. B, 2). All these cilia are arranged in vertical rows. The paroral cilia may be three to five microns in length. There are about seventy of these rows of cilia and they are never differentiated locally into a lateral field as in *Tintinnopsis* (Campbell, 1926). Since this number of ciliary lines corresponds closely to the number of denticles which surround the mouth of the lorica, there is a suggestion of correlation between them. The longer cilia which are present suborally may serve as moulding organs and arrange the substance which makes up the lorica in this region into the characteristic denticles. In *F. serrata* these rows may build up denticles, whereas in *F. ehrenbergi* they may smooth down the lip.

The *fiber system*, which is the conducting and integrating system, lies in association with the organs just described. It comprises the (a) neuromotorium, (b) the adoral fiber, (c) the circumoesophageal ring, and (d) the ventral and dorsal fibers which arise from the motorium.

The *neuromotorium* (*mot.*, fig. B, 1, 2) is the large central massive spindle-shaped body toward which all the fibers in the system, by fusion or direct course, ultimately converge. It is located in the ventral ectoplasmic wall at a point below the middle of the gullet. From its aboral end the two *ventral fibers* (*v. f.*, fig. B, 2) arise and from its adoral end springs the *adoral fiber* (*ad. f.*, fig. B, 2). The motorium is rather small and is differentiated, with some difficulty, in whole mounts stained in iron-haematoxylin. The adoral fiber extends from the neuromotorium around the frontal field and below its margin

(*ad. f.*, fig. B, 1). It connects each of the membranelles and forms the principal neuromotor trunk. In addition to the adoral fiber the dorsal fiber appears to connect also with the striations of the oral plug. It was probably this fiber and the adoral fiber which Entz, Jr. (1909) described in *F. ehrenbergi* but which he did not connect with a central neuromotorium, which he did not detect and hence was led to conclude that the function of contractility and conduction resided in the ectoplasm. The ventral fibers appear to vanish freely in the endoplasm, passing downward. The *circumoesophageal ring* (*cir. ring.*, fig. B, 2), which is one of the most interesting parts of the system, surrounds the gullet below the midpoint and connects with the neuromotorium by a fiber. Fibrils extend from it below about the gullet.

The oral and pedicel regions are the areas of greatest morphological differentiation, and the oral region is the seat of the neuromotorium, which is the directing center. The motile organs, the membranelles, and cilia are located on or near the oral end and in the closest association with the areas of greatest modification in the loricas of all or nearly all the Tintinnoina (cf. Brandt, 1906) at binary fission. These facts lead us to suggest that the lorica forms a sound basis for systematic studies, even in the absence of the animal, for it is a biochemical product formed in a characteristic manner for each species and based both on the products and also upon the specific behavior of the species.

ECOLOGY

Favella serrata appears to be largely neritic, but it is also found under oceanic conditions, being recorded in the North Sea by Brandt (1907). In general it is widely distributed in temperate and subtropical seas. It was abundant in the waters of San Francisco Bay in August, 1925, and was found in collections made at La Jolla during January of the same year. In all these collections which I made living animals were present. *Favella serrata* is an epiplankton. Some collections yield many individuals while others taken a few days later may yield only a few.

The food of *Favella serrata* consists of bacteria, small pelagic diatoms and dinoflagellates, mostly common species, and more rarely, radiolarians, silicoflagellates, and some chrysomonads, whose yellow chromatophores add to the coloring matter of the cytosome. Entz,

Jr. (1909) reports the using of coecolithophores and small non-loricate ciliates. These food bodies lie in vacuoles (*fd. b.*, fig. B, 2), where they persist for a long time. There is no indication that these are selected in a particular manner. One may find dinoflagellates, diatoms, and other food matter in the same individual.

Favella serrata moves with the aboral end foremost, or it may reverse and move with the adoral end foremost. Locomotion is less darting than in *Tintinnopsis* (Campbell, 1926), having more the course of a smoothly moving *Paramecium*. *Favella serrata* does not adhere to solid objects, but is gregarious like *Tintinnopsis*. When disturbed it may desert its lorica and swim free. The animal rotates about its long axis as it moves forward.

Turning to the membranelles we find that these organs move in a harmonic, rhythmic, and pulsating manner, which accomplishes the work of locomotion and feeding, and, at certain periods, shell-building. When at rest, isolated, single membranelles may act independently. In locomotion the waves of contraction move distally on the membranelles from one to the next rhythmically. Oral membranelles, found in the mouth, are concerned with feeding and the organization of small food objects into boluses. The animal bores its way through the medium in which it lives in the manner described rather carefully by Entz, Jr. (1909). Mucus, strung out behind the moving animal, may be drawn up during resting periods and organized into food masses, together with the adhering food matter gathered by chance in this way.

There is some evidence that flotation is a function of the lorica in the Tintinnoina. Not only the great specific surface but the lightened structure is of importance to flotation. The alveolar structure whereby the hard wall probably encloses less dense substance enables the greatest surface to be attained with the least weight. This alveolar structure is greatly developed in *Favella* and similar Tintinnoina and may be of advantage in flotation. The long pedicel at the aboral end of the lorica may act as suggested by Brandt (1896) as a counterweight to the swimming animal, or may serve to increase the size of projection (Oswald, 1903*a, b*) and maintain the center of gravity so that a horizontal position is retained. Rapid sinking is prevented by the enlarged specific surface.

DIVISION IN SPECIAL RELATION TO THE FORMATION OF
THE LORICA

The *cytosomal changes* of *Favella serrata*, in division, are in principle not unlike those of *Tintinnopsis nucula* (Campbell, 1926). The cytosome elongates, and, as this continues, the newly forming frontal field on the side of the cytosome appears in increasing detail. As in *Tintinnopsis* the newly formed field after arising as a clear line curls upon itself and finally forms a spiral upon the ventral side of the parent cytosome. As the spiral grows and winds, the body continues to elongate. A fully formed, although very small functional frontal field, provided with short membranelles, appears in this position long before there are nuclear changes. Other stages of the process of cytoplasmic division are similar to *Tintinnopsis* (Campbell, 1926) and are illustrated in *F. serrata* (fig. C, 1, 5, 6, 7).

One cannot help being struck with the great part played by the cytoplasm in differentiation during division. The formation of the daughter peristome precedes all visible morphological changes in the nuclei of both *Tintinnopsis* (Campbell, 1926) and *Favella* (fig. C, 1). There is a daughter peristome formed with beating membranelles for some time before division changes are apparent in the nuclei (fig. C, 1). This fact leads us to believe that the neuromotor system, and the basal granules of the membranelles are derived from a cytoplasmic source and not, as maintained by Entz, Jr. (1909), from granules discharged by the nuclei. We suggest that the granules seen by Entz, Jr. (1909, pl. 16, figs. 8-10) are capable of another explanation, and cite in support of this suggestion the evidence from *Vorticella*, in which the aboral ciliary apparatus arises *de novo* and suddenly, in response to freedom from the stalk, either when freed naturally as in division or experimentally by cutting (Runyan and Torrey, 1914). This evidence is contrary to that expected from a nuclear origin for the basal bodies and the neuromotor system.

Nuclear changes in *Favella serrata* during division occur sometimes after the new frontal field has appeared upon the surface of the column. They are very similar to those of *Tintinnopsis* (Campbell, 1926). The macronuclei rotate into position one beside the other about the anlage and after some time elongate, and the chromatin materials within become strand-like (pl. 21, fig. 3). The reconstruction band in the macronucleus appears probably as the

solution of contents in this area proceeds. Following this the daughter nuclei separate and then reassemble. The micronuclei divide mitotically, forming a large number of chromosomes. They swell up to about five microns in the prophase. There is never any indication of conjugation or condensation as described by Laackmann (1906) or Entz, Jr. (1909), either of the macronuclei or micronuclei. Each always retains its identity throughout all phases of division and interkinesis. There is no evidence that chromidia give rise to nuclei, as was thought by Entz, Jr. (1909). The nuclei may be parasitized by *Karyoclastis* (fig. C, 4), or the cytosome by *Duboscquella* (Chatton, 1920) (fig. C, 3). Monomacronucleate individuals (pl. 22, figs. 5, 7; fig. C, 8) are probably reorganizing after conjugation (Campbell, 1926). These unusual forms may simulate chromidion-gamy. Various phases of division are presented in figure C, 1, 5, 6, 7, and in plate 22, figures 5-7.

The *building of the lorica* is a process involving activity upon the part of the organism. Not only the production of substances which will give rise to its materials is needed, but there is also involved the moulding of this matter into a structure with a regular, characteristic species pattern. The former is a simple matter and needs only a secretory region of some sort or another, while the latter implies some sort of active constructive behavior which is periodic in occurrence and regular in application to the problem set before the organism. Both are part of the process in the Tintinnoina. The building of the lorica implies a behavior based upon structure. The concept of the mechanism of this challenging phenomenon is readily supplied by the description of a neuromotor system which furnishes the integrating and coordinating apparatus whereby the formed material is built into a characteristic lorica.

As in *Tintinnopsis* (Campbell, 1926) the animal elaborates substances which are formed into the lorica. The sources of this matrix might be, it has been suggested, (a) a general surface peeling (Entz, Jr., 1909), (b) general surface extrusion from peripheral vacuoles in the ectoplasm (Busch, 1925), (c) material derived from the break-up of the old lorica and reworked by the two daughters at division (Meunier, 1910), (d) the division of the lorica into two parts, the uppermost being taken by the anterior and the lower part by the posterior daughter (Entz, Sr., 1884), (e) secretion of a ring by a temporary annulus of the cytosome (Schweyer, 1909), and finally, (f) the lorica may be derived from a local secretion from an already

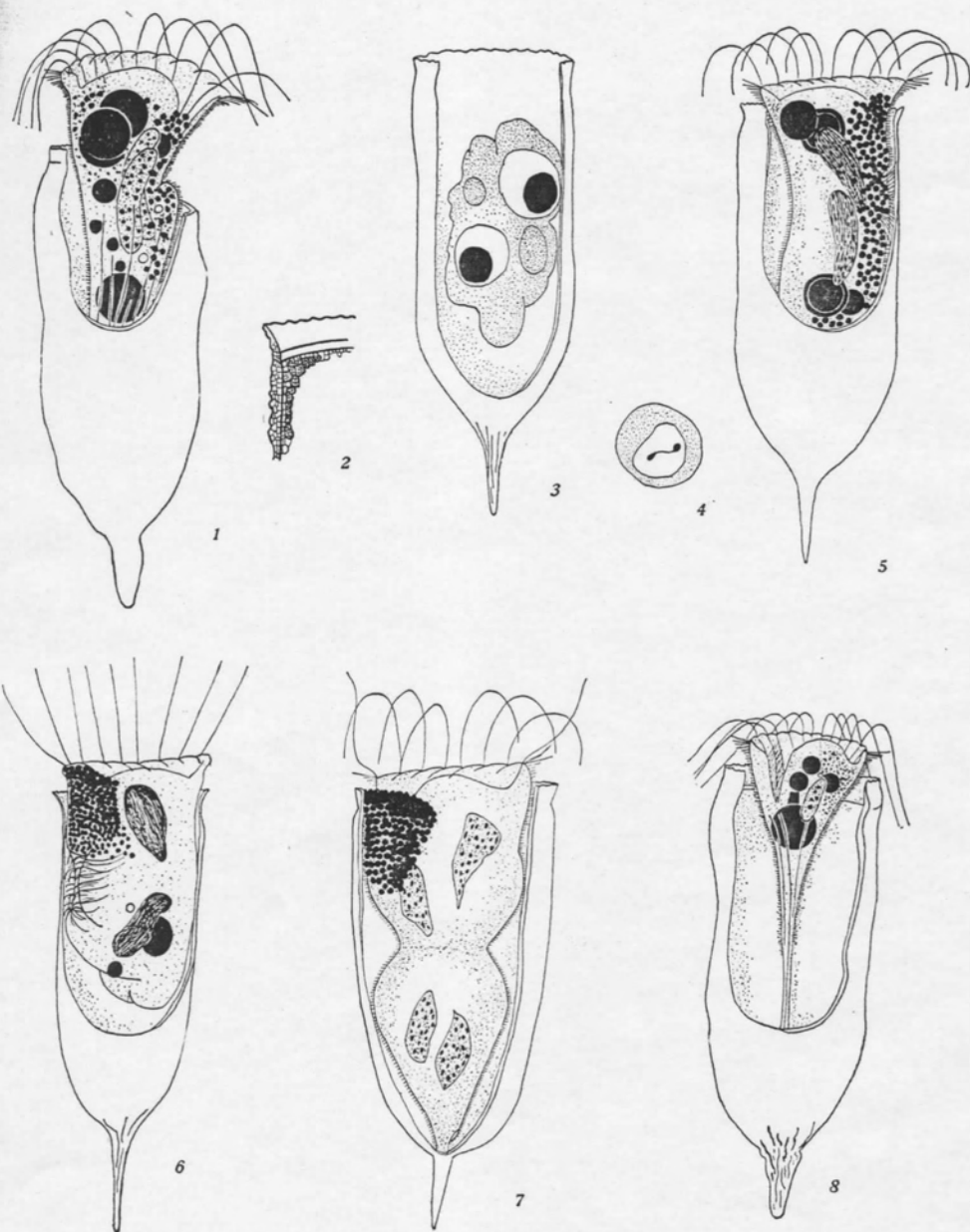


Fig. C. Camera lucida drawings of *F. serrata* showing various phases of division and other features. 1, 5, 6, 7, show division phases and especially the distribution of siderophile granules. 2, shows the structure of the wall. 3, parasitism due to *Duboscquella tintinni*. 4, isolated *Karyoclastis*, greatly enlarged. 8. Monomacronuclear form. $\times 260$.

formed organ, as the mouth, and moulded by neuromotor organs as suggested by Kofoid (1905) and later by myself (1926). These many suggestions, some of them based upon actual observations, are difficult to reconcile.

Jørgensen (1924) regards it as only provisional that the loricas of aborally closed species are built as described by Schweyer (1909) and believes the observations of Entz, Sr. (1884) upon *Tintinnus fluviatile* to be essentially correct for these forms; he doubts that the loricas of all Tintinnoida are constructed in a uniform manner. In his account (1924) of *Rhabdonella spiralis hydria* he suggests that the loricas may be formed as short, thimble-like structures which later on, by some unknown sort of stretching or growth, acquire the form of the matured lorica with a long pedicel and elaborate apophyses. It is exceedingly difficult to imagine by what process growth might take place in those figured (1924, fig. 70a, b, c, d). It might be intussusceptional, in which case we are compelled to assume more than we can believe possible in such a non-living system as the lorica. If, on the other hand, its growth may be described by stretching the explanation of the form of the elaborate posterior pedicel of that species depends again upon some unknown and curious factor of moulding; the animal scarcely deserts its lorica and swims outside to complete its dwelling. On the whole Jørgensen leaves one much to desire regarding the formation of the lorica of *Rhabdonella*. His *Rhabdonella spiralis hydria* is probably, as he suggests is possible, only a deformed member of another species. The suppositions of Entz, Jr. (1909) and Busch (1925) that the lorica forms from surface excretions have little observation to support them. The latter author, who figures particles adhering to the surface of the cytosome of the same refractility as the lorical substance, and claims that they arose *in situ* fails, in my mind, to produce evidence that these particles were not derived from the mouth or anus. I have never seen, in an extensive series of prepared slides, any evidence of a general surface extrusion in any tintinnid. Meunier (1910) hardly accepts his own theory, advancing it only provisionally. Entz, Sr.'s (1884) account seems not to have been substantiated, although the species, *Tintinnus fluviatile*, is common.

There is definite evidence in *F. serrata*, of the source of the material used in lorica construction. The *siderophile granules* formed in dividing animals (fig. C, 1, 5, 6, 7, and pl. 22, figs. 5-7) in a dorsolateral position surrounding the mouth and often in late

stages densely packed together, serve as the intracytoplasmic source of the material of the lorica. The greater mass of the material of the lorica is thus formed, another part being derived from accumulated fecal débris from the anus, especially in *Tintinnopsis*. The evidence for this is the occurrence in the wall of the lorica of skeletal remains of organisms used as food, such as coccoliths and diatoms. They would be extruded from the anus rather than the mouth. - The dense mass of siderophile granules figured by Entz, Jr. (1909, pl. 16, fig. 2c; pl. 18, fig. 2c; pl. 19, figs. 5, 8c) and thought by him to represent chromidia may be similar granules. This mass of granules forms a dense, shield-like unit always in a constant position above the newly-forming membranelles. They appear to arise (pl. 22, fig. 5) as loose single granules in the region of constriction, which is an area of great activity, and to move into the mass one by one, or in small groups, becoming compacted later. Upon extrusion through the mouth they expand (pl. 22, fig. 6; and fig. C, 7), fuse and harden slowly, and are beaten into shape by the neuromotor organs adjacent, such as the membranelles and paroral cilia. The clear annular band (of the living animal) seen by Schweyer (1909) may be the swollen region full of this lorical-forming substance in *Tintinnus inquilinus*, and the annulus pictured (Schweyer, 1909, pl. 10, fig. 6) a diagram only of extruded lorical substance. Material is poured out of the mouth and the anus as may be observed in the living organism. Kofoid (1905) was struck with the possible relation existing between a localized secreting area and the general prevalence of annulations and coiling in the loricas of *Coxiella* (*Cyttarocylis*) *pulchra*, which he described from the San Diego plankton. This material is within the reach of neuromotor organs and may be transferred by their activity to form the rugose refractile layered alveolar structure of the lorica, which is a colloidal aggregation and formed from materials derived from the animal. This ebullition of foamy material especially from the mouth provides an asymmetrically placed source, and, as Kofoid observes (1905), the animals in common with other ciliates rotate about their long axes and thereby may distribute this matter symmetrically by their membranelles and cilia. The material may then be transferred by the neuromotor organs which by their activities shape up the lorica. The lorica reflects, in its permanent structure, the manner of its formation, as in *Coxiella* and *Climatocylis* where strong coiling is evident, or in *Favella*, where rugose pleats are prominent and denticles are provided about the oral lip. *Neuromotor*

organs are the moulding agents. Spines, apophyses, and other elaborations are the work of these organs, at binary fission. The serrations and repeated annulations of some, as the denticles of *Favella serrata*, are probably the work of the inhabitant itself as noted by Kofoid (1905) in *Tintinnus serratus* and *Tintinnopsis reflexa*. We suggest that the strong correlation between the number of denticles about the oral margin of *F. serrata* and the number of ciliary lines, especially of the longer paroral cilia, is of the greatest importance in this connection. The pedicel may be the work of the posterior daughter at division, and its knobbed, spiked, or irregular end the finishing stroke of the tools below. These correlations are too significant to be passed unnoted. As I have suggested in another connection the regions of the greatest differentiation of the lorica in all the Tintinnoina are those which are in contact at the time of the formation of the lorica, or at all times, with the neuromotor organs.

The regularity of pattern resulting from the behavior of the neuromotor organs is exemplified in the regularity of the loricas in the many finely separated species of tintinnids. The process of speciation in this large group has gone very far as even a cursory examination of Brandt's monograph (1906, 1907) demonstrates. The determination of this speciation in Brandt's monograph is founded upon the structural modifications of a single organ of the animal, the lorica. But the lorica reflects in its construction the fundamental, peculiar organization of the animal within it (Campbell, 1926) and it shows the specificity, not only of the structures used in its formation but equally of the behavior which formed it. It may therefore be held that behavior-pattern which is uniform in action within the species, and periodic in its expression in a given form, may aid the understanding of the manner of formation of the lorica not only in *Favella serrata* and *Tintinnopsis*, but also in the Tintinnoina as a whole. It finds its anatomical basis in a central, dominating neuromotor apparatus, within the complex body of these multicellular protozoans, and in the number, position, and relations of the cilia and membranelles, the tools available for moulding the lorica in the period of formation.

The stereotyped behavior of the neuromotor organs is repeated at each bipartition. Possibly the widely prevalent asexual reproduction and the repetition of countless generations by this method, each with a similar genetic, chromosome inheritance, may favor the regularity of behavior which accounts for the little dissimilar and

narrowly speciated loricas of each genus in every sea. Sexual behavior by conjugation or by phases of internal reorganization may then account for the mechanism of the evolution of the lorica and its inhabitant, provided a modern conception of heredity applies in the protozoa (Kofoid, 1923), as well as in the Metazoa; this unites in one system all such organisms.

SUMMARY

Favella is a largely neritic genus of the Tintinnoina. Its cytosome is trumpet-like with a flattened, spiral frontal field. There are two macronuclei and two micronuclei. There is a complex neuromotor apparatus of intracytoplasmic fibers linking the motile organs with a central neuromotorium.

The large loricas by their form and structure are adapted to pelagic life. The high specific surface and lightened structure add to the buoyancy of the organism. These loricas are formed from material elaborated in the cytoplasm and discharged largely by the mouth, and distributed and fashioned by the neuromotor organs into the characteristic lorica which is of high survival value. The loricas afford an excellent basis for the systematic allocation of the species in the Tintinnoina.

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EXPLANATION OF PLATES

All figures are drawn with a camera lucida from preparations fixed in hot Schaudinn and stained in iron-haematoxylin, except figs. 5-7, which were stained in borax-carmin.

PLATE 21

× 422

- Fig. 1. Lorica of *F. serrata*, cut away to show lumen.
- Fig. 2. Cytosome of *F. serrata*, showing general features.
- Fig. 3. Isolated macronucleus and micronucleus early in division.
- Fig. 4. A small portion of the wall to show primary and secondary alveoles.

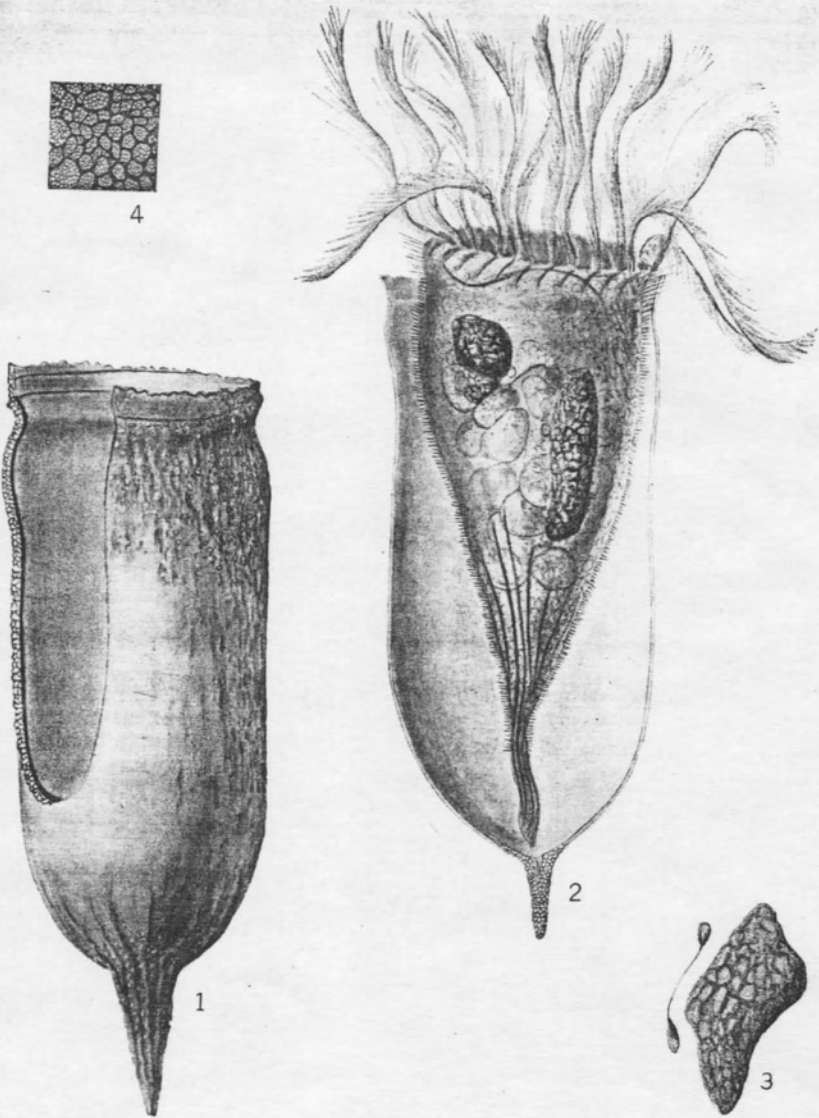


PLATE 22

× 338

Fig. 5. Dividing individual showing the accumulation of siderophile granules about the cytostome.

6. The granules have become massed about the cytostome and compacted closely. The new mouth is well advanced.

Fig. 7. Same individual as fig. 5, but rotated 90°, showing the extent of the siderophile granules and their compacting about the mouth within the cytosome.

