Abstracted by William M. Goldsmith, author
Southwestern College, Winfield, Kansas.

The process of ingestion in the ciliate, frontonia.

The food of the ciliate, frontonia, is primarily diatoms, desmids, euglenas, filaments of oscillatoria, and various other microscopic plants. The mouth is normally very small, but may be expanded to approximately two-thirds the length of the body without injuring the organism. Five factors are involved in the process of ingestion of material longer than the expanded width of the body of the frontonia. A. Action of oral cilia: The cilia about the mouth of frontonia exert a direct pull upon the incoming food. B. Action of the locomotor cilia: The cilia of the body drive the organism forward and thus force the stationary food into the mouth. C. The rotation of the body axis: The end of the fiber usually enters the mouth and passes anterodorsally until it comes in contact with, and exerts a pressure upon, the aboral wall, after which the frontonia swings around and releases the tension. Points of contact between the ingested particle and the inner side of the body membrane are called tension points. D. Body contractions: A series of sharp contractions of the body wall assists in relieving certain other tension points. E. Cyclosis: Cyclosis probably aids by moving the end of the fiber around the wall. Unusual and fantastic figures are produced through the contortion of the organism by the ingested food.

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THE PROCESS OF INGESTION IN THE CILIATE, FRONTONIA[1]

WILLIAM M. GOLDSMITH

Southwestern College, Winfield, Kansas

TWENTY-FIVE FIGURES (THREE PLATES)

INTRODUCTION

The present paper is primarily a record of a series of observations on the ingestion of various kinds of food by the ciliate, Frontonia leucas, and on the relation which this unusual method of ingestion bears to the variation in shape and habits of the organism. The points of chief importance and interest in connection with the present problem are as follows:

1. Frontonia frequently takes food consisting of filaments many times longer than itself. The manner of ingestion of such food is explained in detail.

2. The food of frontonia, is primarily diatoms, desmids, euglenas, filaments of oscillatoria, and various other microscopic plants. Various indigestible particles may also be ingested.

3. The mouth of frontonia is normally very small as compared with that of Paramecium and other common ciliates. However, it may be expanded to approximately two-thirds the length of the body without injuring the organism.

4. The normal shape of the body may be altered by certain characteristic contractions, by simple twisting and bending, and particularly by the presence of ingested materials.

[1] These investigations were carried on in the Zoölogical Laboratory of the Johns Hopkins University during the year 1919–20, in connection with the regular laboratory course in animal behavior. The writer is indebted to Prof. S. O. Mast for many valuable suggestions during the progress of the work. He is also under obligation to Prof. Asa A. Schaeffer, of the University of Tennessee, for reading the manuscript.

5. Food is not taken into the mouth by the usual ciliary action of the cytostome. A number of related factors are involved in this process. These are considered in the text and are listed in the summary.

GENERAL BEHAVIOR

Under normal conditions, in a quiet culture, frontonias may be seen swimming slowly here and there near the substratum apparently in quest of food. Any slight disturbance, such as the jarring of the container or the addition of weak chemicals to the culture, causes the organisms to rise from the bottom and to swim around more rapidly. However, after the removal of the stimulus they soon settle down to the bottom and continue the slowly swimming movements. Schaeffer ("Ameboid Movement," '20) says: "Frontonia feeds mostly by 'browsing,' that is by eating particles lying on or against some solid support." If an individual chances to come in contact with any object approximating the size of the food it is accustomed to eating, such as filaments of oscillatorias, diatoms, desmids, and various other microscopic plants, it usually pauses, places the oral opening near the object and proceeds to brush it with the oral cilia as though attempting to ascertain its nature (fig. 1). While the mouth is in close proximity with the object, the posterior part of the body frequently swings about this point as upon a pivot, sometimes turning through an arc of 90° or even entirely around. It is not uncommon for the organism to leave the object, move off for a short distance, then turn slowly about and swim here and there over the same area, eventually coming in contact with the same object and repeating the process.

THE MECHANICS OF INGESTION

Although frontonias ingest food particles of various shapes, the process of feeding can be more successfully observed when the food is in the shape of a filament. Before actual ingestion is begun the organism usually moves over the food and slowly swings around until the longitudinal axis is parallel with the long axis of the object to be engulfed. It then moves slowly

forward with the oral cilia in contact with the object (fig. 1) until the end of the linear food particle is reached, when the mouth is slowly pushed over the end of the object and thus ingestion begins (fig. 2).

Just as the oscillatoria filament is about to enter the mouth, the frontonia bends the anterior end downward as shown in figure 2. This brings the plane of the mouth perpendicular to the long axis of the fiber, and thus permits the fiber to enter with the least resistance. As the fiber slowly enters the body, the granules and food particles suspended in the endoplasm are pushed aside, leaving a clear space on either side of the entering food. This space usually presents the general appearance of the ectoplasm. From all indications it seems quite certain that a small amount of water is taken in with the fiber which adds to the transparency of the surrounding space. This clear area is not definitely set off from the endoplasm material as is the case during the last two or three hours of digestion. The protoplasmic granules and smaller food particles may pass from one area to the other, and often crowd in and at times, and at certain places, obliterate the transparent space. The movement of these granules in front of and to the side of (fig. 3) the incoming food fiber is quite characteristic of the movements accompanying the entrance of any solid into a viscous medium containing particles in suspension. As will be suggested later, there is little streaming of the granular endoplasm unless there is first a movement of the incoming fiber or possibly a contraction or other movement of the body wall.

A. Ciliary action—first and second factors of ingestion

The mechanics by which the oscillatoria filament (or any other material) is caused to enter the body of the frontonia is of vital interest in connection with the present investigations. At the outset it should be emphasized that the customary method employed by the ciliates, namely, the sweeping of food particles into the mouth in a current of water created by the cilia, is obviously out of the question, since the food is oftentimes much longer than the organism. First, the oral cilia may be in actual

contact with the food and exert a direct pull thereon and thus actually pull the object into the mouth. Secondly, the action of the cilia of the body may push the frontonia in the direction of the food and thus force the end of the object through the mouth opening. Prolonged study revealed the fact that both factors of ingestion are employed. The most conclusive evidence in support of the first possibility was found in the fact that the organism was oftimes seen to lie quietly while the food slowly entered the mouth; while, on the other hand, it was not uncommon for the oscillatoria fiber to remain comparatively still, while the frontonia slowly moved forward as the end of the fiber entered the mouth. This forward movement suggests that the frontonia either pushes the fiber into its body by swimming toward and around it or that the oral cilia, pulling upon one end of the stationary fiber, move the frontonia in the direction of the food. The fact that the ciliate at times moves forward when there is a concavity at the oral region (fig. 4) suggests that the push comes entirely from the locomotor organs. However, other situations are noted wherein the oral region moves along the fiber while the ciliate as a whole and the fiber itself are both stationary (figs. 10 and 11, *h* to *l*). Such observations would seem to establish the fact that both the oral and locomotor cilia play a part in the mechanics of ingestion.

B. Body movement—third and fourth factors involved in the mechanics of ingestion

In case the food particle is no longer than the expanded width of the body of the ciliate, the two factors heretofore considered suffice to explain ingestion. In the case of a diatom, for example, the body cilia force the frontonia forward while the oral cilia pull the food into the mouth. However, when one end of the food body is forced against the aboral wall, as at *a*, figure 3, and the other end still protrudes from the mouth, continued ingestion, if no other factors entered, would cause a rigid fiber to be thrust firmly against the aboral wall. Further ingestion is impossible without the play of other factors, and these appear to result from the stimulation due to the pressure of the end of

the fiber against the body wall. It will be convenient to designate the points where this occurs as *tension points*. Specifically, however, the writer would define tension points as those points of contact between the ingested material and the body wall in which a sufficient pressure is exerted to be a stimulus. Such stimuli result in, (*a*) the changing of the angle between the body axis and the fiber, or in, (*b*) certain characteristic body contractions. It will be shown later that cyclosis is also an important factor in relieving the stimulation at the tension points, especially when flexible fibers are being ingested.

When the food fiber comes in contact with and protrudes the aboral wall, special effort seems to be exerted in an attempt to continue ingestion without altering the process. This outward pressure at the tension point seems to serve as a stimulus and to cause one or more things to happen. Sometimes partial or complete ejection of the food takes place, either suddenly by jerky movements, or slowly by reversing the ingestion process. Usually, however, the body of the frontonia goes through certain squirming movements and straightens out more in line with the axis of the fiber, thus aiding in the continuation of the ingestion process, (fig. 4). It will be noted from figures 1 to 8 that the frontonia is now turned through an angle of 180° from the position at the beginning of ingestion. When in this position the incoming food meets the least resistance, as the end of the fiber must now travel posteriorly along the aboral wall (*b*, *c* and *d*) rather than anterodorsally, as it did when it first entered the mouth. Thus, at the completion of this stage of ingestion the organism is turned completely around (compare fig. 1 and 8). It will be noted that during the early stages of ingestion the ciliate is usually directly over the fiber with the anterior end bent downward so that the mouth will come in contact with the end of the food body. This being the case, the end of the fiber which is being ingested is raised from the substratum.

The turning of the body, as shown in figures 3 to 6, causes the point of contact (fig. 3, *a*) of the end of the oscillatoria filament and the body wall to shift posteriorly (figs. 4, 5, and 6; *b*, *c*, and *d*). After the body reaches approximately the position

shown in figure 5, the usual method of ingestion (the pull of the cilia of the mouth and the push of the locomotor cilia) carries the end of the fiber along the aboral wall to the posterior end of the frontonia (fig. 7, *e*). The continued pressure exerted from within not only makes more pointed the posterior end, but also causes an elongation of the entire organism (fig. 8). The anterior end now moves along the fiber, thus causing the mouth to be drawn well toward the anterior end of the organism (fig. 8, *f*). As the mouth is pulled forward the pressure at the posterior end becomes greater and greater. This is the second tension point in the process. The stimulus causes the organism to again undergo sharp body contractions. As in the former case, if the pressure is not relieved the oral cilia are relaxed, causing the body again to shorten. With a whirling backward movement the frontonia ejects the food particle (fig. 12). However, if the fiber bends or breaks, normal ingestion continues.

In the specific case under consideration, the oscillatoria filament was bent as indicated (fig. 9) and the mouth continued to move along the fiber (fig. 10, *h*, *i*, and *j*), causing the posterior end to be drawn toward the mouth. The whole animal was bent upon itself like a hinge (fig. 11). Since under the given pull the ciliate had now reached its limit of expansibility and, furthermore, since the fiber did not bend again, further ingestion was impossible. Accordingly, the frontonia suddenly contracted, whirled about the oscillatoria filament, causing the mouth (*m*) to be pried wide open, and flung itself from the food (fig. 12). With reference to this particular method of ejection, Schaeffer says: "If there are several coils of a filament whose other end is fast, rolled up inside of a frontonia, the mouth sometimes stretches antero-posteriorly until the coil as a whole without unwinding is thrown out of the body."

Rigid fibers were used extensively as food for experimental purposes, as the organism would continue to draw in one of them as long as possible and then eject it, only to repeat the process time after time. Since the fiber was longer than the expanded length of the organism and not sufficiently flexible to be wound up inside of the ciliate, the repeated attempts at complete in-

gestion were, of course, futile, but the process was nevertheless normal. This repetition made it possible to observe in detail again and again all of the movements involved in the ingestion of the same fiber by the same frontonia. These observations were furthermore especially valuable, as the fiber bent at a weak place at a distance from the ingested end equal to the expanded length of the ciliate. This bending permitted each process to continue more than twice as long as it otherwise would have done, since it was possible for more of the fiber to be ingested.

C. Cyclosis, the fifth factor of ingestion

Schaeffer emphasizes the fact that "in Frontonia leucas, rotational streaming is under the control of the organism, and special use is made of it in feeding." Although it will be shown later that cyclosis is effective, and in some cases essential, during the ingestion of certain flexible fibers, observations show that with some food material complete ingestion takes place without this fifth factor. A reconsideration of figures 1 to 9 will illustrate the point under consideration. In this case the rigid alga filament is forced into the body by the pull of the oral cilia and the push of the locomotor cilia of the body wall. The rotation of the body relieves the tension point (fig. 3, *a*) and permits the end of the fiber to pass down the aboral wall. Although there are slight indications of cyclosis during the ingestion of material of this type, careful observation makes it evident that rotational streaming is not essential. It might be concluded, then, that rigid material whose length is no greater than the expanded length of the frontonia can be, and is, ingested without the effective play of cyclosis.

VARIATION IN SIZE OF MOUTH

Such observations on ejection of partly ingested material as those considered above revealed some interesting facts regarding the nature of the mouth of frontonia. In many cases specimens which had ingested a sufficiently long fiber to produce a coil inside of the body suddenly whirled about and caused the mouth

to be expanded sufficiently wide for the spiral to pass out without being first unwound. In many instances the mouth was stretched almost the length of the body. However, the author would conclude from his observations that the stretching of the mouth of frontonia is brought about by mechanical means through the twisting movements considered above rather than through being under the control of the organism itself. At first this unusual process was thought to be simply the breaking of the body wall, but by segregating individuals which had thus ejected rolls of oscillatoria filaments it was found that they were in no wise injured and that the stretching of the mouth was a normal process. Some of the unpublished notes of Schaeffer bear directly upon this point. He says in part: "In case the thread is too long, the coil does not always unwind but in nearly all cases, if the coil consists of many turns, the coil in its entirety comes out of the animal, the mouth apparently stretching for nearly the whole length of the animal. This is a normal process and does not hurt the frontonia." The mouth of the frontonia is not only expanded to an unusual width during ejection, but also many instances of ingestion, or attempted ingestion, have been noted in which the mouth was pushed open almost far enough to ingest objects as large as the animal itself. Figure 13 shows a frontonia attempting the ingestion of a mass of débris larger than its own body. Observations indicate that this enlarging of the mouth during ingestion is brought about by the play of the first two factors involved in ingestion, namely, by the pull of the oral cilia and by the forcing of the organism against and around the material being ingested by the action of the locomotor cilia of the body wall.

INGESTION OF LARGE DESMIDS

At times desmids which seemed to be ciliated (fig. 16) were seen to swim here and there through the frontonia cultures. Since the high power revealed a thin layer of protoplasm between the ciliated wall and the body of the desmid (Closterium), it was evident that these unusual organisms were frontonias which had engulfed desmids of more than twice their normal length.

Since Closterium was the largest rigid body known to be ingested by any frontonia, a study was made of the methods employed.

In order to expediate observation, rich cultures of frontonia were deprived of food for a number of hours (from twelve to twenty-four), and were then removed to depression slides containing numerous specimens of Closterium. Under these conditions, the ciliates readily attacked the desmids until many frontonias attempting ingestion could be observed at the same time. In practically all cases ingestion was indeed only an attempt, as complete ingestion was of very unusual occurrence as compared with the number of trials. For example, on December 10, 1919, at 8:00 A.M., numerous specimens of Closterium were added to a rich culture of hungry frontonias in a Syracuse watch-glass, and the culture observed at brief intervals throughout the day. Although the ciliates spent the day in almost continuous attempt at ingestion, only three could be found at 5:30 P.M. which contained closteria.

The method of taking in these unusually large food particles was found to be almost identical with that involved in the eating of oscillatoria filaments as recorded in the earlier part of this paper, except that, of course, the mouth was more expanded. The average limit of linear expansion is shown in figure 15. At this point the organism either suddenly jerked back, whirled about, and left the desmid, or allowed the mouth to recede slowly down the desmid and completely ejected same, or relaxed as shown in A, figure 14, after which other attempts might be made before the food was completely ejected.

INGESTION OF SMALLER BLUE-GREEN ALGA FIBERS, OSCILLATORIA PROLIFICA, ETC.

The five factors considered in the earlier part of this paper are all noticeably effective during the ingestion of small flexible fibers. Figures 17 to 21 show the fibers being formed into a coil. The particular significance of this set of observations was in the further demonstration that cyclosis, regardless of the cause, is effective, if not essential, in some cases of ingestion. Without assuming that this is actually the case, it would be

very difficult to explain how the tension point at *c*, figure 19, could be relieved. Since the contractions, mentioned as the fourth factor, are direct compressions of the body wall, they would seem to force the end of the fiber through the body membrane. Therefore the movement produced by cyclosis would probably be the only factor which would alleviate this tension. When long fibers, as illustrated in figure 20, were completely ingested, the ciliate became very sluggish and discontinued the usual movements until digestion was nearly completed.

EFFECT OF THE INGESTED MATERIAL UPON THE SIZE AND GENERAL APPEARANCE OF THE BODY

Ingested food causes an unusual variety of shapes of the frontonia's body. Cultures taken directly from the brook have been found to contain individuals of almost every imaginable shape. The various shapes, of course, depend upon the variety of food available. After a few weeks' work the experimenter could cause to be produced many desired fantastic figures. For example, it was a very simple matter to produce the characteristic 'half-moon' frontonia shown in figure 23. This was done simply by cutting oscillatoria fibers into pieces slightly longer than the linear expanded length of the average frontonia. The imperfect 'half-moon' shown in figure 24 resulted from the ingestion of a longer fiber than was used in the case of the typical 'half-moon,' while the bow-and-arrow-like ciliate (fig. 22) is an unusual case in which a shorter piece of blue-green alga lodged perpendicular to the fiber which produced the 'half-moon.' The interesting case shown in figure 25 is simply a 'half-moon' frontonia in which the action of the digestive fluids caused the ends of the fiber to curl. Had the fiber given way in the center, the shape would have been markedly different. Since the food material includes not only hundreds of the smaller and more or less common fresh-water algae and the slowly moving protozoa, but also the limitless variety of foreign matter and débris which one finds in the sediment of a brook or which may be added to a culture, one is not surprised to find almost any imaginable shape. Moreover, the general appearance of the frontonia not

only varies with the shape, size, color, density, and flexibility of the ingested material, but also with the arrangement as well.

Although material of almost any color might appear in the body of the frontonia, the more common colors, especially during the progress of digestion, are the various shades of brown, green, and blue.

DIGESTION

Although the problem of digestion need not necessarily be considered with the mechanics of ingestion, a number of simple observations were made along this line. As was suggested in the earlier part of this paper, the smaller solid particles of the cell are not usually found in contact with the long food fibers. This clear space forms the beginning of the future food vacuole. The digestive fluid attacks certain parts of the fibers, especially the ends, more readily than others, and this causes the replacing of the graceful curves by sharp bends, breaks, and general distortion. The walls of the oscillatoria filament give way and after two or three hours of digestion the free ends usually begin to roll up. Later the fibers break at various points and the pieces roll up until only small spherical food vacuoles containing irregular masses remain. The entire process consumes approximately six hours.

SUMMARY

1. Observations and experiments were made upon frontonias while these organisms were ingesting euglenas, diatoms, desmids, and oscillatoria filaments.

2. The ingestion of blue-green algae, especially oscillatoria filaments, furnished the most conclusive demonstrations of the method involved, as the process continued a greater length of time and involved more factors than did the ingestion of smaller organisms.

3. Five factors are involved in the process of ingestion of material longer than the expanded width of the body of the frontonia. In case of smaller particles, the third, fourth, and fifth factors mentioned below are not essential to ingestion.

A. *Action of oral cilia.* The cilia about the mouth of the frontonia exert a direct pull upon the incoming food.

B. *Action of the locomotor cilia.* The cilia of the body in general drive the organism forward and thus force the stationary food into the mouth.

C. *The rotation of the body axis.* The end of the fiber usually enters the mouth and passes anterodorsally until it comes in contact with and exerts a pressure upon the aboral wall (fig. 3), after which the frontonia swings around through an angle of almost 180°, using the mouth as a pivot. This change of position permits the fiber to pass dorsally along the aboral side of the ciliate. Through the play of either factor A or B, or both, ingestion continues until the fiber exerts such a pressure on the body wall at the extreme posterior end that the organism is extremely elongated and pointed (fig. 8). Such pressure on the body wall acts as a stimulus, causing movements that relieve the stimulation. The rotation of the body axis assists in relieving the stimulation at certain of these tension points.

D. *Body contractions.* A series of sharp contractions of the body wall assists in relieving certain other tension points.

E. *Cyclosis.* Cyclosis aids by moving the end of the fiber around the wall, thus making further ingestion possible (fig. 19).

4. Unusual and fantastic figures are produced through the contortion of the organism by the ingested food which varies in size, shape, density, elasticity, and color (figs. 21 to 25).

PLATES

PLATE 1

EXPLANATION OF FIGURES

1 A normal frontonia approaching the end of an oscillatoria fiber prior to ingestion.

2 Oscillatoria fiber entering the body of the frontonia. Characteristic shape of the organism during the early stage of ingestion of linear objects.

3 and 4 Turning of the body of the frontonia in order to relieve the stimulation at the first tension point (fig. 3, *a*).

4 to 6 The body cilia is pushing the frontonia in the direction of the food and thus forcing the end of the object posteriorly along the aboral wall.

7 and 8 The fiber reaches the posterior end of the organism and causes an elongation of the body of the frontonia.

9 The fiber breaks and ingestion continues by the oral cilia pulling the mouth along the object.

INGESTION IN THE CILIATE, FRONTONIA

WILLIAM M. GOLDSMITH

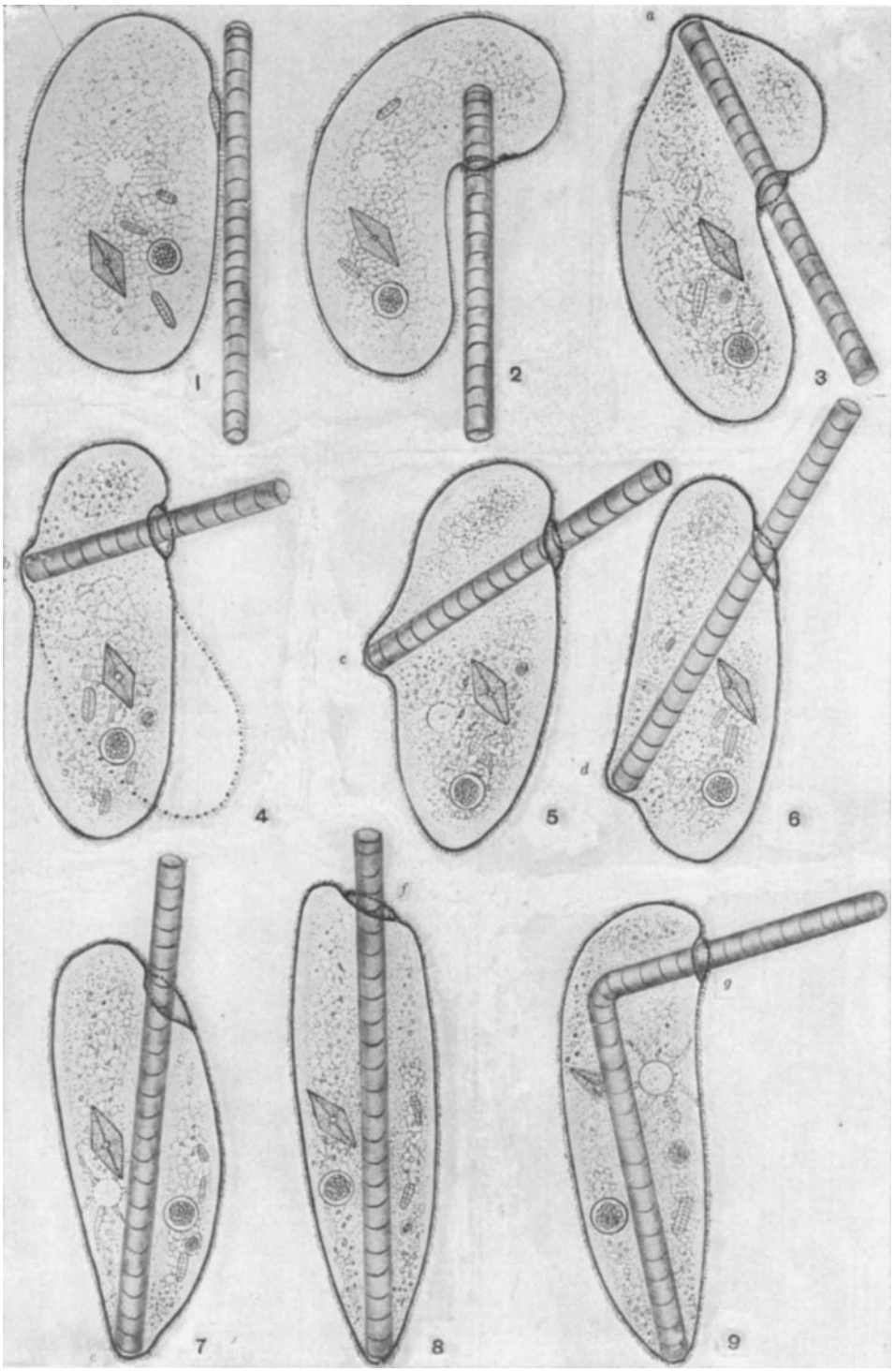


PLATE 2

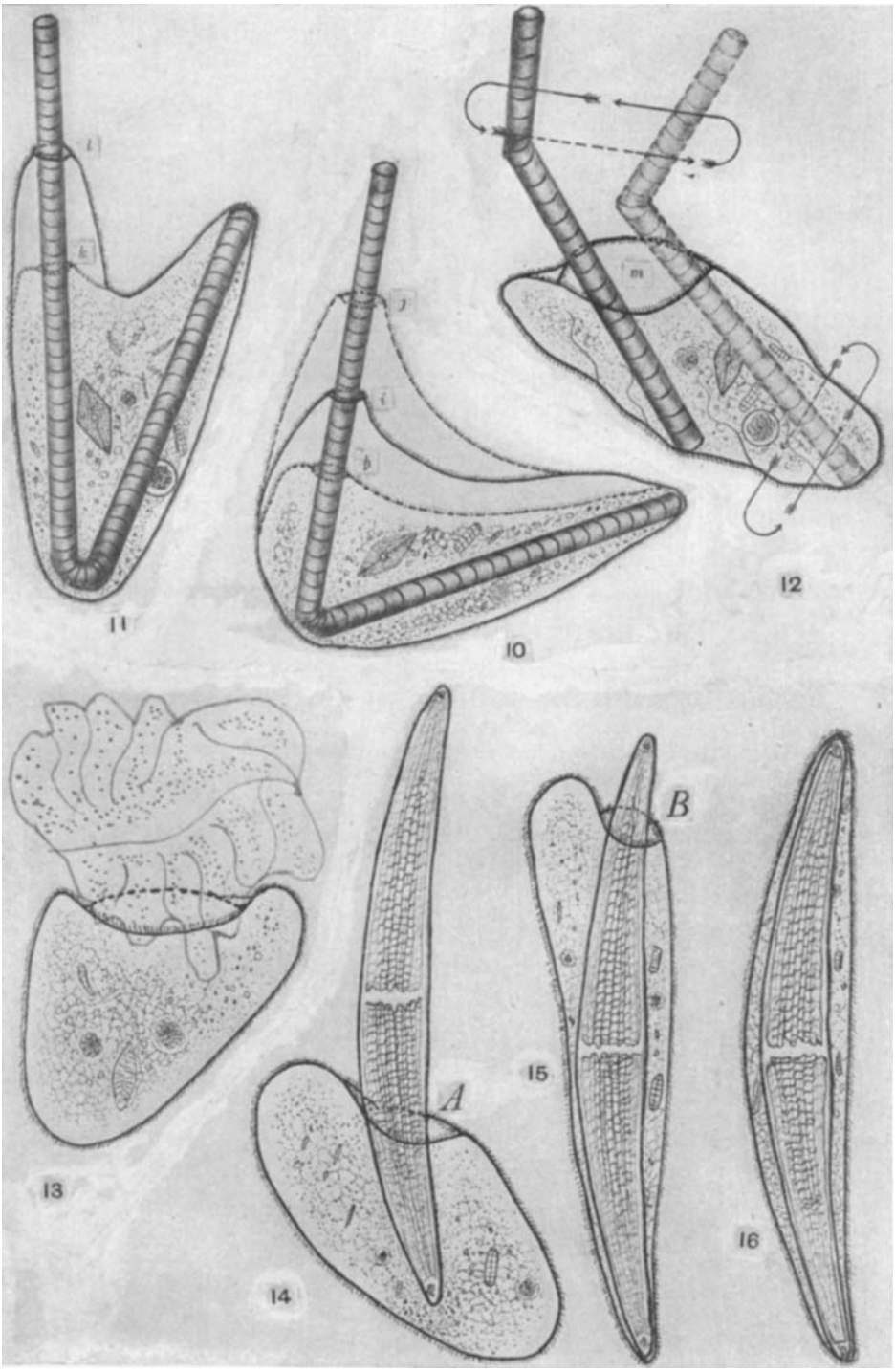
EXPLANATION OF FIGURES

10 and 11 The mouth of the frontonia continues to be pulled along the fiber (*h, i, j, k, and l*) until the body is stretched to its maximum.

12 Further ingestion being impossible, the mouth stretches anteroposteriorly while the entire organism whirls about and flings the fiber from the body.

13 A frontonia attempting the ingestion of an object larger than its own body.

14 to 16 Ingestion of a large desmid (Closterium).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10
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A
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B
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PLATE 3

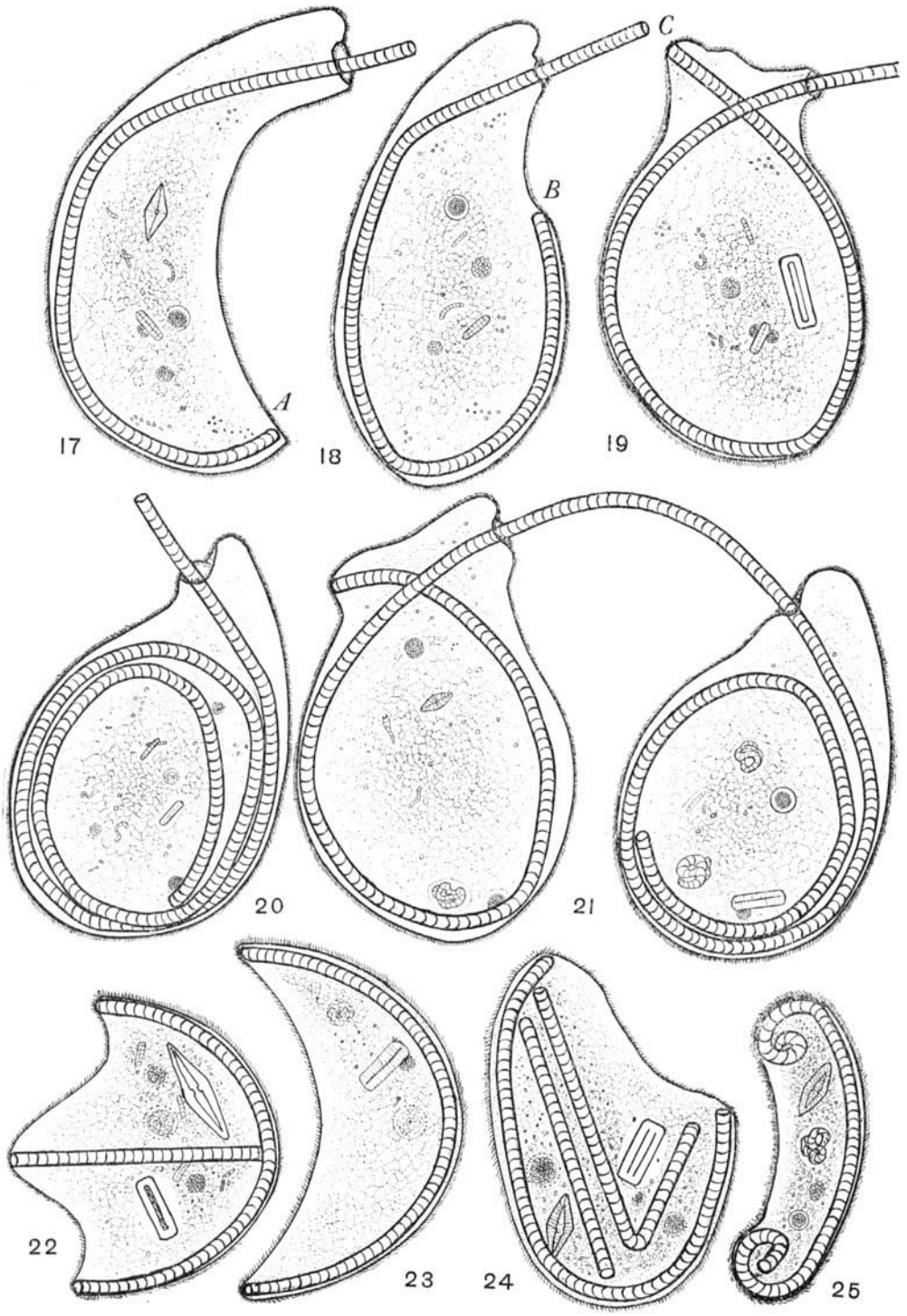
EXPLANATION OF FIGURES

The ingestion of flexible fibers (Oscillatoria prolifera)

17 to 20 Method by which a number of coils of an alga filament are rolled up inside of a ciliate.

21 Two frontonias attempting to ingest the same filament. In this particular instance the mouths met and the organism on the left slowly ejected the fiber as it passed into the mouth of the one on the right.

22 to 25 The ingested material alters the size, shape, and general appearance of the body of the frontonia.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