A Study of Spiraling in the Ciliate *Frontonia* with a Review of the Genus and a Description of two new Species.

By

W. E. Bullington

(Biology Department, Randolph Macon College).

With 11 figures and 9 plates in the text.

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I. Introduction.

The writer (1925) in a general study of spiraling in the ciliate Infusoria, finding direction of spiral in free swimming in the individual members of each species so constant as to be characteristic, concluded that spiraling might be of some value in the taxonomy of the Infusoria.

Later (1930) it was found that left spiraling *Paramecium bursaria* could swim in either direction. But in a careful study and comparison of the two directions it was found that the individuals of this species swam more often in left spirals. Left spiraling was always the direction followed when the animals swam great distances and it was always the direction in which greatest speed occurred; right spiraling was slower, the spirals wider, the distances traveled in a given forward direction much shorter, and was usually seen when the animals were "browsing" around over the debris or swimming to and from the surface film. But most striking of all was the instant change of direction from right to left spiraling by every right spiraling individual when it was greatly disturbed. Because of these facts left spiraling was considered the characteristic direction in normal free swimming for *P. bursaria.*

A special and careful restudy of spiraling, then made necessary for every species of *Paramecium* obtainable, showed four other species able to swim in either direction. But, in each of the four species, one direction again appeared easier, more natural, was the direction of greatest speed, and was used when the animal traveled greatest distances in a given forward direction. This direction was characteristic of free swimming. The other direction had exactly the appearance of something just being learned and therefore required attention to maintain. The spirals were wider and speed slower. Three species, however, were characteristically left spiraling; one characteristically right spiraling.

Later still (1930) Palolo embryos (24 hours old) were found able to swim in both right and left spirals. And again there was a distinct difference in the two spirals.

And now a special study of spiraling in the ciliate *Frontonia* has been completed. Here, too, certain species have been found able to swim in either right or left spirals. During the period covered by this work, which has extended over several years, I have found two species not previously described. Their description, as well as a study of their spiraling, is included in this paper.

Furthermore, since in this study of spiraling I have been compelled to make a careful study of the general morphology of each species in order to be sure of my identification, which is absolutely essential, and since I have found in this study certain characteristics which stand out, but which appear not to have been sufficiently described nor correctly shown in drawings of previous investigators, I feel it is necessary to give here a very brief redescription of the genus together with a key to the species and a short redescription of each species studied. In addition to this, for the sake of clarification, I am considering eight other species, or so called species, which have been described from time to time, in their relation to one another, and to the eight I have studied for spiraling. All this in the hope, and with the belief, that it will be of help to future investigators in the study of these animals.

A part of the observational work included in this paper was done at the Biological Laboratory, Cold Spring Harbor, Long Island, the U. S. Bureau of Fisheries Laboratory, Woods Hole, Mass., and Beaufort, N.C., and at the Carnegie Biological Laboratory, Tortugas, Fla.

II. Materials and Methods.

Materials. The animals studied in this paper came from pools and ponds in various sections of the country wherever and whenever they could be found. They include both fresh and salt water forms and are believed representative. Measurements of body size and of spirals are included here from Cold Spring Harbor; Lawrence, Kansas; Woods Hole, Mass.; Beaufort, N.C.; Tortugas, Fla.; and Ashland, Va.

Methods. For the determination of structure, which was necessary for purposes of identification, living individuals, and stained where possible, were studied under the 4 mm. and oil immersion objectives, and $10\times$ and $15\times$ oculars, with a carbon arc lamp as a source of light. In order to determine the direction of spiraling the animals were studied under the binocular microscope, first in mass culture, then individuals found spiraling in both directions were isolated in clean watch glasses and studied separately. In order to determine lenght of spiral, I counted the number of spirals required by an individual to swim continuously in a generally straight path, across the entire field of the microscope — a known distance. The diameter of the field in micra divided by the total number of spirals gave the average length of spiral in micra. The diameter of the field was usually 8000, sometimes 18000, and it was a relatively easy matter to count the spirals if the animal crossed the entire field in continuous swimming. The difficulty was, however, that they did not always swim entirely across the field. Since any distance less than the diameter of the field had to be estimated, all such partial measurements were, therefore, considered not sufficiently accurate to justify their use and were discarded. For speed of swimming, the time in seconds required to travel the distance across the field was obtained with a stop watch. The distance divided by the number of seconds required to cros the field gave the speed in micra per second.

III. The genus *Frontonia.*

The name *Frontonia* was created by EHRENBERG in 1838 as a sub-genus of bursaria to take care of those ciliates with a 'brow' or projection extending out over the anterior portion of the mouth.

DUJARDIN (1841) disregarded the name *Frontonia* and created the generic name *Panophrys* for this group of ciliates.

STEIN failed to recognize either name, *Frontonia* or *Panophrys*, and created the name *Cyrtostomum.*

CLAPAREDE and LACHMAN (1858) recognized the priority of the name *Frontonia* and raised it to the rank of a genus.

KENT (1881—1882) disregarded CLAPAREDE and LACHMAN'S *Frontonia* and went back to STEIN'S *Cyrtostomum* and described *Frontonia leucas* under the name *C. leucas.*

BÜTSCHLI (1887—89), MINCHIN (1912), TÖNNIGES (1914), CALKINS (1926), DOFLEIN (1929), and KAHL (1931), have all recognized and used the name *Frontonia* as the correct generic name for this group of animals.

The animals making up this genus are found in both fresh and salt water, are elongated in form, more or less dorso-ventrally flattened; usually rounded at both ends but usually wider anteriorly; narrowed and somewhat more cylindrical posteriorly; body extremely flexible, entirely and evenly ciliated, cilia arranged in fine longitudinal rows; trichocysts abundant in all species; mouth ventral, subterminal, not lateral as described by KENT, relatively large, oblong, pointed at the anterior extremity, more rounded or cut off squarely at the posterior end, and entirely surrounded by several rows of very fine, closely set cilia, which extend from this lower expanded portion of the mouth as a gradually narrowing band along the post oral groove described below. An undulating membrane is present in most, if not all species. The pharynx, if such it can be called, is very short, but is not lined with rod-like teeth as described by Ehrenberg and as shown in his drawings. Kent interpreted these 'teeth' as being more ovate modifications of the sub-cylindrical rod fascicles characteristic of *Nassula* and *Prorodon*. But in none of my examinations have I found rod-like teeth or rod fascicles, even under oil immersion objectives and the 15 × ocular, and with a carbon arc lamp as a source of light. I have, however, found trichocysts, which are so thickly studded over the body of all species, extending down the walls of the pharynx, and when seen in surface view i. e., when looking directly down into the mouth, give at times the impression of pharyngeal rods until they are examined very closely. This is undoubtedly what Ehrenberg saw and mistook for pharyngeal rods. The genus is further characterized by a long narrow groove leading from the lower right side of the mouth down the body in a gentle curve to the animal's left, and extending, in some cases, to the extreme posterior end of the animal. This groove seems to be an opening into the body — an extension of the mouth opening — and is almost, if not entirely closed, except when particularly long pieces of algae are being taken into the body when it opens as wide as necessary to aid in the process. This was reported by Kahl (1931), and I have seen it several times. This mouth and the groove are so characteristic in this genus, and so different from that in any other genus, that they may be taken as fundamental, easily determined characteristics for generic identification. Kahl shows in his drawings (1931), a band or line at the pointed anterior end of the mouth and extending from there to the extreme anterior part of the body. This is shown by him as a sort of band, particularly in *F. leucas* and *F. marina*. No previous investigator seems to have shown anything comparable to this, and in the several thousand individuals which I have studied I have failed to find it on any species. I am inclined, therefore, to believe it an optical illusion. This line, as he shows, is located at the point where the body striations and the finer oral cilia, on each side of the mouth, come to a point or meet in their curvature around the mouth. This might at times give one the impression of a line or band extending anteriorly, but an actual band or line I have failed to find.

IV. Key to the species of *Frontonia*.

a 1. Free swimming, not parasitic.
- b 1. Body distinctly foot-shaped.
  - c 1. Fresh water species.

d 1. With one contractile vacuole; body size averages approximately. 258 μ × 96 μ *Frontonia leucas* EHRBG.
d 2. With several (3—8) contractile vacuoles; body size averages approximately.
463 μ × 162 μ *Frontonia vesiculosa* DA CUNHA.
c 2. Marine species.
d 1. Spirals characteristically to the left.
e 1. With one contractile vacuole but without canals; body size averages approximately.
251 μ × 95 μ *Frontonia marina* FABRE-DOMERGUE.
d 2. Spirals characteristically to the right.
e 1. With 2—3 contractile vacuoles, pigment spot sometimes present; body somewhat oily green in color; body size averages approximately.
197 μ × 108 μ . . . *Frontonia vernalis* EHRBG.
e 2. No pigment spot; body size averages approximately. 120 μ × 65 μ *Frontonia schaefferi* sp. nov.
b 2. Body kidney-shaped; two contractile vacuoles; prominent pigment spot; body averages approximately.
141 μ × 76 μ . . . . *Frontonia ocularis* sp. nov.
b 3. Body oval or somewhat pointed, not foot nor kidney-shaped.
c 1. Fresh water species.
d 1. Body pointed at one end, sometimes at both; one contractile vacuole; prominent pigment spot; body size averages approximately.
117 μ × 80 μ . . . *Frontonia acuminata* (EHRBG.)
d 2. Body gently pointed posteriorly; pigment spot not present; body characterized by prominent pimples or 'perles' on surface; sometimes a caudal bristle present; body length 60 μ—80 μ.
. . . . *Frontonia depressa* (STOKES).
d 3. Without pigment spot; posterior end extended out like handle of a ping-pong paddle; body averages approximately. 255 μ × 158 μ *Frontonia atra* (EHRBG.).
c 2. Marine species.
d 1. May or may not have pigment spot; pointed posteriorly; one contractile vacuole; body length about 100—130 μ . . . *Frontonia complanata* (WETZEL).
b 4. Body ellipsoidal; ends equally rounded.
c 1. Fresh water species; body length about 115—150 μ
. . . . *Frontonia elliptica* BEARDSLEY.

c 2. Marine or brackis water species; body length may vary from 80 μ to 200 μ; may have a pigment spot. . . . . *Frontonia algivora* (KAHL) emend.

b 5. Body extremely slender, elongated; length about 200—300 μ; brackish water . . . . . . *Frontonia microstoma* KAHL.

a 2. Parasitic or commensal.

b 1. Commensal on gills of Amphioxus.

c 1. Body shaped like F. acuminata; without pigment spot; body measures.
75—100 μ × 55—75 μ *Frontonia branchiostoma* CODREANU.

V. *Frontonia leucas* EHRBG., 1838.

Frontonia leucas was described by EHRENBERG in 1838 under the generic name *Bursaria*, sub-genus *Frontonia*, as a flattened ciliate, almost equally rounded at the two ends, and having a body length of approximately 177 μ, with a mouth extending about one-fifth or one-sixth the length of the body from near the anterior end.

The individuals which are generally accepted as *Frontonia leucas* EHRBG., however, vary so greatly in size, (I have found them varying from 133 μ to 705 μ), that for some time I have questioned the correctness of the classification. But due to the fact that I was at first unable to pure culture them in the laboratory, and was limited in my studies for the most part to fleeting glimpses of 'wild' individuals found from time to time, very little could be determined concerning the reactions of specific individuals, and nothing concerning the reactions of the progeny of certain individuals.

But in the fall of 1932 great numbers of what appeared to be *Frontonia leucas* suddenly came up in an old laboratory culture made up of pine needles and spirogyra from King's Pond, and some decaying oak leaves from Railroad Pond. The smallest individuals in this culture measured only 133 μ in length by 66 μ in width; the largest 660 μ in length by 220 μ in width. I was able to isolate some of the very small and some of the very large ones and to establish pure cultures of each. These cultures flourished on boiled hay and wheat. These 'Algae eaters' of DOFLEIN (1929), ordinarily feeding upon Oscillatoria, diatoms, and other algae, seemed in this case to have adapted themselves to a bacterial diet. This was indicated by the fact that they collected around bits of hay and wheat exactly as do paramecia, although no bacteria-filled vacuoles comparable to those of paramecia were ever seen. BEERS (1933) reported *Frontonia leucas*, in some of his cultures, feeding upon amebas. Some of my cultures had great numbers of amebas in them but no frontonia were ever seen feeding upon them. Some were, however, observed feeding upon orcella and an unidentified species of rotifer.

Some of these cultures ran for two years and more, and during that time both groups maintained their identity.

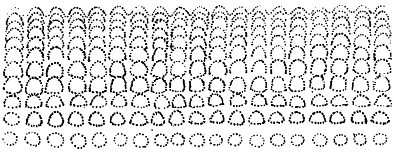
An examination and comparison of stained preparations of both groups for nucleus has shown very little difference in the macronucleus. Both have a single large, oval macronucleus, alike except perhaps for size, in which respect it has seemed to correspond more or less with size of body, agreeing in this respect apparently with the findings of Hood (1927). The macronucleus can be seen clearly in most individuals even without staining.

The micronucleii are also alike in general form and size, being relatively large oval bodies, similar in shape to the macronucleus, and located in the same relative position in both the small and the large individuals, either embedded in the macronucleus, lying along side of it, or scattered through the cytoplasm near it (Pl. 1 Fig. 1). The only difference noted was in the number of micronucleii. The smaller individuals seemed to have no more than five usually 3 to 4; the larger individuals commonly had 6 to 8. Whether this is a clear cut basis upon which a differentiation can be made is not definitely known at the present time and awaits further investigation.

Of more importance than size of body and number of macronucleii, however, is the number and character of the contractile vacuoles. The smaller individuals had uniformly one relatively large, centrally located contractile vacuole, while the large individuals had always 5 to 8 smaller laterally located vacuoles.

The difference in body size, number of micronuclei, and particularly in the number and arrangement of contractile vacuoles definitely indicate two entirely different species. And since the size of body, and number and location of the contractile vacuoles of the smaller one meets the requirements of Ehrenberg's description of *Frontonia leucas*, and correspond to the drawings of Ehrenberg (1838), and succeeding investigators, Fromentel (1847), Butschli (1887—89), Tönniges (1914), Doflein (1929), and Kahl (1931), it is identified as *Frontonia leucas*, and is the one described here under that name. The other, never before reported from this country, has, however, been found described from Brazile in 1914 as *F. vesiculosa* by Da Cunha, and will be discussed further under that name.

Frontonia leucas Ehrbg., belongs in general form, to a group which, in dorsal view, in shaped distinctly like the left human foot.



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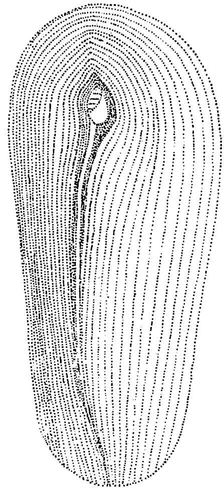

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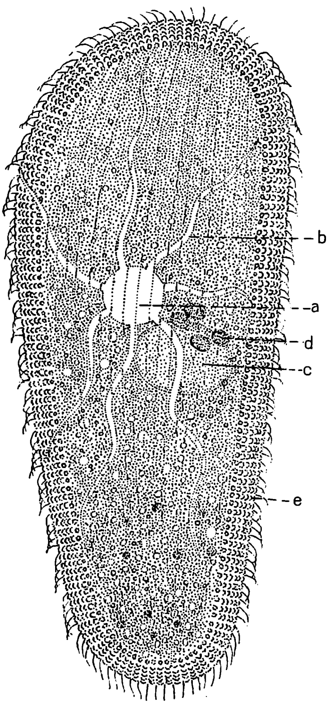

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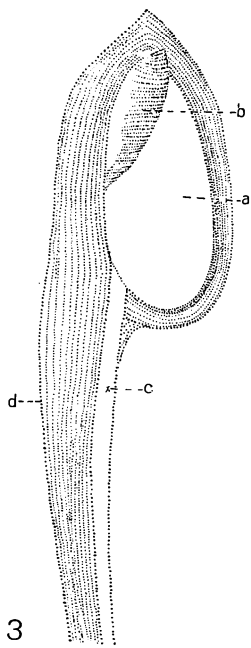

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Plate 1. *Frontonia leucas* EHR.

Fig. 1. Dorsal view, × 334. a Contractile vacuole, b Feeder canals, c macronucleus, d Micronucleii, and e Trichocysts.

Fig. 2. Ventral view, × 250, showing mouth and groove.

It is elongated, widened at the anterior end corresponding to the ball of the foot; is thinned out ventrally just back of this point and near the center of the body to correspond to the instep; narrowed and more or less cylindrical in the posterior region corresponding to the heel.

As for size, I have found individuals in this species varying in length all the way from 133 μ to 350 μ (Table 3), and in 110 measurements, length has averaged 258 μ. Width has varied from 66 μ to 150 μ, and in 93 measurements has averaged 96 μ. Of course most of these measurements were made of individuals from the laboratory cultures mentioned above. It may be entirely possible that other cultures will be found of the single vacuolated individuals, in which the maximum measurements exceed these figures, but they have not yet been found by the present author.

Trichocysts. Trichocysts, as reported by previous investigators, are abundant over the entire body of *F. leucas*, and appear, in side view, as small spindle-shaped rods, as described by EHRENBERG (1838), ALLMAN (1866), TONNIGES (1914). This can easily be seen when the microscope is focused down on the edge of the body. These trichocysts are attached in the cortex near the surface which their outer ends appear to punch up in the form of small pimples. These pimples appear along the edge of the body as serrations, but on the surface as small circles (Pl. 1 Fig. 4). The inner ends of the trichocysts extend inward into the fluid endoplasm where the endoplasmic granules can be seen flowing in and out among them. The trichocysts are usually arranged parallel to one another and perpendicular to the surface of the body, but they sometimes are found pointing at all angles to the surface. This is clearly seen in trapped individuals under the high power, — sometimes even under the low.

Mouth and groove. The mouth and groove call for special mention for the reason that no previous description or drawing seems to show these structures quite correctly. The mouth is ventral, sub-terminal, about $^1/_3$ to $^1/_4$ the length of the body from the anterior end, and near the right side. It is elongated, pointed at the anterior end, widened and cut off almost quarely at the posterior end (Pl. 1 Fig. 3). It is bordered all around by several rows of very

Fig. 3. Mouth and a portion of the groove highly magnified. a Mouth, b Undulating membrane, c Posterior groove, d Row of larger granules bordering the cilia surrounding the mouth.

Fig. 4. Pimple-like projections over the ends of the trichocysts, greatly enlarged.

fine, closely arranged cilia. Immediately outside of and surrounding these fine cilia is a single row of larger granules, as seen under the 4 mm objective, and are probably the basal granules of longer stouter cilia — but the cilia themselves were not seen. From the right side of the posterior end of the mouth is a narrow, whitish or transparent wavy band extending almost to the posterior extremity of the body where it gradually fades out. This is the oral or post oral groove. The fine oral cilia on the right side of the mouth extend down along the right side of this groove as a sort of band which also gradually fades out to a very thin line near the lower end of the groove. On the left side of the mouth, and at the posterior end, these oral cilia bend around the mouth sharply to the right and extend over to the groove. The inner row of fine cilia extends across the opening of the mouth into the groove. The mouth and groove, together with the band of surrounding cilia and the heavy row of granules, are very prominent and characteristic structures (Pl. 1 Fig. 2, 3). They at times give the impression of a broadsword with the groove representing the handle, the right side of the mouth representing the back of the blade, and the left side representing the cutting edge of the blade. A short undulating membrane, not shown by Kahl, has been found attached to the upper one-third or one-half of the right side of the mouth and extending diagonally across toward the animal's left.

Contractile vacuole. The single large contractile vacuole of *Frontonia leucas* is characterized, as has been shown by previous investigators (Allman (1855), Fromentel (1874), Tönniges (1914), Kahl (1930), and others), by the presence of several long, narrow, irregular, feeder canals which extend from the vacoule out through the cytoplasm in some cases almost entirely across the body (Text-Fig. 1).

Spiraling in Forward Swimming.

Direction of spiraling (Text-Fig. 2). *Frontonia leucas* can swim in either right or left spirals, but like *Paramecium bursaria* Bullington (1930), it does not swim equally well in both directions. A careful and long continued study of isolated individuals which were able to swim in both directions has shown that speed in right spiraling is slower, swimming more deliberate, and is continued for a much shorter distance in a given forward direction — usually for only 3—4 spirals — when the animal jerks backward and moves off in a new forward direction, exactly like *Paramecium bursaria*. Seldom does it continue in a given forward direction long enough to cross the entire field of the microscope, and for this reason it is difficult to obtain measurements of speed and size of right spirals. Right spiraling is more often seen when the individuals are swimming toward or away from the surface film — usually in a zig-zag manner — or feeding about over the debris.

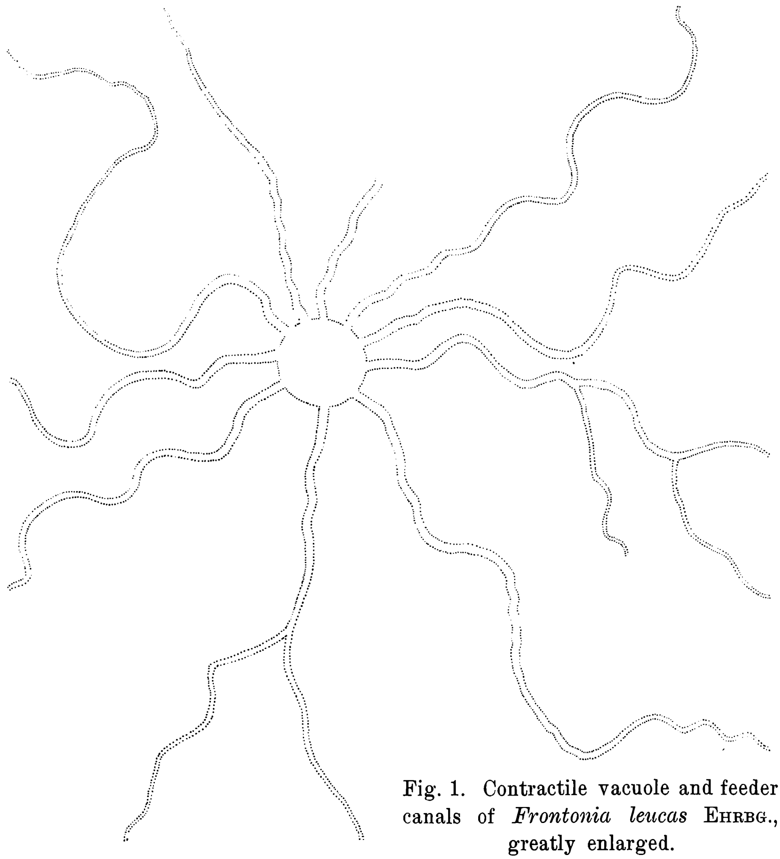

Fig. 1. Contractile vacuole and feeder canals of *Frontonia leucas* Ehrbg., greatly enlarged.

Greatest speed occurs, and greatest distances in a given forward direction are traveled, in left spirals, and this is the direction assumed automatically and instantaneously by all right spiraling individuals when greatly irritated,as when jabbed with a needle or transferred to a clean watch glass with a few drops of distilled water. Left spiraling may be toward the surface film or away from it, slow or rapid, but is usually in a horizontal plane and is continued for a distance sufficient to cross the entire field of the microscope. It is relatively easy to measure its speed and length of spiral. Left spiraling is therefore, considered the characteristic direction of spiraling for this species, and on this basis *F. leucas* is classified as a left spiraling species.

Size of spirals (Text-Fig. 2). Left spirals have averaged 1267 μ in length by approximately 100 μ in width; right spirals 967 μ in length by a width at least twice as great as that of left spirals. These averages are based upon measurements of 120 left spirals ranging in length from 1000 μ to 1600 μ, and 62 right spirals ranging in length from 666 μ to 1333 μ. Left spirals are therefore, at least one third longer than right spirals, and only half as wide.

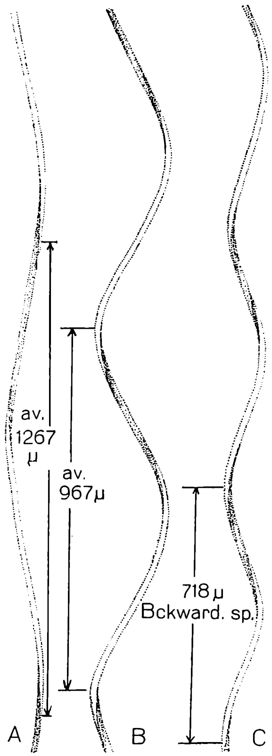

Fig. 2. Spiral paths of *Frontonia leucas*, 50 times actual size, showing size and direction of spiral. A. Average left spiral, B. Average right spiral, and C. Average spiral in backward swimming.

Speed of swimming. Swimming in left spiraling has averaged approximately 2050 μ per second in measurements varying from 1554 μ to 2960 μ per second; right spiraling has averaged 1081 μ per second, or only about one-half the speed of left spiraling.

Spiraling in Backward Swimming.

Backward swimming, which occurs frequently in this species, is always in right spirals. This is an absolute change of direction of spiral over that in normal forward swimming. No reason is known for this change of direction but it has been followed consistently in all backward swimming which I have been able to observe. One would I believe, ordinarily, expect a mere reversal of forward direction, which, in that case, would not constitute a change of direction of spiral but a reversal of the end going forward.

As to speed and size of spiral in backward swimming, the 76 spirals which have been measured averaged 718 μ in length, or a little more than half the length of spirals in normal forward swimming, and occurred at a speed of approximately 3000 μ per second or $1\frac{1}{2}$ times the average speed of normal forward swimming

(Text-Fig. 2). Speed in backward swimming, however, varies greatly. Sometimes under extreme conditions the animal may even perform spiraling movements without any progression whatsoever.

Turning while Feeding.

When these animals are feeding around over the bottom of the dish they are constantly circling to their left without spiraling. They do this by jerking backward, pivoting on the posterior portion of the body, then starting off in a new forward direction several degrees to the left of the previous one. Sometimes several turns are necessary to make the complete circle; sometimes one is sufficient. This turning is exactly the same that is used in changing direction of forward movement during right spiraling, and is the same circling seen in *Paramecium bursaria* BULLINGTON (1930).

Reaction to Additions of Sea Water.

Since it became necessary, in the identification of these species, to determine whether the same species could live in either fresh or salt water, each fresh water species was subjected to gradually increasing percentages of salt water. *Frontonia leucas* as here described, is very sensitive to slight additions of sea water to the culture medium, and if the additions are not made very gradually the animals quickly ball themselves up and die. And even when the sea water is added gradually they die when the medium has reached a percentage of about 25.

Diagnosis.

Frontonia leucas EHRENBERG sp., is a foot-shaped fresh-water species averaging approximately 258 $\mu \times 96 \mu$ in size; clear or slightly pinkish in color sometimes green; covered with fine, relatively short cilia arranged in fine longitudinal striations; mouth and groove relatively prominent, characteristic, ventral, subterminal in position; trichocysts abundant over the entire body; contractile vacuole single, central usually with 8—10 radiating canals; nucleus centrally located and consists of one large oval macronucleus and sometimes as many as five relatively large oval micronucleii; left spiraling is normal, characteristic, used in all speed and distance swimming, the one instantaneously assumed by all right spiraling individuals when greatly disturbed, and occurs at an average speed of 2050 μ per second, in spirals averaging approximately 1267 μ in length by 100 μ in width; right spiraling is a feeding rather than a free swimming

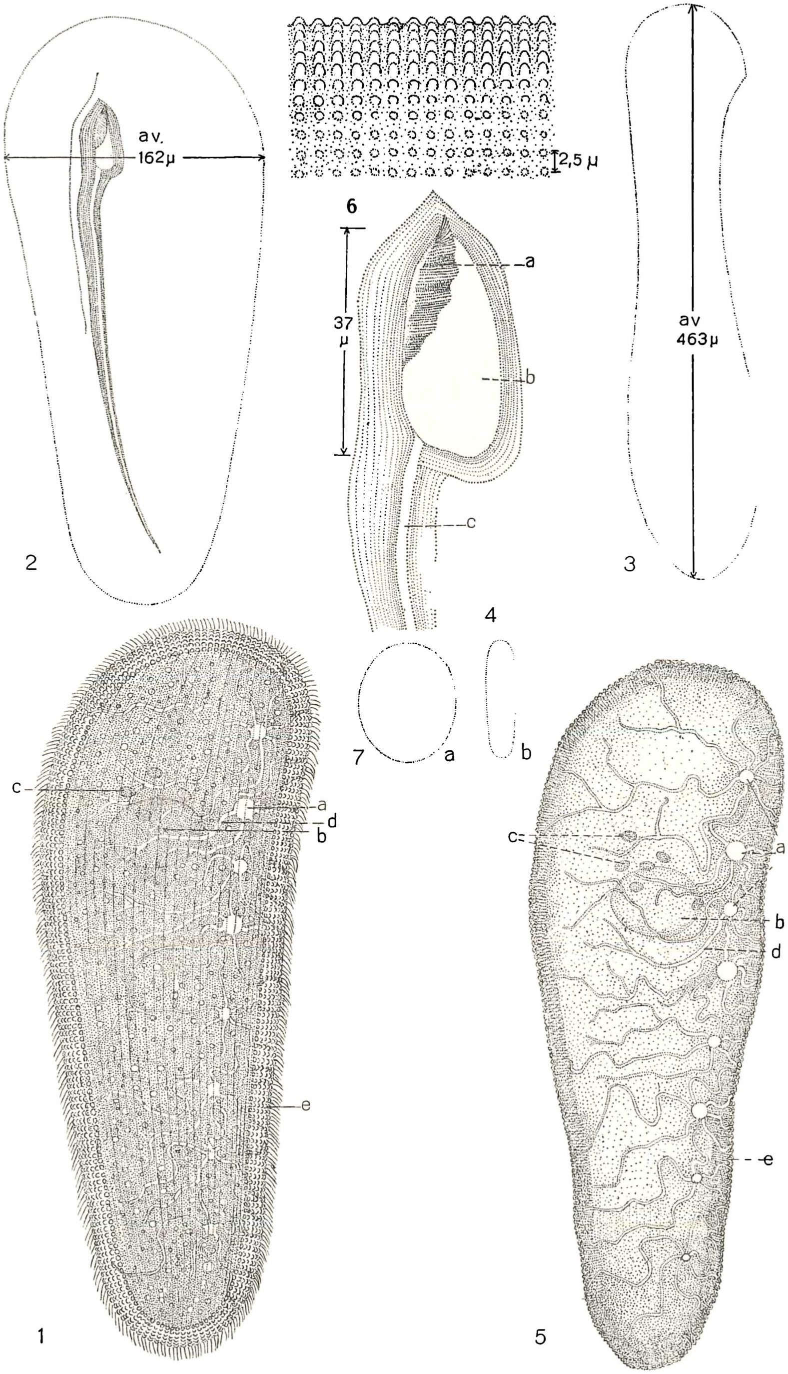

Plate 2. *Frontonia vesiculosa* DA CUNHA.

movement, has only about half the speed of left spiraling, the spirals approximately twice the width and only about three-fourths the length, and its forward direction is frequently changed. BACKWARD swimming frequently occurs and is always in right spirals. Circling movements to the left without spiraling occur constantly while the animals are feeding around over the bottom of the dish.

VI. *Frontonia vesiculosa* DA CUNHA, 1914.

General Morphology.

This is the large fresh water species found associated with *Frontonia leucas* above. In shape it is much like *F. leucas* but differs from it in being larger, usually more flattened in the anterior half (Pl. 2 Fig. 1, 2, 3), narrower and more cylindrical in the posterior half. It is extremely flexible, bending very easily, sometimes even doubling back upon itself, but always, if left unhindered, it reassumes its original form. And when seen from the edge it is found that the anterior portion of the ventral side projects out in a beak-like manner over the upper end of the mouth which it appears partly to surround (Pl. 2 Fig. 3). This corresponds exactly with EHRENBERG's "brow" which he described as projecting out over the mouth and lips of the members of this genus. The body is often more or less cylindrical throughout and irregular in outline which gives it at times a peculiar club-like appearance (Pl. 2 Fig. 5). It is finely and evenly ciliated, the cilia being arranged in closely set longitudinal rows (Pl. 2 Fig. 1).

Mouth and groove. The mouth and groove are typical as described for *F. leucas*, and are located in a similar ventral, subterminal position, somewhat nearer the animal's right side and facing its left. The

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Fig. 1. Dorsal view of a normal average individual, × 200. a Contractile vacuole, b Macronucleus, c Micronucleii, d Feeder canals, and e Layer of trichocysts.

Fig. 2. Ventral view, × 170, showing mouth and groove.

Fig. 3. Lateral view, × 165, showing thickness and beak-like projection over the mouth.

Fig. 4. Mouth and part of the groove greatly enlarged. a Undulating membrane, b Mouth cavity, c Groove.

Fig. 5. Dorsal view showing club shape. a Contractile vacuole, b Macronucleus, c Micronucleii, d Feeder canals of contractile vacuoles, e Layer of trichocysts in the body wall.

Fig. 6. View of one edge of body, × 1000, showing pimple-like projections above the trichocysts, and their arrangement over the surface of the body.

Fig. 7. Macronucleus, highly magnified. a Flat surface, b Edge view, showing thickness.

mouth measures 37 μ long, and, as in *F. leucas*, is surrounded by several rows of very fine closely set cilia, which, in this species end anteriorly under the sharp beak-like projection over the mouth. An undulating membrane similar to that of *F. leucas* is present in the anterior portion and extends down the right border from the anterior extremity, in the same oblique manner, and for about the same relative distance. But it is not very prominent, since usually the 4 mm objective is required in order to see it clearly (Pl. 2 Fig. 2 A). Da Cunha describes an undulating membrane on the left side border of the mouth, and by left, I suppose he means the animal's left, but mine was distinctly on the right side of the mouth. If he has reference to his own left, which he does not make clear, then his statement agrees with my findings.

Contractile vacuoles. Outside of its larger size, this species is characterized by the number and arrangement of its contractile vacuoles. There are from 5 to 8 of these small vacuoles arranged in a row down the right dorsal side of the body. They, and the larger body size, easily differentiate this species from the smaller *F. leucas* with only one large centrally located vacuole. Each of these small vacuoles has from 7 to 10 small irregular feeder canals radiating out from it and extending almost entirely across the body near the dorsal surface, exactly like the canals extending out from the large single vacuole of *F. leucas* (Pl. 2 Figs. 1, 5). Da Cunha apparently failed to see these radiating canals. He does not mention them in his description and he fails to show them in his drawing.

Nucleus. The nucleus consists of a single large macronucleus, oval in form, surface view, but flattened, elongated, and rounded at the ends when seen from the side (Pl. 2 Fig. 7). The micronucleii are relatively large, have the same oval shape, but vary in number, as explained above, from 3 to 8. They have the same general position as in *F. leucas* — either embedded in the macronucleus, lying along side of it, or even scattered out in the cytoplasm near it (Pl. 2 Fig. 1).

Trichocysts. The body of this species is covered with regularly arranged pimple-like projections spaced 2.5 μ apart, and appear on the edge of the body as serrations and on the surface as small circles (Pl. 2 Fig. 6). These pimples are, as in *F. leucas*, projections of the ectoplasm over the outer ends of the underlying trichocysts. By focusing on the surface of the body, only the pimples appear, but by focusing upon the edge of the body the serrations appear. Beneath the serrations and embedded in the ectoplasm, may be seen the dense, relatively small, spindle-shaped trichocysts. They are relatively short and lie generally perpendicular to the surface of the body. But sometimes they become detached from the ectoplasm, particularly when the animal is flattened out under a cover glass, and float around in the endoplasm with the granules and other structures. Sooner or later they collect, however, at various places underneath the ectoplasm in rafts of various shapes. Upon proper stimulation they suddenly discharge themselves from the body in the process of which they become greatly elongated, extremely slender, needle-like structures, 2—3 or more times their original length (Text-Fig. 3 A).

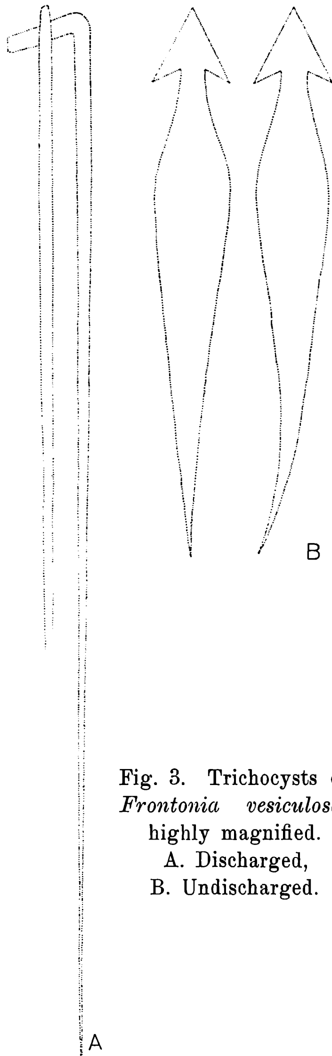

Fig. 3. Trichocysts of *Frontonia vesiculosa*, highly magnified. A. Discharged, B. Undischarged.

Ehrenberg (1838) observed these trichocysts in *Frontonia vernalis* and described the undischarged trichocysts as fusiform (spindle-shaped) bodies. He observed that under certain conditions, e. g., mechanical stimulation or the application of weak acetic acid, these bodies suddenly greatly elongated, pierced the cuticle, and stood out on the surface of the body like stiff hair-like setae.

But Allman (1866) seems to have made the first accurate observations of these structures in *F. leucas* before and after discharge. He found, asdid Ehrenberg, that external stimulation, such as drying, application of acetic acid, or mashing, brought about the sudden transformation of the spindle structures into the greatly elongated hair-like setae. His drawings correctly represent these discharged trichocysts. But he seems to have gone further and been the first to dissect out the undischarged trichocysts and then to discharge them while observing them under the microscope.

As to the shape of the outer end of the trichocysts. Previous investigators, ALLMAN (1866), TÖNNIGES (1914), JACOBSON (1931), KRUGER (1931), have shown the undischarged trichocysts of *F. leucas* as an enlarged structure, somewhat rounded on the outer (distal) end, and thus the trichocysts of *F. vesiculosa* appeared to me upon first observation. A more careful study of them under the oil immersion objective and the 10 × ocular, however, has shown them to be definitely barbed on the outher end, and tapering to a very slender point at the inner end (Text-Fig. 3 B). So far as I have been able to find no such structures have been previously reported for any species of Frontonia.

Size. DA CUNHA gives length as varying generally between 300 μ and 400 μ — seldom as much as 500 μ; width 120 μ to 160 μ. In my cultures length, in 182 measurements, has averaged 463 μ in a variation of from 308 μ to 660 μ; width in 105 measurements varying from 110 μ to 262 μ has averaged 162 μ.

Spiraling in Forward Swimming.

Direction of spiraling. *Frontonia vesiculosa* DA CUNHA is a left spiraling species — so classified because it is in left spirals that it swims greatest distances in a given forward direction, in left spiraling that greatest speed occurs, and it is left spiraling that is always used when the animal is greatly disturbed. The same individual can however, swim in right spirals, but these are slower, the spirals usually wider and shorter, and are frequently broken into by a change of forward direction. This frequent change of direction makes it difficult so measure right spirals and determine the speed of swimming. Few right spiraling individuals ever swim far enough straight ahead to cross the field of the microscope. Moreover, every right spiraling individual when greatly disturbed, changed immediately from right to left spiraling. To bring about this change it is only necessary at times to transfer them from the large general culture to a watch glass with only a few drops of culture medium. At other times it may be necessary to add a few drops of distilled water. Sometimes jabbing them with a steel needle is necessary to cause them to change.

Size of spirals. Left spirals in 192 measurements varying from 1200 μ to 2000 μ have averaged 1552 μ; right spirals in 62 measurements varying from 833 μ to 1333 μ have averaged 1073 μ, or only about two-thirds the length of left spirals (Text-Fig. 4).

Speed of swimming. Left spiraling has averaged approximately 2821 μ per second in 20 measurements ranging from 2286 μ to 4000 μ per second; right spiraling averaged only 873 μ per second, or less than one-third the speed of normal left spiraling, in 8 measurements ranging 588 μ to 1173 μ.

Spiraling in Backward Swimming.

This species frequently swims backward, and in every case observed this has been in short right spirals. Ninety-six such spirals have been measured. They averaged approximately 674 μ in length, or about one-third the length of left spirals in forward swimming. One individual traveled 8000 μ backward in spirals averaging only 400 μ in length (Text-Fig. 4c).

Circling while Spiraling.

There seems to be a tendency in some individuals of this species to move in wide circles to their left while swimming in otherwise normal left spirals. These circles have a diameter a little greater than the field of the microscope, or approximately 8000 μ. No explanation has been found for this reaction but it reminds one of the tendency in man to veer off from a straight line to the left or right and travel in circles when the normal orienting mechanism is prevented from functioning (SCHAEFFER 1928). Not all individuals have been seen swimming in this manner, but enough have been seen to indicate that the tendency is quite general. This is the only species found with this tendency to circle while spiraling.

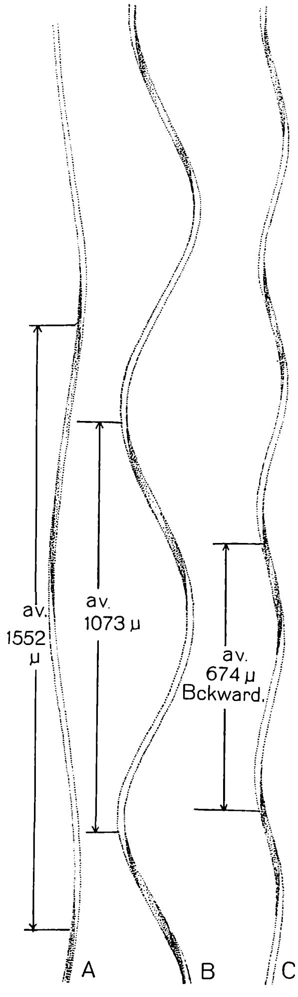

Fig. 4. Spiral paths of *Frontonia vesiculosa*. ×50. A. Average left spiral. B. Average right spiral. C. Average spiral in backward swimming.

Reaction to Sea Water.

This species, like *F. leucas*, is very sensitive to slight additions of sea water. I have been umable to keep them living in a medium containing more than approximately 50 % sea water.

Diagnosis.

Frontonia vesiculosa DA CUNHA is a fresh water species similar in form to *F. leucas*, sometimes cylindrical, often club-shaped, measures approximately 463 $\mu \times$ 162 μ; clear or slightly pinkish in color; covered with fine cilia arranged in fine longitudinal striations; barbed, spindle-shaped trichocysts abundant; mouth and groove typical, anterior end of mouth covered over with a slight beak-like projection of the body; contractile vacuoles several, usually 5—8, small in size, located in a row down the animal's right dorsal side; nucleus, consisting of a large single oval macronucleus and from 3 to 8 relatively large oval micronucleii centrally located; Left spiraling, characteristic in normal free swimming, occurs at an average speed of 2821 μ per second, and in spirals measuring on an average 1552 μ in length; right spiraling has only about one-third the speed, and the spirals two-thirds the length, of left spiraling. Backward swimming is always in right spirals.

VII. *Frontonia marina* FABRE-DOMERGUE (1890—91).

1899: *Frontonia leucas* var. *marina* FLORENTIN. Ann. Sci. Nat. Zool. p. 237—240. pl. 9.
1931: *Frontonia marina*, KAHL, Die Tierwelt Deutschlands. 21 teil, p. 319.

Frontonia marina FABRE-DOMERGUE, has been found in brackish water pools, salt marshes, and in sea water in widely separted places in point of both time and distance. It was first found by the author at Cold Spring Harbor, Long Island, during the summers of 1921, 1923, and 1924; was found at Woods Hole, Mass., during the summers of 1925, 1926, and 1929; at Tortugas, Fla., during the summers of 1930, 1931; and at Beaufort, N. C., in 1934.

At Cold Spring Harbor it came from the Overflow Pond (sea water); from inner harbor near the dock; from marsh pools near Jones boat house (brackish); from the salt marsh pools on Gilgo Beach, South Shore (brackish to salt); and even came up in cultures made from dredgings from Long Island Sound.

At Woods Hole it came from the brackish pond just north of Eel Pond, and from a small unnamed pond on the aestern end of Chippiquiddick Island between Pond No. 1 and Panchec Pond on the high bank near where Catama Bay empties into the Atlantic Ocean. This pond was very salty, being frequently added to by the waves at high tide, but apparently losing water only by evaporation.

At Tortugas it came from the smallest of the enclosed sea water pools on the west side of Fort Jefferson, Garden Key.

At Beaufort, it came from the turtle ponds on the east side of the U. S. Bureau of Fisheries Laboratory, and also from tow taken from the channel.

General Morphology.

Body form. This species has the typical foot-shape of *F. leucas* and *F. vesiculosa* (Pl. 3 Fig. 1), but is broader at the anterior end, and somewhat thicker dorso-ventrally. It is thinned out ventrally in the center of the body, similar to the others, but is more cylindrical posteriorly. The entire body of those at Beaufort seemed more cylindrical, due, it was thought, to the amount and kind of food eaten, since often the generally flattened condition so characteristic, is changed greatly by the ingestion of large numbers of Diatoms, Oscillatoria, etc. Pieces of Oscillatoria are sometimes taken into the body so long that they form one or more loops entirely around the inside. This stretches the body so much that it becomes a very thin, flat, circular film, at times almost like a sheet of paper. Shorter pieces often stretch the body in the shape of a half moon, as in *F. leucas* (Goldsmith 1922). Longer pieces often do not bend but push the body out at each end into a thin rod-shaped form many times the original length of the animal.

The body of *F. marina* is very flexible, and extremely granular — the granules being relatively large and appearing under the 4 mm. objective and the 15 × ocular as small spheres (Pl. 3 Fig. 4). These are more prominent in the posterior end. Sometimes these granules appear as oily globules embedded in a mass of smaller globules.

Cilia. The body cilia are very fine, are arranged in longitudinal and transverse rows, and are all of about the same length except on the posterior end of the body where there appears at times to be a longer tuft of cilia. No mention is made of longer caudal cilia by previous investigators.

Mouth and groove. The mouth is typical, perhaps slightly more pointed at the anterior extremity, and not so wide but more rounded at the posterior end (Pl. 3 Fig. 2). Its location is the same as in *F. leucas* and *F. vesiculosa*, and has the same typical long narrow groove, described for the other two species, extending down from the lower right side of the mouth. Under the 16 mm. objective and the 10 × ocular this groove appears only as a short streak, but under the 4 mm. objective and the 15 × ocular it can be seen as a long wavy streak extending to the extreme posterior end of the body. As in the other two species several rows of very fine cilia

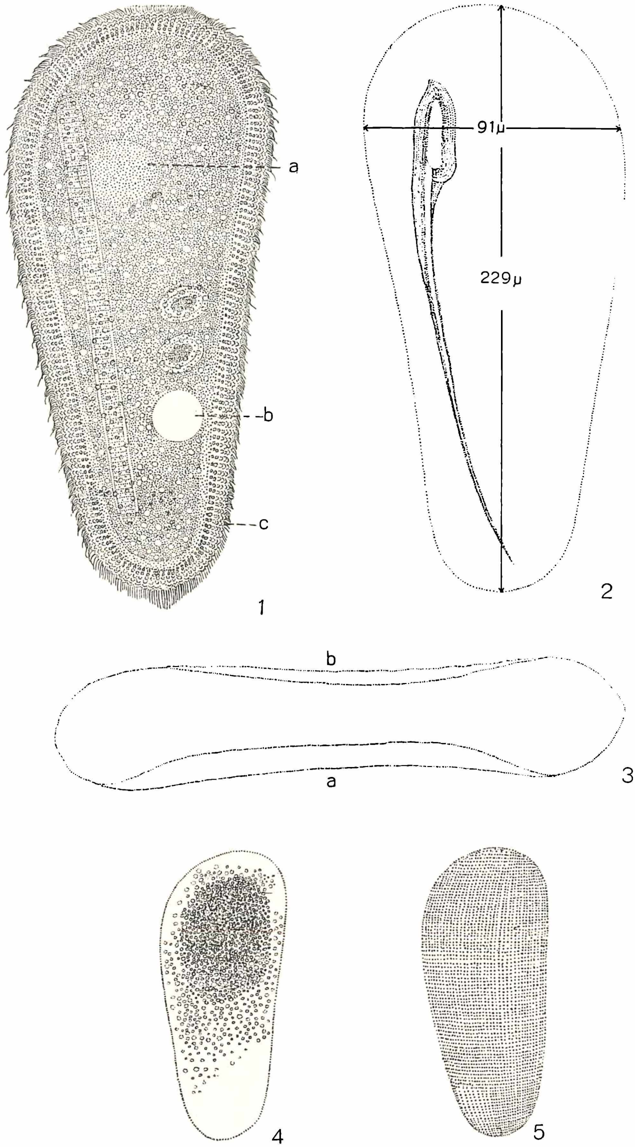

Plate 3. *Frontonia marina* FABRE-DOMERGUE.

Fig. 1. Dorsal view, × 350. a Macronucleus, b Contractile vacuole, c Pimple-like serrations over the underlying trichocysts.

Fig. 2. Ventral view, × 350, showing mouth and groove.

Fig. 3. Lateral view showing thickness of body, the thinning out in the center, and the thickness at the two ends. a Ventral, b Dorsal.

Fig. 4. Dorsal view showing massing of the small spherical granules.

Fig. 5. Dorsal view showing arrangement of trichocysts over the body.

surround the mouth, and those on the right side of the mouth extend down along they groove where they fade out gradually, and entirely disappear near the lower end of the groove. FABRE-DOMERGUE and FLORENTINE show an undulating membrane attached to the right side of the mouth opening. I have not been able to find one.

Nucleus. The nucleus consists of one large oval or oblong macronucleus, similar to that of *F. leucas* and *F. vesiculosa*, located in the anterior half of the body, and two or three micronucleii. FABRE-DOMERGUE (1891) failed, in his description, to mention micronucleii; FLORENTIN (1899) failed to find any micronucleii in those he studied, but KAHL (1931) reports two in his, perhaps more, but never a single one. I have found three micronuclei, similar in shape to those of *F. leucas* and *F. vesiculosa*, but not quite so large, lying in the cytoplasm near the macronucleus.

Contractile vacuole. Only one contractile vacuole has been seen. It is located near the center of the body and contracts very slowly — only once in 2—5 minutes. Upon contraction it gradually reforms by the formation first of two or three smaller vacuoles which then run together to make the large central vacuole (Pl. 3 Fig. 1).

Size of Body. This species has been found as small as $132\,\mu \times 55\,\mu$ and as large as $701\,\mu \times 146\,\mu$, but in this entire study (131 measurements of length and 124 of width) they have averaged $231\,\mu \times 91\,\mu$ (Table 3). Considerable variation in size has been found at different places and times, but very little variation at the same place and time.

Spiraling in Forward Swimming.

Direction of spiraling. This species swims also in both right and left spirals, but one direction again is characteristic, and is the one generally followed in free swimming; the other is a feeding movement. Right spiraling is used when the animal is "browsing", or feeding. It is seen most generally when the individuals are swimming back and forth from the bottom of the dish to the surface film, or moving about over the debris; left spiraling on the other hand, is used when greatest speed is required. It is the direction always assumed by right spiraling individuals when greatly disturbed. Isolating right spiraling individuals in a small drop of culture fluid and adding a few drops of distilled water, or touching the animal with a steel needle, or even jarring the dish, is usually sufficient to cause the change. Left spiraling individuals subjected to the same treatement only increassed their speed — never changed direction.

Size of spirals. Left spirals have ranged from 611 μ to 2000 μ in length, and, in 1014 measurements they have averaged 1147 μ; width of spiral has not averaged more than 100 μ. Right spirals, on the other hand, in only a few measurements (20) — 62 spirals — have averaged 1780 μ in length, or more than 600 μ greater than left spirals (Text-Fig. 5). If these few measurements are typical then in this species there is a direct reversal of length relationship between right and left spirals, as found in *F. leucas* ano *F. vesiculosa.* In these two, left spirals were longer by at least 25 percent. No reason is known for this difference but no particular significance is attached to it since the chief differences in the two spirals are width, speed, and the change from right to left spiraling when greatly disturbed. Width of right spirals in *F. marina*, from general observation — no measurements being possible — is greater than that of left spirals, as in the other two species. In free swimming, therefore, left spiraling characterizes *F. marina.*

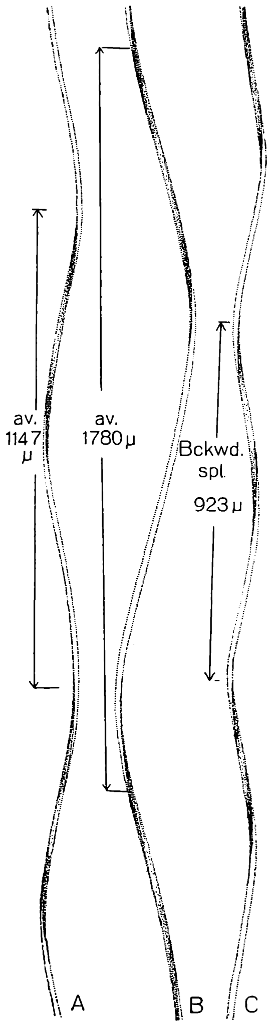

Fig. 5. Spiral paths of *Frontonia marina.* ×50. A. Average left spiral. B. Average right spiral. C. Average spiral in backward swimming.

Speed of swimming. So far as right spiraling is concerned, not a single measurement of speed has been possible due te the difficulty of getting the right spiraling individuals to swim across the entire field of the microscope without changing forward direction, but in general, speed in right spiraling is much reduced. On the other hand, very little difficulty has been experienced in determining speed of left spiraling. Seventy-eight measurements varying from 982 μ to 3666 μ per second have averaged 2382 μ, or about 9 body lengths, per second (Table 7).

Spiraling in Backward Swimming.

Whenever individuals of this species are greatly disturbed in the anterior region either chemically or physically, they instantly dart backward in right spirals. It is usually next to impossible to get measurements of these spirals, however, due to the short distances traveled at one time. Only seven such measurements, including 42 spirals, have been made. These averaged 923 μ in length by 85 μ in width (Text-Fig. 5), or slightly smaller in both length and width than the spirals in normal free swimming in a forward direction.

Reactions to Additions of Fresh Water.

There has been some doubt in the minds of some investigators as to the validity of the identification of *Frontonia marina* as a definite species — they thinking it a mere variety of *Frontonia leucas* which had adapted itself to life in sea water. FLORENTIN (1889) believed he could establish transition stages of *F. leucas* from fresh water all the way through brackish water, sea water, to salt water.

I have undertaken to test this species for its reaction to additions of fresh water to the culture medium. It has been found very sensitive to fresh water. When sufficient fresh water was added to make the culture medium about 25—30 % fresh water, these animals immediately became cylindrical like Prorodon and died in a short time.

Diagnosis.

Frontonia marina is a marine species, very sensitive to slight additions of fresh water; similar in body form to *F. leucas* and *F. vesiculosa*; measures approximately 231 $\mu \times 91 \mu$; pinkish or transparent in color; contains one contractile vacuole which is reformed after each contraction, usually by the formation of two or three smaller vacuoles which then fuse to form the one single large vacuole; trichocysts abundant, prominent, similar to those in *F. leucas*; nucleus consists of one large oval or oblong macronucleus and two or three micronucleii. In forward swimming left spiraling is characteristic, the spirals shorter, narrower, speed greater, and is instantaneously assumed when the animal is greatly disturbed; right spiraling is slower, the spirals wider and longer, occurs less frequently and the distance traveled in a given forward direction in unbroken stretches much shorter. Always this is changed to left spiraling when greatly disturbed. Backward swimming is always in right spirals.

VIII. *Frontonia vernalis* EHRBG., 1838.

1838: *Bursaria (Frontonia) vernalis* EHRBG., Inf. Volk. Or., p. 329, pl. 34, fig. 7.
1841: *Panophrys chrysalis* DUJARDIN, Hist. Nat. Inf., p. 492, pl. 14.
1841: *Panophrys vernalis* DUJARDIN (Ibid.).

1858: *Frontonia leucas* Clap. et Lach., Etudes sur les Inf. et les Rhiz., p. 260.
1859: *Cyrtostomum leucas* Stein, Der Org. der Inf.-Thiere.
1869: *Panophrys fusca* Quenn., Acta Univ. Lund.
1881—82: *Cyrtostomum leucas* Kent, Man. Inf., V. 11, p. 497, pl. 26.
1931: *Frontonia elliptica* Kahl, Die Tierwelt Deutschlands, 21. Teil, p. 321.

Ehrenberg (1838) found in sea water near Berlin, Copenhagen, and Cadix, a ciliate which he described under the name *Bursaria*, sub-genus *Frontonia*, as oval, oblong, swollen, green, having two vacuoles, rounded at the two ends, thinned in the rear, and with a mouth extending about back about $^1/_4$ to $^1/_3$ the length of the body. Ddjardin (1841) placed it in his genus Panophrys under the name *P. vernalis.* He also described another marine ciliate under the name *Panophrys chrysalis* which appears undoubtedly a frontonian and certainly identical with his *Panophrys vernalis*, and with Ehrenberg's *Bursaria* (*Frontonia*) *vernalis.* Stein (1859) identified Ehrenberg's *Bursaria* (*Frontonia*) *leucas*, *Bursaria* (*Frontonia*) *vernalis*, and Dujardin's *Panophrys vernalis*, as one species and placed them in his new genus *Cyrtostomum* as *Cyrtostomum leucas.* Kent (1881—82) followed Stein's example. Quennerstedt (1869) described a ciliate under the name *Panophrys fusca*, which seems to me, undoubtedly belongs here. Kahl (1931) identified a frontonian as *Frontonia elliptica* Beardsley, but his *Frontonia elliptica* and Beardsley's *Frontonia elliptica* are entirely different. Both have two vacuoles but Beardsley's species was from fresh water while Kahl's was brackish or marine. Most investigators have thought Ehrenberg's *Bursaria* (*Frontonia*) *vernalis* identical with his *B.* (*Frontonia*) *leucas*, the only difference being the green color in *B.* (*Frontonia*) *vernalis* which is not sufficiently important to be used as a basis for the erection of a new species. But the ciliate described by Ehrenberg under the name *B.* (*Frontonia*) *vernalis* was not the same species described by him under the name *B.* (*Frontonia*) *leucas. B.* (*Frontonia*) *leucas* was a fresh water species with only one contractile vacuole; *B.* (*Frontonia*) *vernalis* was marine and had two contractile vacuoles. Claparede and Lachmann (1858) noticed this difference but described both under the name *Frontonia leucas* and left for future investigators to decide whether the difference in habitat and number of contractile vacuoles were of specific value.

My observations on *F. leucas* and *F. vesiculosa* lead me to the definite conclusion that the difference in contractile vacuoles is one which cannot be ignored in the differentiation of the species of *Frontonia*, and definitely eliminates Ehrenberg's *B.* (*Frontonia*) *vernalis* from further consideration with *F. leucas.*

While making a general study of spiraling in the ciliates, I found at Cold Spring Harbor, 1925, in cultures from the large brackish pool located at that time just back of Jone's boat house, and later at Woods Hole, 1925, 1926, in Schoolhouse pond — a small pond fed by salt water from Eel Pond at high tide, and by a very small fresh water stream at low tide — a species of *Frontonia* which corresponds with DUJARDIN's *Panophrys chrysalis*, and EHRENBERG's *Frontonia vernalis.* They therefore, appear to be one and the same species and are here classified and described as *Frontonia vernalis.*

General Morphology.

Form. The body, as in *F. leucas* and *F. vesiculosa*, is typically foot-shaped but the proportionate width is somewhat greater. The anterior end is more rounded and does not project so far to the animal's right (dorsal view); the posterior end is narrowed, similarly rounded, and almost cylindrical.

Cilia. The body, as in the other two, is entirely and evenly ciliated with fine, relatively short cilia arranged in very close longitudinal rows, beginning at the mouth and gradually extending over the body from this point (Pl. 4 Figs. 1, 2).

Trichocysts. The cortical area of the body is thickly studded with trichocysts similar so far as observed to those in the others.

Mouth and groove. The mouth and groove are typical (Pl. 4 Figs. 2, 3), except for an undulating membrane which has not been seen.

Color. This species has a peculiar oily greenish cast which may be due to many relatively small oily appearing globules, which are present particularly in the posterior region. This color appeared characteristic at the time the observations were made, but whether it is really of any specific significance remains for later observations.

Contractile vacuoles. There are two large contractile vacuoles, both located on the right (dorsal) side, one in the anterior half, the other in the posterior half (Pl. 4 Fig. 1). This is distinctive, and corresponds with the vacuoles described both by DUJARDIN for *Panophrys chrysalis*, and by EHRENBERG for *Bursaria* (*Frontonia*) *vernalis*.

Pigment spot. A pigment or eye spot located in the anterior extremity, has been seen in some of the members of this species — but not in all — but was entirely distinctive in those individuals in which it was seen. This is a characteristic which DUJARDIN assigns to his genus *Panophrys*, and which QUENNERSTEDT saw in his *Panophrys fusca.*

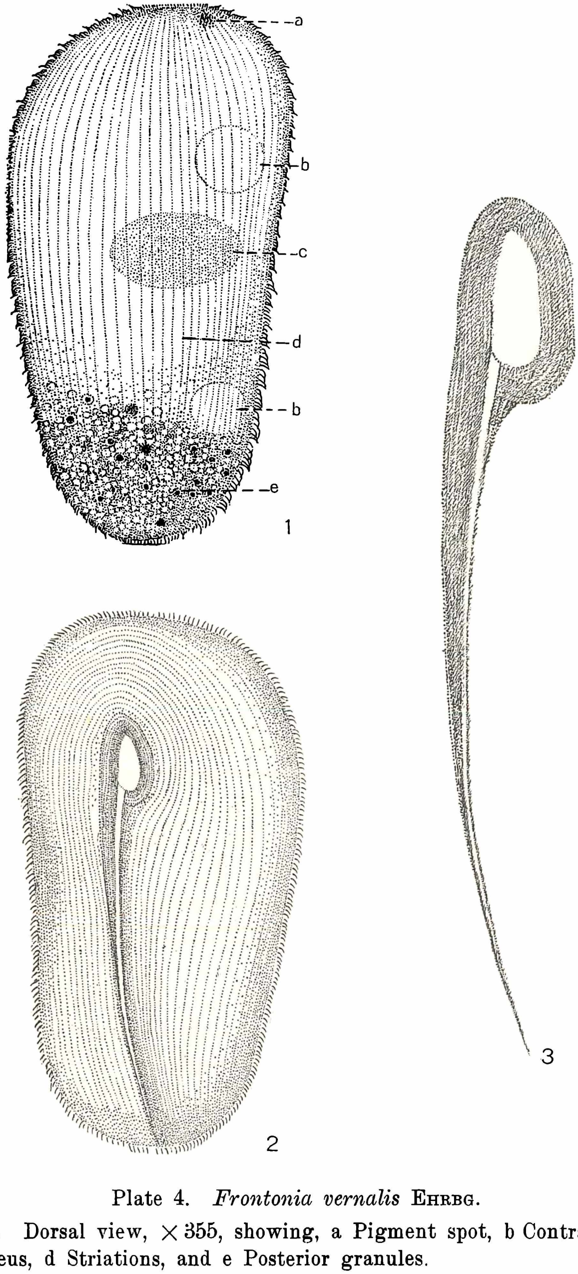

Plate 4. *Frontonia vernalis* Ehrbg.

Fig. 1. Dorsal view, × 355, showing, a Pigment spot, b Contractile vacuole, c Macronucleus, d Striations, and e Posterior granules.

Fig. 2. Ventral view, showing mouth, groove, and ventral striations.

Fig. 3. Mouth and groove highly magnified.

Nucleus. The macronucleus is the only portion of the nucleus seen thus far. It is similar to that already described for the other species. It has the same relatively large oval form, and is located in the same relative position near the center of the body (Pl. 4 Fig. 1).

Size. The members of this species have averaged 197 μ in length in measurements ranging from 166 μ to 311 μ, by 108 μ in width in measurements ranging from 66 μ to 133 μ. DUJARDIN'S *Panophrys chrysalis* measured 181 μ in length (Table 3).

Spiraling in Froward Swimming.

Direction of spiraling. All members of this species seen up to the present time have spiraled uniformly and consistently to the right. This differentiates them very clearly from the other marine species *F. marina*, already described, which is characteristically left spiraling.

Size of spirals. An average right spiral in this species measures approximately 859 μ in length, based upon 92 spirals varying from 780 μ to 1000 μ, by approximately 75 μ to 100 μ in width — width being determined by general observation — no measurements being possible (Text-Fig. 6).

Speed of swimming. Right spiraling occurs at an average speed of approximately 1625 μ per second, based upon only 10 measurements in which speed varied from 1300 μ to 1950 μ per second.

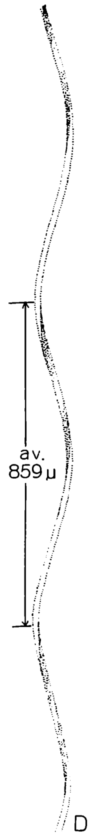

Fig. 6. Spiral path of *Frontonia vernalis* — average right spiral. $\times$ 50.

Spiraling in Backward Swimming.

This species has also been observed swimming backwards and in every case this has been in right spirals. This is brought about in this species by the exact reversal of the direction of beat of the body cilia, and the spiral is the exact back tracking of the spiral performed in forward swimming. All other *Frontonia* studied up to this point have changed direction of spiral in backward swimming.

Diagnosis.

Frontonia vernalis is a brackish to salt water species, clear or somewhat oily green in color; typically foot-shaped, but somewhat broader at the anterior end in proportion to length; body size approximately 197 $\mu \times$ 108 μ or slightly more than half as wide as long; trichocysts abundant and rather prominent; contractile vacuoles usually two in number located — one in the anterior half, the other in the posterior half; macronucleus single, oval or oblong, micronucleii have not been seen; pigment or eye spot sometimes present — the only member of the foot-shaped group having such a spot. Right spiraling is characteristic, the only direction seen, and occurs at an average speed of 1625 μ per second, in spirals averaging approximately 859 μ in length. Backward swimming is frequent and always in right spirals.

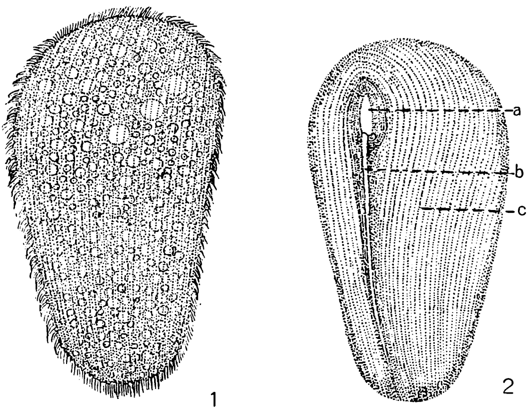

Plate 5. *Frontonia schaefferi* sp. nov.

Fig. 1. Dorsal view, × 433, showing general form, size, etc.
Fig. 2. Ventral view, × 433, showing, a Mouth, b Groove, c Ventral striations.

IX. *Frontonia schaefferi* sp. nov.

Frontonia schaefferi is a very small marine species seen only at Tortugas, Fla., where it was found during the summer of 1930 in a small pool blasted out on East Key a few years before for some of Schaeffer's ameba work. I take great pleasure therefore, in naming this species *Frontonia schaefferi.* This pool was completely dried up in 1931 and the species has not been found elsewhere.

General Morphology.

Form. This species has the typical foot-shape characteristic of all those discussed up to this time, but is different in that it is very much smaller. It is the smallest of the foot-shaped group (Pl. 5 Fig. 1).

Mouth and groove. Mouth and groove are typical (Pl. 5 Fig. 2) in both location and general shape.

Contractile vacuole, and nucleus have neither one been seen and await later observation when and if the species is found again.

Cilia. The body is entirely and evenly ciliated with short slender cilia arranged in fine longitudinal rows (Pl. 5 Fig. 1).

Size. As stated above this species is the smallest of the footshaped group. It measures on an average only 120 μ in length (9 measurements ranging from 86 μ to 167 μ), by 66 μ in width (10 measurements ranging from 43 μ to 106 μ, or slightly more than half as wide as long (Table 3).

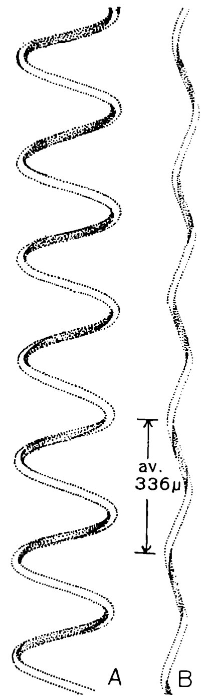

Fig. 7.
Spiral paths of *Frontonia schaefferi*. × 50.
A. Average left spiral.
B. Average right spiral.

Spiraling in Forward Swimming.

Direction of spiraling. This species is able to swim in either right or left spirals, but, like the others in which this is possible, it does not swim equally well in both directions. In this species, however, right spiraling is characteristic occurs at greater speed and in narrower spirals; left spiraling occurs at slower speed, and in longer, wider spirals, as in *Paramecium calkinsi*, Bullington (1930). This is the only right spiraling species of *Frontonia* known at present which is able to swim in left spirals.

Size of spiral. Left spirals could not be measured and are represented here only approximately: right spirals are normally very short and narrow, their length corresponding apparantly rather closely with body length. They have averaged 336 μ in length in 28 measurements — 418 spirals — ranging from 238 μ to 500 μ; width of right spirals could not be measured (Text-Fig. 7).

Speed of swimming. Normal spiraling occurs at relatively slow speed, averaging only about 449 μ per second.

Spiraling in Backward Swimming.

Backward swimming occurs frequently — always in right spirals. Thirty of these spirals averaged 55 μ in length or only about $^1/_6$

the length of spirals in normal forward swimming. Width of spiraling in backward swimming is proportionately narrow no measurements being possible.

Circling while Feeding.

When members of this species are feeding along the bottom of the dish they are constantly moving in small circles to their left without spiraling, and usually without jerking backward.

Reaction to Mechanical Stimuli.

If the individuals of this species are touched at the anterior end rather lightly while they are feeding, they usually jerk backward, turn to the left, and swim off in a new forward direction. If touched forcibly on the anterior end they jerk backward in the same manner, but swim rapidly backward in right spirals — the same spirals as in forward swimming but in reverse order. If touched lightly at the posterior end no attention is usually paid to it, but if jabbed forcibly they swim off rapidly forward withoug any preliminary movements. This is directly contrary to the reactions reported for *Oxytricha fallax*, *Loxodes rostrum*, and *Dileptus anser* (Jennings, 1900). In eash case when the irritation became too severa for *Frontonia schaefferi*, either anteriorly or posteriorly, it appeared to react in a manner which would enable it to escape most quickly from the point of irritation.

Diagnosis.

Frontonia schaefferi is a very small marine species seen only in cultures from East Key, Tortugas, Fla. It has the same typical foot-shape characteristic for all those discussed up to this time, but is the smallest of the group. Mouth and groove are typical; nucleus and contractile vacuole have not been seen; right spiraling is characteristic, occurs at an average speed of 449 μ per second in spirals averaging 351 μ in length. Backward swimming occurs in right spirals only. Circling to the left without spiraling when the animals are moving about over the bottom of the dish, occurs frequently.

X. *Frontonia ocularis* sp. nov.

This is a widely distributed marine species which has been found at Cold Spring Harbor, Woods Hole, and Tortugas. It was first seen during the summer of 1923 at Cold Spring Harbor in cultures of decaying plants from Overflow Pond, and in Inner harbor at high tide on floating eel grass. During the summer of 1925 it was seen at Woods Hole in cultures of eel grass from Cuttyhunk Harbor. Later during the same summer it was found in great numbers in Mill Pond in the algae which forms such a dense mass over the surface of the south side of the pond. Here it was seen also in similar cultures during the summers of 1926 and 1929. At Tortugas, it was located during the summer of 1930 in cultures of turtle grass from First Pond on Long Key.

General Morphology.

Form. The body of this species is somewhat kidney-shaped, with the left side (dorsal view) convex. This is the view one usually has of these animals as they feed about over the bottom of the dish. The anterior one-third of the body is slightly flattened dorso-ventrally; the posterior two-thirds more cylindrical. Both posterior and anterior ends are rounded, but the anterior one is usually narrower and slightly pointed to the animal's right (Pl. 6 Figs. 1, 3, 5).

Mouth. The mouth and groove, as in the preceding species, are typical except that the mouth is not cut off so abruptly at the posterior extremity as it is in *F. leucas* and *F. vesiculosa* (Pl. 6 Fig. 4). An undulating membrane may be present but none has been seen. The groove leading away from the right side of the mouth curves to the animal's left and reaches almost to the posterior extremity of the body.

Contractile vacuoles. From 2—3 contractile vacuoles are usually present. When two are present, one is generally found in the anterior half; the other in the posterior half (Pl. 6 Figs. 1, 3). When three are present they may be grouped near the center of the body.

Nucleus. The macronucleus is single, oval or slightly oblong, centrally located, and may even be seen clearly in living unstained specimens (Pl. 6 Fig. 2, 3). No micronucleii have been seen.

Cilia. The body is entirely and finely ciliated, and finely and longitudinally striated (Text-Fig. 14), the striations, as seen under oil immersion objective and the 10 × and 12.5 × oculars, being formed by the basal granules of the body cilia, as shown by Maier (1903) for *Prorodon*, *Paramecium*, *Stentor*, etc.

Trichocysts. Trichocysts are very prominent in this species and are thickly studded over the entire body. They, too, are arranged in lines running both longitudinally and transversely (Pl. 6 Fig. 5).

Eye spot. The characteristic thing about this species outside of its kidney shape is its prominent pigment or eye spot — a dense reddish brown spot on the extreme right border of the anterior extremity (Pl. 6 Figs. 1, 2, 3, 4). It is very noticeable, and, together with body form, readily identifies this species even under the low power of the binocular microscope.

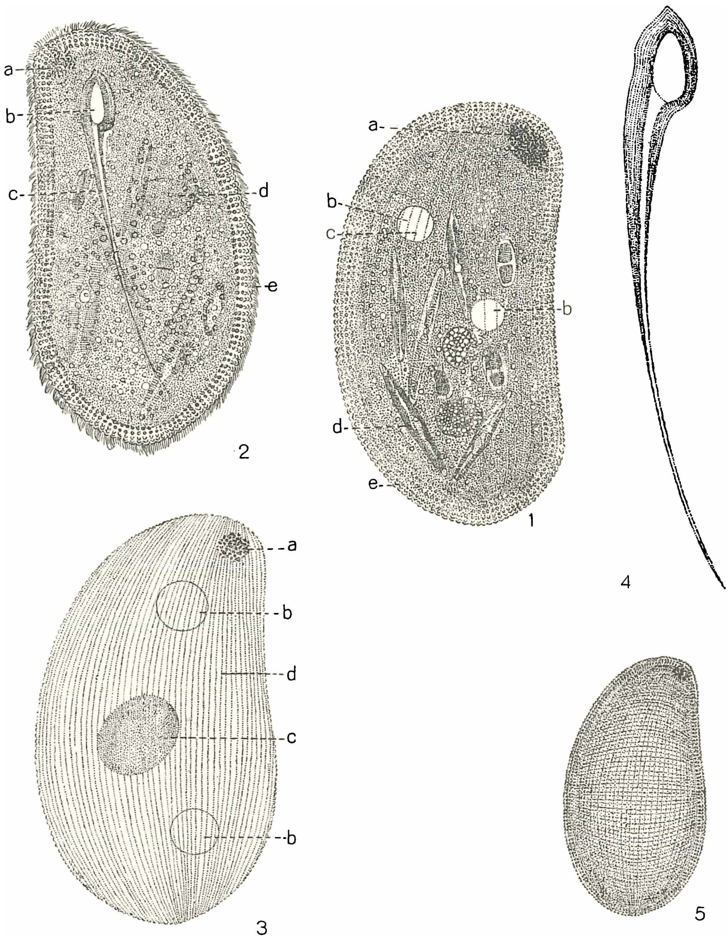

Plate 6. *Frontonia ocularis* sp. nov.

Fig. 1. Dorsal view, × 400. a Pigment spot, b Contractile vacuole, c Striations, d Food material (Diatoms), e Serrations over the underlying trichocysts.

Fig. 2. Ventral view, × 400, showing, a Pigment spot, b Mouth, c Groove, d Macronucleus, e Edge-view of pimple-like projections over trichocysts.

Fig. 3. Dorsal view, outline, × 400, showing, a pigment spot, b Contractile vacuoles, c Macronucleus, d Striations.

Fig. 4. Mouth and groove highly magnified.

Fig. 5. Longitudinal and transverse arrangement of trichocysts.

Size. Body length, in this species, has averaged approximately 141 μ, in 51 measurements varying from 102 μ to 200 μ; width has averaged 76 μ in 41 measurements ranging from 43 μ to 107 μ. Width, in other words, has been found equal to approximately half the length (Table 3).

Spiraling in Forward Swimming.

Direction of spiraling. This is characteristically a right spiraling species, and in the great number of individuals under observation at one time or another since 1925 no left spiraling has been seen. Transferring individuals, even to 40 % fresh water failed to produce left spiraling. The individuals merely swelled up, became cylindrical, and continued to spiral to the right. This shock was sufficient to kill them by the next day and certainly should have been sufficient to bring about left spiraling had it been general.

Size of spirals. Length of right spirals has averaged 798 μ in 131 measurements varying from 400 μ to 2000 μ; width has averaged 144 μ in measurements varying from 96 μ to 192 μ (Text-Fig. 8).

Speed of swimming. Speed has averaged 1166 μ per second in 70 measurements varying from 429 μ to 1920 μ per second.

Spiraling in Backward Swimming.

Backward swimming has been observed only once in this species but this was in distinct right spirals — the same direction as in all forward swimming with the exception that the end of the animal going in front had been reversed.

Reaction to Fresh Water.

A few individuals have been tested for their reaction to additions of fresh water. They seemed to suffer no bad effects from additions of 25 % fresh water, but when this, by gradual increase had reached a strength of 40 % the animals became cylindrical and went to pieces.

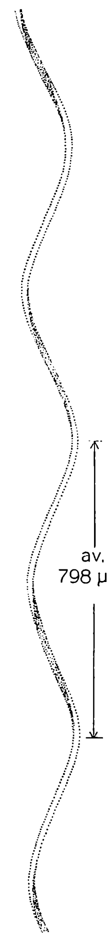

Fig. 8. Average right spiral of *Frontonia ocularis*. × 50.

Diagnosis.

Frontonia ocularis is a marine species, more or less kidney-shaped, averaging approximately 141 $\mu \times 76$ μ in size; has a prominent pigment or eye spot on the right dorsal side, anterior extremity;

trichocysts abundant and prominent, arranged in both longitudinal and transverse rows. Forward swimming has been seen in right spirals only — the spirals of which average 798 μ in length by 144 μ in width at a speed of approximately 1166 μ per second. Backward swimming also occurs in right spirals.

XI. *Frontonia acuminata* (EHRBG., 1833), BÜTSCHLI 1889.

1833: *Ophryoglena acuminata* EHRBG.
1889: *Frontonia acuminata* BÜTSCHLI, Bronn's Kl. u. Ord., Thier-Reich, p. 1703, pl. 62.
1931: *Frontonia acuminata* var. *angusta* KAHL, Die Tierwelt Deutschlands, 21 teil, p. 320, fig. 55—10, 11.

EHRENBERG (1833) described under the name *Ophryoglena acuminata*, a fresh water ciliate having a flattened ovate body, pointed and acuminate posteriorly, a length equal to one and one-half times the width; a scarlet pigment spot near the anterior end; a single vacuole, and a length of about 139 μ.

BÜTSCHLI (1889) recognized this as a species of *Frontonia* and described it as *Frontonia acuminata.*

KAHL (1931) described as a new variety of *F. acuminata* under the name *F. acuminata* var. *angusta*, some individuals in which he did not find an eye spot. I do not know how many individuals KAHL examined before he came to the conclusion he should dub it a new variety, but it seems to me that before one in justified in describing as a new species or new variety, some individuals which differ only slightly from a previously described species, and that difference perhaps only temporary, they should be pure cultured to determine whether the point in question is constant and characteristic. To my mind, therefore, more information is needed before this should be considered a variety.

Frontonia acuminata (EHRBG.) is a fresh water species found in most ponds having an abundance of green algae, particularly diatoms and spirogyra. It has been found by the present author at Knoxville, Tenn., Cold Spring Harbor, Long Island, Woods Hole, Mass., and has been collected in small numbers at various times since 1925 from Railroad Pond, Ashland, Va.

General Morphology.

Form. The members of this species are flattened ventrally but have a pronounced hump in the center of the dorsal surface, as shown by KAHL (1931) except that in my observations I have found the anterior end of the animal turned up like a sled runner (Pl. 1

Fig. 5). This is not shown in KAHL's drawing. This bending up in front and the hump in the middle are characteristic. These are not

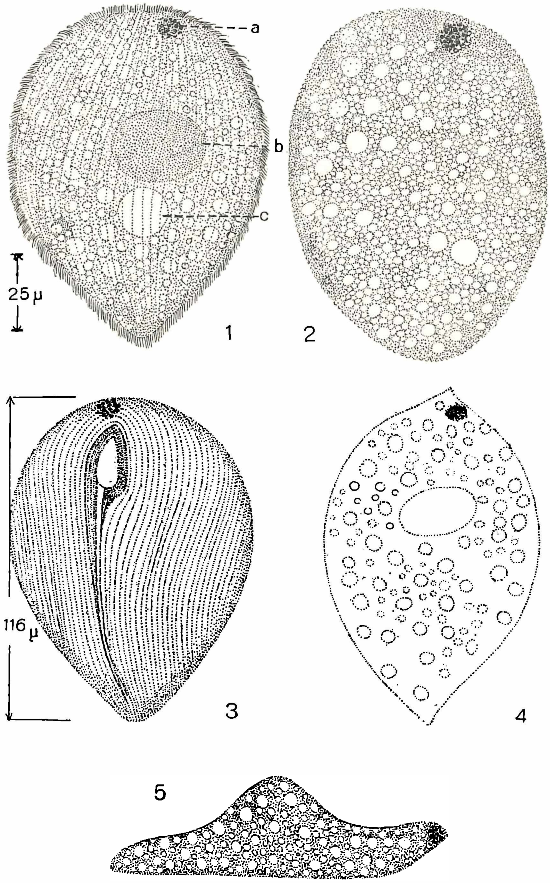

Plate 7. *Frontonia acuminata* (EHRBG., 1838) BÜTSCHLI, 1889.

Fig. 1. Dorsal view, × 388, a Pigment spot, b Macronucleus, c Contractile vacule.

Fig. 2. Dorsal view, × 388, showing form variations.

Fig. 3. Ventral view showing mouth, groove, arrangement of ventral cilia, pigment spot, etc.

Fig. 4. Dorsal view, individual with both ends pointed.

Fig. 5. Side view, × 388, showing dorsal hump and sled-runner appearance.

noticeable, however, except from a side view. That part of the body posterior to the hump is slightly more flattened dorso-ventrally, and is sometimes sharply pointed, but probably more often rounded;

the central portion wider, and the anterior end sometimes pointed — but usually rounded.

Cilia. The cilia are fine, short, cover the entire body in fine longitudinal rows originating at the mouth and extending out over the body from this point (Pl. 7 Figs. 1, 3).

Mouth and groove. The mouth and groove are typical (Pl. 7 Fig. 3) and have been used here as a basis for the inclusion of this species.

Contractile vacuole. Only one contractile vacuole has been seen in this species and it is very small, contracts very rapidly, and is located just behind the central nucleus (Pl. 7 Fig. 1). No feeder canals of any sort have been seen. Many smaller clear, vacuolar-like structures are scattered through the body and are more or less characteristic, but they have not been seen contracting, nor have they flown together to form larger vacuoles.

Fig. 9. Average left spiral of *Frontonia acuminata.* × 50.

Nucleus. A single, oval, sometimes oblong macronucleus is present. This is located just to the left and somewhat to the rear of the mouth (Pl. 7 Fig. 1). Micronucleii, if present, have not been seen.

Pigment spot. This species is characterized by the presence of adark reddish pigment spot located usually near the right side of the anterior end — the same general position as in *F. ocularis* and *F. vernalis.*

Size. Body length has varied from 88 μ to 174 μ, and in 27 measurements has averaged 116 μ; width has varied from 44 μ to 121 μ, and in 7 measurements has averaged 77 μ (Table 3).

Direction of spiral. This is a left spiraling species and no right spiraling has been seen (Text-Fig. 9).

Size of spirals. Due to the difficulty of getting the members of this species to swim in a general forward direction long enough to cross the field of the microscope, only 18 spirals have been successfully measured. These averaged 416 μ in legth (Text-Fig. 9).

Speed of swimming. It has not been possible to determine speed for the same geason given above

Spiraling in Backward Swimming.

Backward swimming occurs frequently and has in every case been to the right. These spirals have averaged about 400 μ in length.

Circling to the left while Feeding.

When the individuals of this species are feeding over the bottom of the dish they are constantly jerking back, pivoting to their left on the posterior portion of the body, and moving off in a new forward direction. In this manner they are constantly moving in left circles.

Reaction to Sea Water.

This species dies when it is subjected to a concentration of sea water greater than about 25 % to 30 %.

Diagnosis.

Frontonia acuminata is an extremely small fresh water species, widely distributed, but usually in relatively small numbers; has a ventrally flattened body, a conspicuous dorsal hump in the center; anterior end turned upward, both anterior and posterior ends rounded or pointed; body measures only 116 μ in length by 77 μ in width; mouth and groove typical; macronucleus single, oval in form. Kahl reports 1 large micronucleus but I have not seen any. Pigment spot very conspicuous and characteristic, located in the right side of the anterior extremity (dorsal). This species swims in left spirals only so far as known. Backward swimming occurs only in right spirals. Circling to the left is commonly seen, but occurs without spiraling.

XII. *Frontonia atra* (Ehrbg., 1833) Kahl, 1931.

1833: *Ophryoglena atra* Ehrbg.
1889: *Frontonia acuminata* Bütschli, Bronn's Kl. u. Ord., Thier-Reich, p. 1703, Vol. 1, part 3, pl. 42.
1905: *Frontonia* sp.? Conn, Protozoa Fresh Waters of Conn., p. 47, fig. 198, pl. 18.
1922: *Frontonia nigricans* Penard, Etude sur les Inf. Deau Douce, pp. 142—43, fig. 140.
1931: *Frontonia atra* Kahl, Tierwelt Deutschlands, p. 321, fig. 55, 8, 17.

Frontonia atra is a large fresh water species seen by the present author in only one place — in cultures from Railroad Pond, Ashland, Va., and always in association with the smaller *Frontonia acuminata.* Ehrenberg (1833) described this ciliate under the name *Ophryoglena atra.* Bütschli (1889) recognized it as a frontonian but thought it the same species as *Frontonia acuminata.* Conn (1905) apparently saw the same ciliate in Connecticut but failed to identify it as to species. Penard (1922) described a species under the name *Frontonia nigricans*, with a general form at times somewhat like a stentor, and having a purplish color. Kahl recognized a difference in Ehrenberg's *Ophryoglena acuminata*, and *Ophryoglena atra* and described

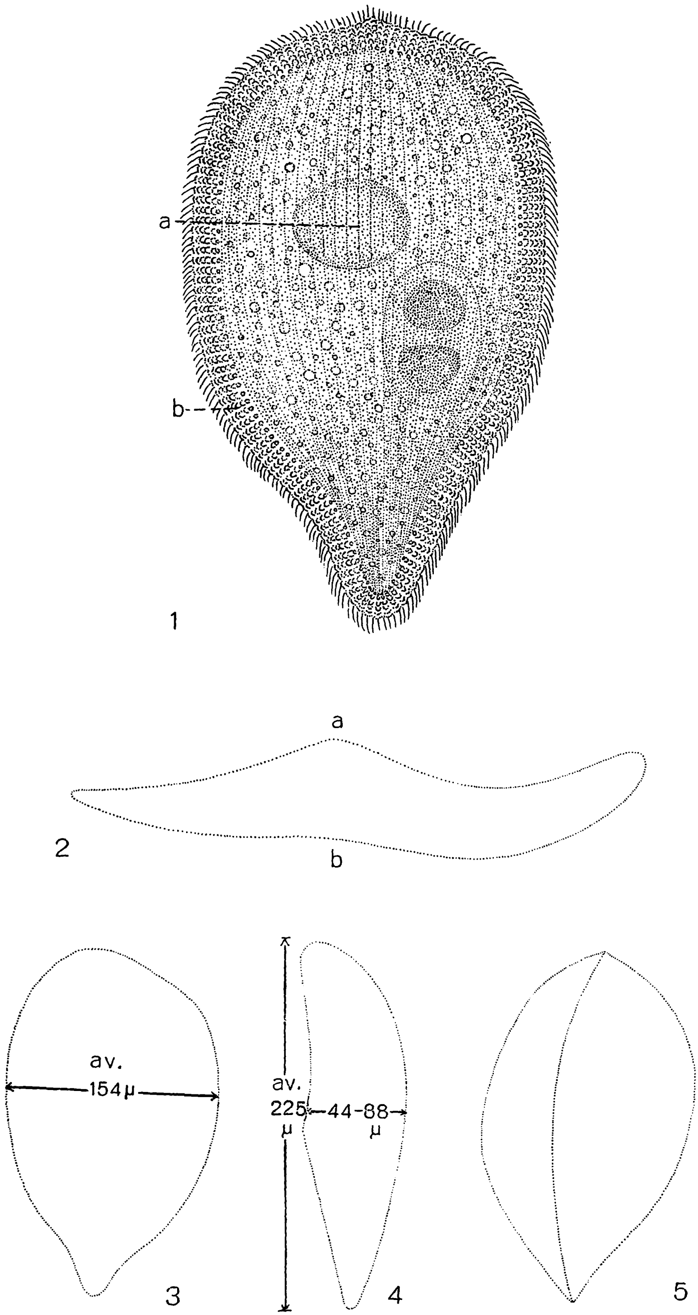

Plate 8.

O. atra as *Frontonia atra* thus eliminating it from further consideratio with BÜTSCHLI'S *Frontonia acuminata* (EHRBG.). KAHL also thinks *F. atra* identical with BURGER'S *Paramecium nigrum*, the literature of which I have been unable to see. Now from my study of those found at Railroad Pond, and a study and comparison of descriptions and drawings of CONN'S unidentified species, PENARD'S *F. nigricans*, and KAHL'S *F. atra*, I am inclined to believe all of them to be one and the same species. The only apparent difference in PENARD'S *F. nigricans* and KAHL'S *F. atra* seems to be the purplish color of *F. nigricans* as against the dark or black of *F. atra*. And the only noticeable difference in the one CONN saw in Connecticut and the other two, outside of color, is the slightly shorter caudal projection in the former. Not anough is known about these differences at the present time, it is believed, to justify this differentiation.

General Morphology.

Form. The body of this species is usually elongated, flattened, and usually bluntly rounded at the anterior end, widest centrally, narrowed posteriorly to about the posterior $^{1}/_{4}$ where it comes in sharply and then projects out in the form of a blunt tail. This gives the body the distinct shape of a ping-pong paddle except that the tail is not so long, narrower at the tip, i. e., somewhat more pointed than the handle of the paddle. From side view the body has the same distinct central hump, and the same sled-runner appearance seen in *F. acuminata* except that it is longer (Pl. 8 Figs. 1, 2).

Mouth and groove. Mouth and groove are typical.

Nucleus. Macronucleus large, oval, as in all previous species; micronucleii have not yet been seen (Pl. 8 Fig. 1). KAHL found two micronucleii in his *F. atra*.

Contractile vacuole. At the present time a contractile vacuole has not been positively identified in my cultures. Once I thought I got a glimpse of a vacuole contracting near the macronucleus, but a close inspection afterward failed to show any other contractions. KAHL reported one for his *F. atra*, and PENARD one for his *F. nigricans*,

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Plate 8. *Frontonia atra* (EHRBG., 1838) KAHL, 1931.

Fig. 1. Dorsal view, × 300, a Macronucleus, b Trichocysts.

Fig. 2. Side view showing sled-runner form, a Dorsal, b Ventral.

Fig. 3. Outline drawing, ventral view, showing form variation, width of body, etc.

Fig. 4. Side view to show thickness.

Fig. 5. Ventral side-edge view.

located, in *F. nigricans* just beneath the nucleus, which corresponds in position with the one I thought I saw in the individuals from Railroad Pond. Contraction must indeed be very slow in this species.

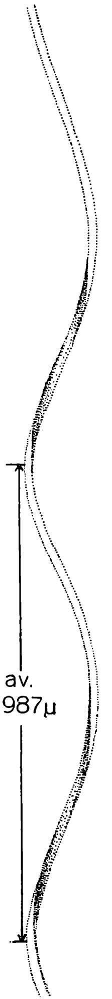


Fig. 10. Average left spiral of *Frontonia atra.* × 50.

Size. In point of size, this species is approximately twice as large as *F. acuminata.* KAHL found length in his *F. atra* varying from 100 µ to 220 µ; PENARD reports it varying in his *F. nigricans* from 200 µ to 220 µ. The ones I have seen are, on an average, larger than this. They have varied from 176 µ to 396 µ in length, and in 87 measurements have averaged 255 µ; width has varied from 66 µ to 264 µ, and in 64 measurements have averaged 154 µ (Pl. 8 Fig. 3). In thickness dorsoventrally the individuals vary from 44 µ to 88 µ at the center of the body (Pl. 8 Fig. 4) and from this point the body gradually decreases in thickness toward the two extremities.

Spiraling in Forward Swimming.

Direction of spiraling. This is a left spiraling species and nothing else has been seen.

Size of spirals. Spirals in this species have ranged in length from 625 µ to 1250 µ (Text-Fig. 10), and in 117 spirals have averaged 987 µ; width of spiral has been determined only comparatively due to difficulty in getting this species to swim entirely across the field at one time.

Speed of swimming. Normal free swimming occurs at an average speed of approximately 1786 µ per second.

Circling while Feeding.

While the individuals of this species are feeding over the bottom of the dish they are constantly circling to their left without spiraling, and without jerking back or pivoting.

Diagnosis.

Frontonia atra is a fresh water species, approximately twice the size of *F. acuminata* which it most closely resembles, measuring on an average in my cultures 255 µ × 154 µ; resembles a ping-pong paddle in general shape, and when seen from the side, has a distinct dorsal hump similar to *F. acuminata*, and the same turned up sled-runner appearance in front; mouth and groove are typical; macronucleus single, large, oval; micronucleii probably two in number; contractile vacuole one, near the nucleus (?). Left spiraling is all that has been seen, and occurs at an average speed of 1786 μ per second; circles to the left frequently while moving over the bottom of the dish without spiraling.

XIII. Other species of *Frontonia*.

1. *Frontonia branchiostomae* Codreanu, 1928.

Codreanu (1928) identified a ciliate he found living as a commensal on the pharyngeal area of *Amphioxus* (*Branchiostoma lanceolatum* Pall), as a species of *Frontonia*, and described it under the name *Frontonia branchiostomae*. Judging from the general shape of body, presence of numerous trichocysts, and the type and arrangement of the mouth and groove, this is without doubt a valid species. The mouth and groove constitute a sufficient basis for this classification, even though Codreanu shows the undulating membrane extending all the way down the side of the mouth, and more prominent than it has appeared in any species I have studied. This is the only species known at the present time which lives either as a commensal or parasite on other animals. It very much resembles *F. acuminata* in general body form, but has no pigment spot, and is very much smaller. It measures only 75 μ to 100 μ in length by 55 μ to 75 μ in width (Codreanu 1928), as against 88 μ to 174 μ in length by 44 μ to 131 μ in width for *F. acuminata*. Kahl (1931), in his reproduction of Codreanu's drawing, shows a distinct band or groove at the anterior pointed end of the mouth, and extending from there to the anterior extremity of the body. This band has previously been mentioned in this paper, and since Kahl's drawing is a reproduction one might conclude that Codreanu saw this band. But Codreanu's drawing shows no such band (Pl. 9 Fig. 10).

2. *Frontonia depressa* (Stokes, 1888), Kahl 1931.

1888: *Colpoda depressa* Stokes, Jour. Trent. Nat. Hist. Soc. V. 1, No. 3, p. 157, pl. 4.
1922: *Frontonia parvula* Penard, Etudes sur les Inf. D'eau Douce, pp. 141—42.
1931: *Frontonia depressa* Kahl, Tierwelt Deutschlands, 21 teil, p. 320, fig. 56.

Stokes (1888) identified and described as *Colpoda depressa*, a species of ciliate from sphagnum water having an ovate body, "depressed, slightly widest anteriorly, less than three times as long as broad, the frontal border rounded", bluntly acuminate posteriorly, with the cilia of the posterior extremity longer, and sometimes with a single cilium projecting beyond the others, single contractile vacuole, a single ovate nucleus, and the body covered, except in the mouth region, with "minute elevations arranged in longitudinal rows", with numerous trichocysts, and a body length of 55 μ to 80 μ. PENARD (1922) found in moss on old walls a similar ciliate which he identified as a new species and described under the name *Frontonia parvula.* This species had an ovate body, rounded in front and bluntly acuminate in the rear, covered with fine serrated cilia, trichocysts small, but cuticle of body covered with pimples "perles", mouth oval, groove short, nucleus ellipsoidal, elongate, or sausage-shaped, with one micronucleus, single large contractile vacuole, and a body length of 60 μ to 70 μ; rerely up to 75 μ.

KAHL (1931) found a similar species in moss on walls and rocks which he identified as identical with both STOKES' *C. depressa* and PENARD'S *F. parvula,* to which he assigned the name *Frontonia depressa* STOKES sp. KAHL found longer posterior cilia on those he observed, but PENARD does not mention this, and neither KAHL nor PENARD saw a single, long, projecting caudal cilium which STOKES found on some of his. The mouth and groove are not shown as clearly on STOKES drawing as might be desired, but I think they, together with body form, and the presence of trichocysts are sufficient to indicate very strongly that he probably had a frontonian. And I think it sufficiently clear that both KAHL and PENARD had the same species. This species is very similar to *F. acuminata* except that it has no pigment spot (Pl. 9 Figs. 15, 16).

3. *Frontonia elliptica* BEARDSLEY, 1902.

BEARDSLEY (1902) described, under the name *Frontonia elliptica,* a fresh water ciliate, ellipsoidal in form, slightly flattened, rounded equally both front and rear, somewhat smaller post., covered with fine cilia arranged in fine longitudinal rows; one large spherical macronucleus, and one or more micronucleii embedded in the mac.; mouth and groove typical but with an undulating membrane on the left side of the mouth; contractile vacuoles two in number. This species differs from *F. leucas* by smaller size, (115 μ to 150 μ BEARDSLEY, 1902), 2 contractile vacuoles, spherical nucleus, and an undulating membrane attached to the left side of the mouth. It more nearly resembles *F. vernalis* (EHRBG.) in position and shape of mouth and groove, the presence of two contractile vacuoles, but differs from it in that it is brackish or marine while *F. elliptica* is from fresh water, has a spherical macronucleus instead of an oval — this is the only one reported with a spherical macronucleus, but this may or may not mean much — and has an undulating membrane attached to the left side of the mouth instead of to the right. The habitat is considered of most importance since my experiments indicate distinctly that *F. vernalis* cannot readily, if at all, be transferred back and forth from sea water to fresh water. For this reason *F. elliptica* is not believed to be a fresh water form of *F. vernalis.* For the same reason KAHL's two-vacuolated *F. elliptica* is identified as *F. vernalis* — not BEARDSLEY'S *F. elliptica.*

Frontonia elliptica BEARDSLEY, therefore, is a fresh water species having two contractile vacuoles, probably a spherical macronucleus, one or more micronucleii, a typical mouth and post oral groove, and a slightly flattened, ellipsoidal body equally rounded at both ends, and perhaps, in some cases, a longer, more prominent caudal cilium and measuring 115—150 μ in length (Pl. 9 Fig. 9).

4. *Frontonia microstoma* KAHL.

KAHL (1931) described a brackish water ciliate under the name *F. microstoma*, which corresponds to no species I have seen. It measures 200 μ to 300 μ in length, is colorless, very slender and elongated, length much greater in proportion to width than any other species; mouth small, only about 15 μ long, with a short post oral groove (40 μ in length); macronucleus single, long lenticular, micronucleus single, located behind the macronucleus. Its brackish water habitat, long slender body, short oral groove, and the lenticular nucleus, prevent its being classified with *F. leucas.* It is too long and slender, and has the wrong sort of macronucleus to be classified with *F. marina*, unless the slenderness is due to food eaten, which seems possible. So at present it must be accepted at its face value but more information is needed (Pl. 9 Fig. 17).

5. *Frontonia algivora* KAHL.

KAHL (1931) described a *Frontonia* from a sea water ditch, but without a drawing, under the name *Frontonia algivora*, measuring 130 μ to 200 μ in length, resembling *Frontonia elliptica* in shape, 2—4 micronucleii, one contractile vacuole. In 1935 he described two others — both marine — one he thought probably a new species but to which he failed to assign a specific name, describing it simply under the head *Frontonia* sp. This one measured 100 μ to 120 μ in length, had one contractile vacuole and exactly the same body form as the one above, in so far as can be determined from his description without a drawing, but had a very large mouth. The other he thought a variety of *F. fusca* QUENN., measured only 80 μ to 100 μ in length, had a green pigment spot in the anterior end, and one contractile vacuole, and exactly the same body shape as the other two. All three of these are insufficiently described but so far as I can determine from the information at hand they are probably the same species. About the only points of difference are size of body — 80 μ to 100 μ in length in the smallest and 130 μ to 200 μ in length in the largest, the presence apparently of a very large mouth (35 μ to 40 μ) in the one given as *F.* sp., and the presence of a green pigment spot in the anterior end of the one considered by KAHL as a variety of *F. fusca* QUENN. But before body size, apparently a larger mouth, and perhaps the presence of a pigment spot, observed perhaps in only a few individuals, should be used as the basis for establishing either new varieties or new species, their constancy needs to be determined by pure culturing. For lack of information sufficient to justify other conclusions, therefore, they are all three identified in this paper as one species which would rightly take the name *Frontonia algivora* (Pl. 9 Figs. 13, 14).

6. *Frontonia complanata* (WETZEL, 1927).

1927: *Frontoniella complanata* WETZEL, Arch. Protistenkde **60**, 130—141.
1933: *Frontonia arenaria* KAHL, Die Tierwelt Deutschlands, 30. Teil, p. 832, Fig. 154—8.

KAHL (1933), as given in his Die Tierwelt Deutschlands, 30. Teil, 1935, described a frontonian under the name *Frontonia arenaria* which seems to me to be identical, at least in many respects, with the ciliate described by WETZEL (1927) under the name *Frontoniella complanata.* Both are marine, have the same general form — very much like *F. acuminata* — the same size, 100 μ to 130 μ in length for *F. arenaria* (KAHL) and 100 μ to 120 μ in length for *Frontoniella complanata* (WETZEL). Each has a single contractile vacuole. There is only one question in my mind at the present time, and that is with regard to the mouth and groove. KAHL'S *Frontonia arenaria* seems to have the typical *Frontonia* mouth, and I feel fairly certain also that WETZEL'S *Frontoniella complanata* has. But with this possible exception WETZEL was dealing with a species of *Frontonia*, and in so far as I can judge, was probably identical with KAHL'S *Frontonia arenaria.* True, *Frontoniella complanata*, as shown in WETZEL'S drawing is not so pointed posteriorly as *Frontonia arenaria*, and *F. arenaria* is shown with a pigment spot in the anterior end, but until more convincing information is at hand they are for me one and the same species. This being true, and since they fit into no other species known at the present time, and since WETZEL described his *Frontoniella complanata* first, the specific name of this species becomes, by right of priority, *Frontonia complanata* (WETZEL) (Pl. 9 Figs. 11, 12).

XIV. Other described Species and other Ciliates which have been considered *Frontonia*.

1. *Frontonia cypraea* ZACHARIAS, 1904.

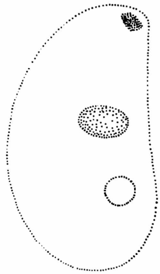
ZACHARIAS (1904) described, without a drawing, under the name *Frontonia cypraea*, a ciliate resembling a "Porzellanschnecke (*Cypraea*)", with a yellowish color, a bulgy short mouth, an undulating membrane, but without a groove. Since ZACHARIAS gives no drawing of this ciliate, I am unable to make out from his description just what he did have. The bulgy mouth and shape of body are not typical for *Frontonia*. KAHL (1931) thinks it must have been a *Lembadion* or a *Disematostoma*. Certainly, with the information available, it cannot be considered a species of *Frontonia*.

2. *Frontonia nassuloides* LEPŞI, 1926.

The fresh water *Frontonia nassuloides* described by LEPŞI, 1926, most certainly cannot be accepted as a valid species of *Frontonia*. The one striking characteristic possessed by each species I have studied, as I have already stated, is the peculiar shape of the mouth, and the possession of a post oral groove extending from the right side of the mouth. No other ciliate possesses such a groove. LEPŞI's *F. nassuloides* does not have this groove, and very little can be determined from his description and drawing about the mouth itself. For this reason, and in this way, therefore, it is believed this described species eliminates itself from further consideration as a member of the genus *Frontonia*.

3. *Sigmostomum indicum* GULATI, 1925.

Sigmostomum indicum described by GULATI, 1925, from India, was given by KAHL (1931) as an uncertain species of *Frontonia*. It has some *Frontonia* characteristics — oval-shaped body, oval macronucleus, an oval micronucleus, body studded with trichocysts, and a single contractile vacuole. But it has an S-shaped mouth and no peristomial field leading to it. This S-shaped mouth and the lack of a post oral groove are not *Frontonia* characteristics and



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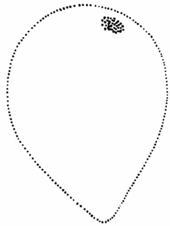

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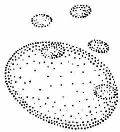

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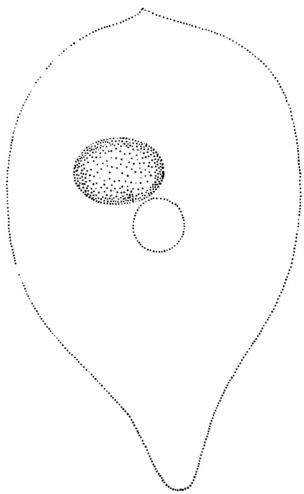

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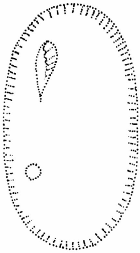
Plate 9.



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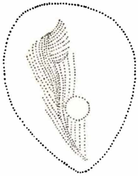

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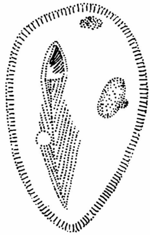

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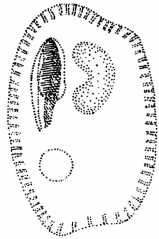

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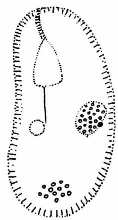

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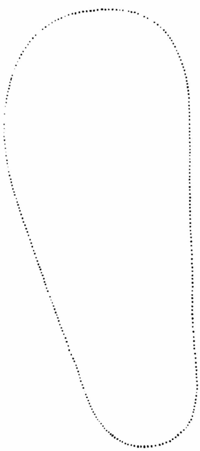

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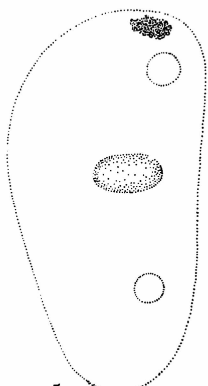

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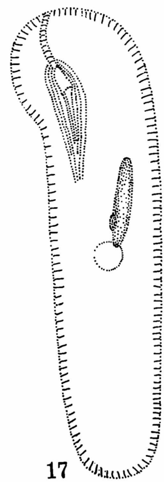

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seem to me to eliminate it from consideration as a species of *Frontonia.* GULATI thought it came nearest to the genus *Glaucoma* in its combination of characters, and to this genus it probably belongs.

XV. General Summary.

1. Fourteen species of *Frontonia* are recognized — eight of which have been studied for spiraling.

2. Habitat. Four of the 8 species of *Frontonia* studied are fresh water species; four are marine (Table 1), and it has not been found possible to transfer either species from one medium to the other, either directly or gradually. Two of the other 6 species are fresh water; 4 are marine.

3. Form of body. Five of the eight species are foot-shaped, one kidney-shaped, and two are oval or somewhat pointed at one or both ends (Table 2, Pl. 9 Figs. 1—17).

Plate 9.

Outline drawings of all known species of *Frontonia*, all drawn to the same scale (500 × actual size), and reduced to 250 times actual size of an average individual, or what is thought to be an average individual, to show comparative size, body form, and chief characteristics of each species.

Fig. 1. *Frontonia vesiculosa* DA CUNHA. × 250.
Fig. 2. *Frontonia atra* EHRBG. sp. × 250.
Fig. 3. *Frontonia leucas* EHRBG. × 250.
Fig. 4. *Frontonia marina* FABRE-DOMERGUE. × 250.
Fig. 5. *Frontonia vernalis* EHRBG. × 250.
Fig. 6. *Frontonia ocularis* sp. nov. × 250.
Fig. 7. *Frontonia acuminata* EHRBG. sp. × 250.
Fig. 8. *Frontonia schaefferi* sp. nov. × 250.
Fig. 9. *Frontonia elliptica* BEARDSLEY (Redrawn from BEARDSLEY × 250).
Fig. 10. *Frontonia branchiostomae* CODREANU (Redrawn from CODREANU × 250).
Fig. 11. *Frontonia complanata* WETZEL (KAHL's *F. arenaria* — Redrawn from KAHL). × 250.
Fig. 12. *Frontonia complanata* WETZEL sp. (WETZEL's *Frontoniella complanata* — Redrawn from WETZEL). × 250.
Fig. 13. *Frontonia algivora* (KAHL's *F. fusca* var.? — Redrawn from KAHL). × 250.
Fig. 14. *Frontonia algivora* KAHL (KAHL's *F. sp.* — Redrawn from KAHL). × 250.
Fig. 15. *Frontonia depressa* STOKES sp. (STOKE's *Colpoda depressa* — Redrawn from STOKES). × 250.
Fig. 16. *Frontonia depressa* STOKES sp. (PENARD's *F. parvula* — Redrawn from PENARD). × 250.
Fig. 17. *Frontonia microstoma* KAHL (Redrawn from KAHL). × 250.

Table 1.
Distribution of *Frontonia* in fresh and salt water.

Fresh water	Marine
Frontonia vesiculosa	*Frontonia marina*
Frontonia leucas	*Frontonia vernalis*
Frontonia atra	*Frontonia ocularis*
Frontonia acuminata	*Frontonia schaefferi*

Table 2.
Frontonia classified on the basis of body shape.

Foot-shape	Kidney-shape	Oval or acuminate
Frontonia vesiculosa	*Frontonia ocularis*	*Frontonia acuminata*
Frontonia leucas	—	*Frontonia atra*
Frontonia marina		
Frontonia vernalis		
Frontonia schaefferi		

4. Size. Although body size overlaps in some species, no two species have averaged exactly the same, but *F. leucas*, *F. marina*, and *F. atra* approach each other very closely. Moreover, when they are arranged in a table according to body size, with the largest at the top and the smallest at the bottom, they take the order shown (Table 3). If this be arranged in chart form they are found to form a definite staircase (Text-Fig. 11).

Table 3.
Classification of *Frontonia* on the basis of body size.
Meas. = Number of measurements, Mn. = Minimum, Mx. = Maximum.

Name	Length in micra				Width in micra			
	Meas.	Mn.	Av.	Mx.	Meas.	Mn.	Av.	Mx.
Frontonia vesiculosa	182	308	463	660	105	110	162	262
Frontonia leucas	110	133	258	350	93	66	96	150
Frontonia marina	131	132	231	701	124	55	91	146
Frontonia atra	87	176	255	396	64	66	154	264
Frontonia vernalis	13	166	197	311	9	66	108	133
Frontonia ocularis	51	102	141	200	41	43	76	107
Frontonia schaefferi	9	86	120	167	10	43	66	106
Frontonia acuminata	27	88	116	174	7	44	77	121

5. Color. The individuals of all species are usually more or less clear to slightly pinkish. Color when present, is usually due to the type of food ingested except perhaps in *F. leucas*, where color is sometimes due to enclosed Zoochlorellae.

6. Trichocysts. Trichocysts are abundant and very prominent in all members of the genus. These are embedded in the ectoplasm

perpendicular to the surface area which their outer ends appear to punch up in the form of pimples. These trichocysts are small spindle-shaped rods which, at least in one species, are definitely barbed on the outer end.

7. Contractile vacuole. Four species have only one contractile vacuole, *F. leucas*, *F. marina*, *F. acuminata*, and *F. atra*; two have from two to three, *F. ocularis* and *F. vernalis*; while *F. vesiculosa* has characteristically 5 to 8. No contractile vacuoles have been seen in *F. schaefferi* (Table 4).

Table 4.
Classification of *Frontonia* on the basis of the number of contractile vacuoles.

One	Two	Two or three	More than three
Frontonia leucas *Frontonia marina* *Frontonia atra* *Frontonia acuminata*	*Frontonia ocularis*	*Frontonia vernalis*	*Frontonia vesiculosa*

8. Nucleus. The nucleus consists of one large oval macronucleus, very much alike in all the eight species with the possible exception of *F. schaefferi* where the nucleus has not yet been seen, and probably of one or more relatively large oval micronucleii. Micronucleii have not been seen, however, except in *F. leucas*, *F. vesiculosa*, and *F. marina.*

9. Pigment spot. Three of the eight species (*F. vernalis*, *F. ocularis*, and *F. acuminata*) have a more or less prominent pigment or eye-spot in the anterior extremity. In *F. vernalis* this spot is least prominent, being seen in only a few individuals, but in *F. ocularis* it is so prominent as to be a specific characteristic.

10. Direction of spiraling in forward swimming. Two of the 8 species (*F. atra*, and *F. acuminata*) are left spiraling; two (*F. vernalis* and *F. ocularis*) are right spiraling; and four are able to spiral in either direction (*F. leucas*, *F. vesiculosa*, *F. marina*, and *F. schaefferi*). But neither of the 4 are able to spiral equally well in either direction. In each species one direction is so constant in all speed and distant swimming as to be characteristic. It is always assumed when the animal is greatly disturbed. The other direction is a feeding movement occurring at a slower speed, in generally wider spirals, continued for a shorter distance, and is always changed when the animal is sufficiently disturbed. Three of the 4 (*F. leucas*, *F. vesiculosa*, and *F. marina*) are characteristically left spiraling; the other (*F. schaefferi*) is characteristically right spiraling. All 8 species of *Frontonia*

Table 5.
Comparison of direction of spiraling in *Frontonia.*

Name	Forward		Backward	
	Left	Right	Left	Right
Frontonia vesiculosa	L	(R)	—	R
Frontonia leucas	L	(R)	—	R
Frontonia marina	L	(R)	—	R
Frontonia atra	L			
Frontonia vernalis	—	R	—	R
Frontonia ocularis	—	R	—	R
Frontonia schaefferi	(L)	R	—	R
Frontonia acuminata	L			

studied can, therefore, be classified on the basis of the characteristic spiral, into right and left spiraling species. On this basis *F. leucas*, *F. vesiculosa*, *F. marina*, *F. atra*, and *F. acuminata* are left spiraling species; *F. vernalis*, *F. ocularis*, and *F. schaefferi* are right spiraling species (Table 5).

Table 6.
Comparison of length of characteristic spiral in *Frontonia.*
Sprls. = Spirals.

Name	Left spiraling				Right spiraling			
	Sprls.	Mn.	Av.	Mx.	Sprls.	Mn.	Av.	Mx.
Frontonia vesiculosa	192	1200	1552	2000	62	833	1073	1333
Frontonia leucas	120	1000	1267	1600	62	666	967	1333
Frontonia marina	1014	611	1147	2000	62	750	1780	3000
Frontonia atra	117	625	987	1250				
Frontonia vernalis	—	—	—	—	92	780	859	1000
Frontonia ocularis	—	—	—	—	1243	400	798	2000
Frontonia schaefferi	—	—	—	—	418	238	336	500
Frontonia acuminata	—	—	—	—	18	—	416	

11. Size of spirals. Average length of spiral in normal forward free swimming in *Frontonia* ranges from 1552 in *F. vesiculosa* down to 351 μ in *F. schaefferi*, and if the 8 species are arranged in a column according to length of spiral, with the species having the longest spiral at the top, and the one having the shortest spiral at the bottom, they are found to take the same position as when arranged for body size (Tables 3, 6 and Text-Fig. 11), with the exception that *F. atra* exchanges places with *F. marina*, and *F. schaefferi* with *F. acuminata* — in both cases of which length of body is very nearly the same. The average length of spiral in *Frontonia* therefore, corresponds very closely with average length of body.

12. Speed in forward swimming. Average speed of swimming in *Frontonia* ranges all the way from 2821 μ per second in *F. vesi-*

culosa to 491 μ in *F. schaefferi*, with speed in *F. acuminata* not determined. And again if the species are arranged on the basis of

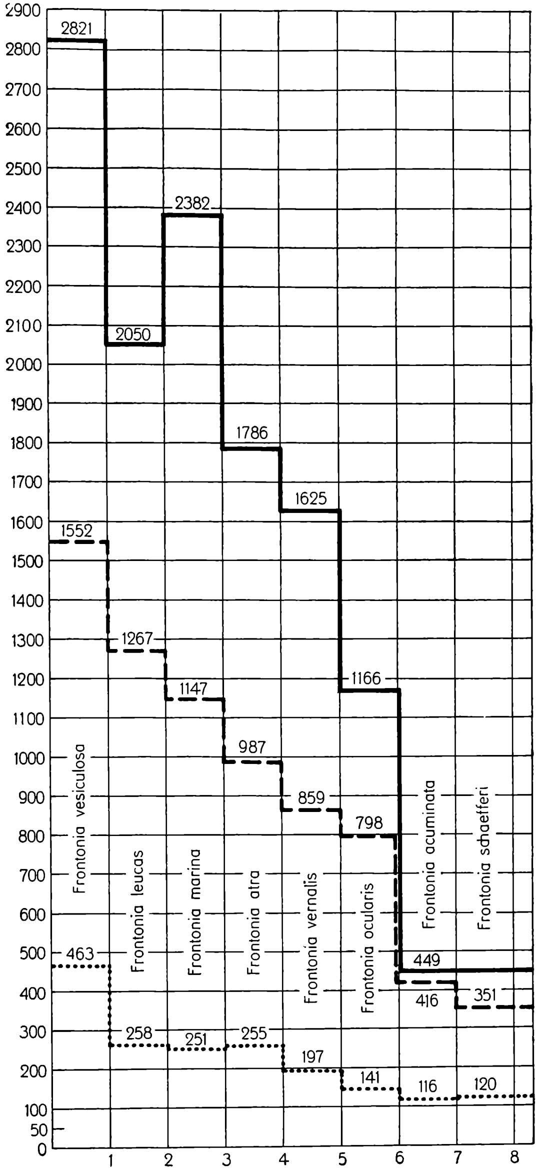

Fig. 11. Relation of size of body, size of spirals, and speed of swimming in 8 species of *Frontonia*. ······ Body size. — — — — Length of spiral. ——— Speed of swimming.

speed of swimming, with the speediest at the top of the list and the slowest at the bottom, they are found to have the same position as when arranged for length of body and length of spiral, except that *F. leucas* and *F. marina* exchange places (Tables 3, 7 and Text-Fig. 11). With the exceptions noted therefore, we can say that in *Frontonia* the average length of spiral and speed of swimming vary with the species according to average body size.

Table 7.
Comparison of species of *Frontonia* as to speed of swimming.

Name	Left spiraling, micra per second				Right spiraling, micra per second			
	Meas.	Mn.	Av.	Mx.	Meas.	Mn.	Av.	Mx.
Frontonia vesiculosa da Cunha	20	2286	2821	4000	8	588	873	1173
Frontonia marina Fab.-Dom.	78	982	2382	3666				
Frontonia leucas Ehr.	—	1554	2050	2960				
Frontonia atra Ehr. sp.	—	1666	1786	2272				
Frontonia vernalis Ehr.	—	—	—	—	10	1300	1625	1950
Frontonia ocularis sp. nov.	—	—	—	—	70	429	1166	1920
Frontonia schaefferi sp. nov.	—	—	—	—	—	—	449	
Frontonia acuminata Ehr. sp.								

13. Spiraling in backward swimming. Six species of *Frontonia* have been observed swimming backward, and in each case the spiral was to the right, although in forward movement three of the 6 swim in right spirals and three in left spirals. In other words only three species swim in the same direction backward as forward. This corresponds exactly with backward spiraling in *Paramecium* Bullington (1930).

14. Circling while feeding. Five species have shown a distinct and peculiar tendency to circle to the left in addition to their normal spiraling movements. In *F. vesiculosa*, there is a more or less general tendency to move in large circles to the left even while swimming in normal left spirals. *F. atra* and *F. schaefferi*, on the other hand continually circle to the left while feeding but without spiraling and without jerking back; *F. leucas* and *F. acuminata* circle to the left also, while feeding, but only by jerking backward and pivoting.

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