On the Bicoecidae: A Family of Colourless Flagellates

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ON THE BICOECIDAE: A FAMILY OF COLOURLESS FLAGELLATES

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[Plate 26]

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Two distinct species appear to have been confused by James-Clark in his original description of *Bicoeca lacustris*. The two forms have been re-examined and photographed. It is suggested that the differences between them justify their separation into two species, as suggested by Štolc, the one form to retain the name *B. lacustris*, the other to receive that of *B. vacillans* Štolc.

A new species, *B. maris*, is described, and the affinities of the Bicoecidae, Bodonidae and Craspedomonadidae are discussed.

1. Introduction

The notes and photomicrographs collected here have resulted from observations extending over a period of two years on certain members of the Protomonadina belonging to the family Bicoecidae (=Bikoecida Stein). It is hoped that they may serve to define the classic species, *Bicoeca lacustris* James-Clark, and to distinguish it from a somewhat similar species with which it appears to have been confused. These notes also include a description of what seems to be a new marine species of *Bicoeca*. The paper concludes with a brief discussion of the systematic position of the Bicoecidae.

Although the genus *Bicoeca* was first described seventy years ago, its taxonomy is anything but clear, as Penard (1921) pointed out. An examination of the literature since James-Clark's first description (1868) has revealed so many discrepancies and inaccuracies that it seemed desirable to review the information available about this interesting family, chance having provided an opportunity of examining three of its members and of making photomicrographs of living individuals, which may perhaps serve as a more objective record for future reference than has hitherto been available.

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Since the observations recorded have led to interpretations of structure differing considerably from those of earlier writers, it is proposed to consider first the original description of the genus for which the family Bicoecidae was created. The definition of this family given by Doflein and Reichenow (1929) (see p. 469) is perhaps the most reasonable, but the departures from this definition in earlier and later literature are so considerable that it appears imperative to reconsider all such definitions. In many cases descriptions have been based on rationalizations from the accounts of earlier observers, or on misinterpretations of Stein's figures. Indeed the history of this family leads one to regret once more that Stein's great work remains incomplete.

2. *Bicoeca lacustris* James-Clark

The genus *Bicosoeca* (βῖκος a vase, and οἰκέω to inhabit) was created by James-Clark (1868) to contain two species, with one of which we are concerned. *B. lacustris* is a fresh-water form, occurring in quiet streams and lakes, attached to filamentous algae. The name *Bicosoeca* was changed to *Bikoeca* by Stein (1878), and the corrected form, *Bicoeca*, will be used throughout this paper, even where earlier forms were used by the authors whose views are cited. The family Bikoecida was made by Stein (1878) to include this genus and *Poteriodendron*, a somewhat similar but colonial form, probably identical with *Stylobryon* Fromentel (1874). James-Clark describes with great conviction both the structure of *Bicoeca lacustris* and the changes occurring during 'development'. But, admirable as are James-Clark's descriptions and figures, there are reasons for supposing that certain features were misinterpreted, and that the forms which he observed do not, as he implies, represent stages in a developmental sequence, but are, in fact, separate species.

B. lacustris (see figure 1) is said (in his account) to have a yellow tinge; the animal occupies the anterior half of the calyx and projects a little beyond the edge. The shape is rather elliptical than elongate-oval, varying between the two conditions, and is the latter in the largest individuals. The body is rounded posteriorly and broadest in the middle, tapers to a truncate front, and ends on one side in a laterally projecting flagellum and on the opposite side in a long, incurved lip. A furrow (less deep than in *B. gracilipes*, the marine form described by James-Clark) extends from the flagellum base to the contractile ligament. James-Clark interpreted this furrow as a greatly prolonged ostial notch, and the retractor as a trailing lash originating at the greatest possible distance from the other flagellum. The lip is twice as long as wide and has an incurved, digitate form. The flagellum arises at an angle of 40–45° to the axis of the body. According to James-Clark's account, it assists in forcing food into the mouth, which lies between the base of the flagellum and the lip. The anus is said to lie on the lip-like process. He describes 'the collection of large globular masses in the base of the lip and sometimes further up and their subsequent exit thereabouts'. Two contractile vacuoles lie at the posterior end to right and left of the plane passing through lip, flagellum and furrow; they empty alternately 5–6 times per minute. The fully developed calyx is about twice as long as the body and 4–5 times as long as wide. It has the form of a deep slender urn, the bottom rounded, the waist slightly constricted, and with a faint, scarcely reverted, truncate rim. 'In younger stages the aperture almost closes when the body is retracted and during protrusion the rim embraces the body closely. During undeveloped stages of the calyx the pedicel is less than half its full length (down to little or nothing). When full grown it is at least half as long as the calyx.'

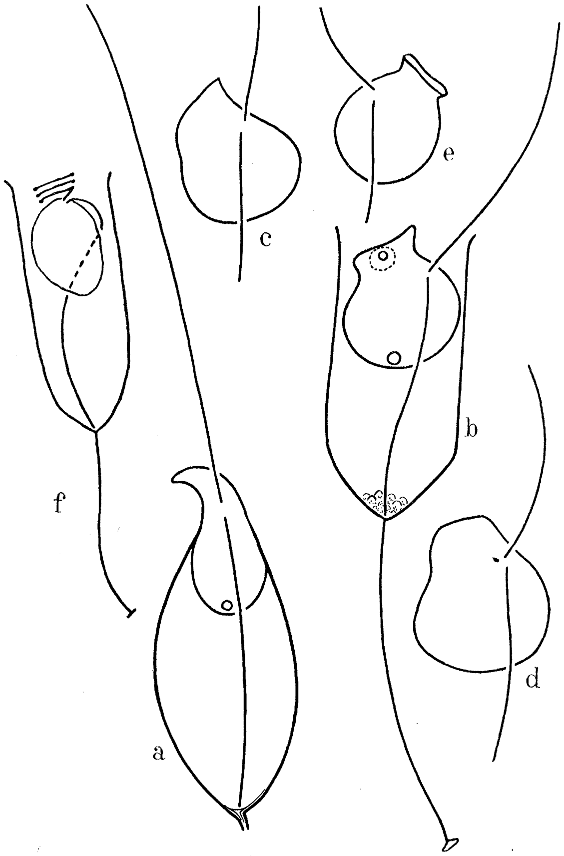

FIGURE 1. (*a*) The form referred to as *a* (*Bicoeca lacustris* James-Clark). (*b*), (*c*), (*d*), (*e*) and (*f*) The form referred to as *b* (*Bicoeca vacillans* Štolc); sketches showing the appearance of the same individual at different times. (*f*) Sketch showing that the posterior flagellum is free to its insertion.

The forms *a* and *b* (figure 1), answering to James-Clark's description of the genus *Bicoeca*, were found in a small aquarium covered with duckweed. In order to determine the systematic rank of these forms, it is proposed now to consider in turn the structural features described by James-Clark in *B. lacustris* as they appear in these forms.

3. A COMPARISON OF FORMS *a* AND *b* WITH *BICOECA LACUSTRIS* JAMES-CLARK

(*a*) *The peristomial process or lip*

The shape and disposition of the lip-like peristomial process in the form *a* is shown in figures 1 *a* and 2, and in figures 10–13, plate 26. The process arises as a leaf-like membrane usually carried almost at right angles to the long axis of the body, occasionally directed backwards as in figure 2. Careful examination of the anterior end showed that there is no suggestion of a collar being formed here as in *B. exilis* Penard, but that there is a slight rim round the base of the flagellum, of which the peristomial process is an extension (see figure 2).

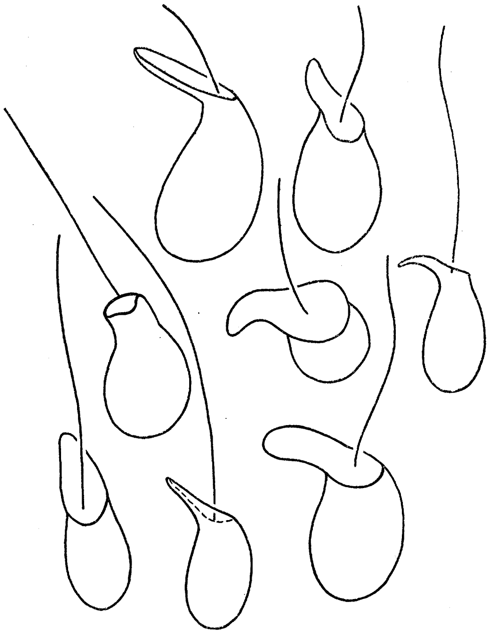

FIGURE 2. The appearance of the lip or peristomial process in form *a*.

In the form living in the widely open house (*b*, figure 1) the structure is entirely different. To one side of the body, well removed from the base of the flagellum, a broad columnar process arises (shown in figure 1 and in figures 16–19, plate 26), which is often drawn out into a point on its upper border (figure 22, plate 26)—just as in Stein's figures of *Poteriodendron*. This ear-like point may have been mistaken by previous observers for the lip present in *a*, and it is just possible that this is the structure which Kent interpreted as a flagellum (see p. 455). The free border of the columnar process is sometimes defined by a rim (see figure 1 *e* and figures 16–20, plate 26). The process may well be called a peristome, since it is the site of a permanent cytostome. James-Clark and Bütschli (1878) describe the ingestion of food particles in *Bicoeca lacustris* in the region between the peristomial process and the base of the flagellum. Kent (1880–1) says that food is incepted at all points of the periphery. Lauterborn

(1899) claims that the food vacuole lies near the base of the flagellum. According to Senn (1900) the mouth lies on the protoplasmic process or between it and the base of the flagellum. Lemmermann (1914) agrees with this. In *b*, however, ingestion takes place on the truncated surface of the columnar peristome. This was also described by Senn (1900) in the case of *Poteriodendron petiolatum* Stein. A recently formed food vacuole is shown in figure 17, plate 26. The process of ingestion involves the formation of a cavity in the end of the column and the raising of lips around this (see figure 1 *b*). These come together enclosing the particle. It was frequently observed in this form that particles falling on the surface near the base of the flagellum are not ingested. They are generally carried to the tip of the pointed extension and are there ejected. Only particles touching the centre of the disk are ingested and rapidly borne away from the surface in a vacuole. It is to be noted that the body frequently does not reach the mouth of the house, and rarely, if ever, does the protoplasmic process project from the opening. With the optical equipment employed (see description of plate 26, p. 472), both forms appeared colourless.

(*b*) *The flagella*

Although the suggestion that the anchoring contractile filament is comparable to the trailing flagellum of the genus *Bodo* was made by Štolc as early as 1887 from observations on *B. lacustris* and *B. vacillans*, and by Lauterborn (1899) from observations on *B. socialis*, the Bicoecaceae are placed by Pascher (1914) in his key (based on the flagellar apparatus) in the group with one swimming flagellum (not with the Bodonaceae which possess one swimming and one trailing flagellum).

Kent (1880–1) insisted on the presence of two anterior flagella, the one being minute and visible with difficulty. Penard (1921) remarks that if there were indeed two, the form must have been *Stokesiella* Lemmermann, not *Bicoeca*. The former genus was created by Lemmermann (1914) to contain five species of flagellates from freshwater ascribed by Stokes (1888) to the genus *Bicoeca*. This question of the presence or absence of an accessory flagellum is one which requires very careful attention. In the three forms which I have had an opportunity of examining I did not find any such flagellum, either in living specimens or in stained preparations. I am informed by Mr Clifford Dobell, however, that he has observed an accessory flagellum—much as in *Monas*—in forms otherwise indistinguishable from *Bicoeca lacustris* James-Clark, and that he believes that forms with two anterior flagella undoubtedly exist. Stained preparations of three species of *Bicoeca* by von Prowazek (1903), Reynolds (1927) and myself (see p. 459) show no trace of a second anterior flagellum. The situation is rendered all the more confusing by the fact that when Kent and Stokes published their descriptions the anchoring filament was not recognized as a flagellum, and the two flagella of the free-swimming form were identified by Kent with the two anterior flagella of the sessile form. Yet since the posterior anchoring filament is undoubtedly a flagellum, the free-swimming form should have *three* flagella, if indeed there are two anterior flagella; but this has never been described. I would suggest that a second, rudimentary, anterior flagellum may sometimes be formed before division, at a time when the flagellate is still active, before it becomes rounded off (see p. 460).

Penard (1921) has described the appearance of *B. exilis* when it is leaving the house, one flagellum being carried forward, the other trailing. This was also described by Kent, who states that the trailing flagellum of the free-swimming form is the feeding flagellum of the sessile form, and that locomotion is due to the smaller of the two anterior flagella. Penard states quite definitely that the *anchoring* flagellum is trailed as a rudder in the case of *B. exilis*. He is here referring, however, not to the division product, which was observed by Kent, but to the vegetative form abandoning its house. Earlier suggestions by James-Clark that the posterior flagellum was a contractile thread arising at the posterior end were already doubtful from Stein's figures. Figure 1*f*, sketched from life, shows that the posterior flagellum is in fact free to its base, which lies in the vicinity of the anterior flagellum. My observations do not confirm James-Clark's description of a permanent groove from the base of the anterior flagellum to the posterior end. This I regard as a misinterpretation of the origin of the posterior flagellum.

Observations made at intervals of about 20 minutes frequently showed that the position of the organism in the house is constantly changing. Rotation about the axis of the posterior flagellum takes place, so that the anterior flagellum is continually fishing in new waters. This movement does not occur continuously; the animal throws out the flagellum in a slightly different direction on emerging from the cup after contraction.

The coiling of the anterior flagellum has impressed all observers. Kent compares it with the coiling of a butterfly's proboscis. Verworn (1889) in the case of *Poteriodendron* likens the coiled flagellum to a helical spring. In the form *b*, coiling leads to the formation of a solenoid, and the coiled flagellum does not stand upright over the retracted body as Penard describes in *Bicoeca exilis*, but sits as a turban on top of it (see figure 3 and figures 23 and 24, plate 26). Penard shows the coils of the flagellum diminishing slightly in diameter towards the tip. This was occasionally observed in *b* (see figure 3), but the coils may also increase in diameter towards the tip as in figures 23 and 24, plate 26.

The uncoiling of the anterior flagellum is shown in figure 3. Verworn says that in *Poteriodendron* it is flicked out like a mooring rope, while Penard compares the process to the uncoiling of a lasso (*Bicoeca exilis*). As uncoiling proceeds, the straightened portion is thrown into waves which appear to travel towards the tip, and disappear when the flagellum is completely extended and rigid save for the invisible vibrating tip. In *b*, the base of the flagellum sometimes arises, as James-Clark describes, at a considerable angle (*c.* 45°) to the long axis of the body (figure 16, plate 26). It may, however, appear as a continuation of the posterior flagellum, parallel to the long axis of the body (figure 19, plate 26). In *a*, on the other hand, the flagellum arises terminally and parallel to the long axis (figure 1 and figures 10 and 11, plate 26).

When the posterior flagellum contracts, withdrawing the body, it is thrown into a lax spiral.

(*c*) *The contractile vacuole*

Whereas James-Clark (1868) described two contractile vacuoles at the extreme posterior end, Bütschli (1878) observed but one near the origin of the posterior contractile thread. Kent (1880–1) gives two or three, posteriorly situated, and this was quoted by Bütschli (1883–7). Lauterborn (1899) describes one contractile vacuole only. Senn (1900) indicates one contractile vacuole at the posterior end. Lemmermann (1914) also agrees with this. Penard (1921) found one contractile vacuole in *B. exilis* at the posterior extremity and behind the nucleus. He observed accessory vacuoles as well. Observations on forms *a* and *b* revealed in each case a single contractile vacuole posteriorly situated.

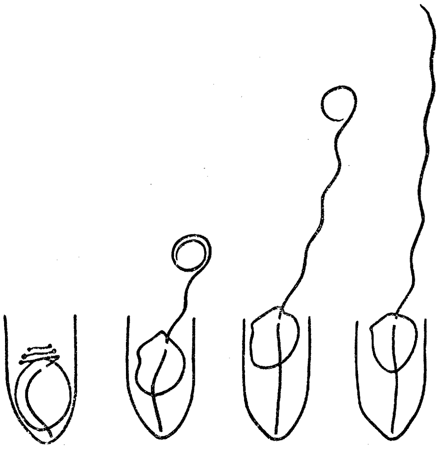

FIGURE 3. The appearance of the organism *b* when contracted; stages in the uncoiling of anterior and posterior flagella.

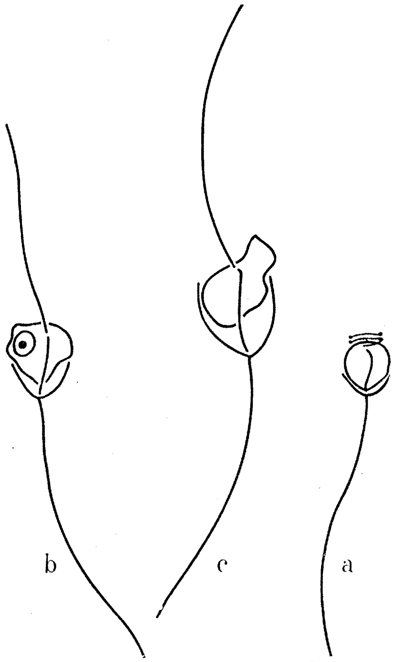

FIGURE 4. Young individuals of form *b* showing stages (*a*), (*b*) and (*c*) in the secretion of the house. A food vacuole is shown in (*b*).

(*d*) *The house*

(i) *Development.*

The course of development implied by James-Clark's account is probably incorrect. Penard (1921) observed individuals of *B. exilis* for periods of 10, 12 and 24 hr. and never saw lengthening of the stalk of the calyx. He did not observe settling of the liberated flagellate forms, nor has this been observed by the writer. Figure 4*a*, however, shows an individual in which the stalk has reached its normal length (that is, normal for *b*) while the house is still far from completion. A slightly later stage is shown in figure 4*b*. Kent (1880–1) appears to have observed fixation and, by implication, the development of the house, but gives, remarkably enough, no description of 'this interesting growth', observing only that attachment is effected at the extremity which previously bore the flagella, these organs being absorbed and developed anew at the opposite or distal extremity.

It is difficult to see how growth of the stalk could take place once the base of the house is secreted. The formation of the stalk may well correspond to the secretion of temporary mucous strands observable in certain ciliates, such as *Uronema filificum* Kahl, where the secretion streaming from the posterior rigid cilium forms a cord attaching the animal to any surface. The base of the cup can only be formed, however, by the coagulation of a secretion from the whole surface, and since the cup is supported by the stalk it is difficult to imagine how the latter can be added to, once the continuous cup-shaped base has been secreted. The evidence available (Penard's observations and figure 4) suggests that the stalk is formed first, once and for all, and cannot be lengthened, and that the house is secreted subsequently. We have reason, therefore, to question James-Clark's statement that during development the pedicel increases from half or less than half its final length to the adult length.

(ii) *The form of the house in youth and age.*

James-Clark also reported that in the younger stages the aperture of the calyx almost closes when the body is retracted, and that the rim embraces the body closely during protrusion. Figures 10–15, plate 26, where the animal is seen both extended and retracted, show that this occurs in *a*. But if the short stalk characteristic of such pear-shaped calyces (see, for example, all Stein's figures) does not increase in length, the question arises whether such forms are indeed early stages or whether they are a separate species. It is important to note that, although James-Clark figures two forms of house, later accounts do not always insist on this point.

Bütschli (1878) describes *B. lacustris* (which he occasionally found living colonially) and agrees with James-Clark that the mouth of the cup may be widely open or constricted. In the latter case he often observed closure of the mouth on withdrawal. He also agrees with James-Clark that this occurs in young forms, but his figures of *B. lacustris* show the 'young' form only. His account differs from that of James-Clark in the suggestion that the cup may be triangular in cross-section—a suggestion which has never been confirmed.

Kent (1880–1) describes the cup as elongate-ovate, widest posteriorly, a little over twice as long as broad, supported on a pedicel which nearly equals it in length; the animalcule when extended projected beyond the aperture of the lorica.

Bütschli (1883–7) describes the house in the family Bikoecina (including the genera *Bicoeca* James-Clark and *Poteriodendron* Stein) as vase- or thimble-shaped, usually attached to a slender stalk. His figures are from Stein, with the exception of one, which is original, and which shows the house as in figure 1 *a*.

Zacharias (1894) in his imperfect account of a supposed variety of *Bicoeca lacustris* James-Clark, var. *longipes* Zacharias, gives the following description: house 10–12 μ tall, moderately inflated and becoming somewhat narrower above; foot 28 μ long.

Blochmann (1895) gives a description of the genus *Bicoeca* Clark (*sic*) with an oval house, open at the narrower end; length of house 14 μ.

Francé (1897) in his account of the Craspedomonadinae figures several forms of *Bicoeca* and says that the house shows almost as much variation in shape as that of *Salpingoeca*. Penard (1921) on the other hand is of the opinion that the shape of the capsule and the length of the flagellum are sufficient grounds for separating his species, *Bicoeca exilis*, from *B. lacustris* James-Clark. The examples of *B. lacustris* drawn by Francé have the form of house shown in figure 1 *a*.

Lauterborn (1899) described a colonial form, *B. socialis*, in which the house resembles a bellied vase, somewhat inflated at the base, narrowing towards the open end, and cut off squarely. This is obviously quite different from the form of vase in figure 1 *a*.

Senn (1900) states that the members of the family Bicoecaceae possess houses which are oval or flask-shaped. *B. lacustris* is illustrated by a typical egg-shaped house and this is described as oval, pear-shaped, rim sometimes contractile; stalked or sessile, 10–15 μ long.

Lemmermann (1914) returns to the description given by James-Clark: young houses oval, narrowed anteriorly; older houses vase-shaped, widened anteriorly, tapering posteriorly, with a short, simple stalk. He gives Bütschli's figure, however, in which the house is as in figure 1 *a*.

It is clear that the species *B. lacustris* has generally been described with a house constricted at the mouth, and that the distinction between 'young' and 'old' members of the species dates from James-Clark (who was supported by Bütschli).

(*e*) *The nucleus and flagellar complex in the Bicoecidae*

The nucleus of *B. exilis* seen in life is described by Penard (1921) as spherical, posterior and to the side; pale, with a large central caryosome. According to Senn (1900) the nucleus lies rather in front of the middle in *Bicoeca* but centrally in *Poteriodendron*. Lauterborn (1899) states that the nucleus and nucleolus are distinct in life. Bütschli (1883–7) observed the nucleus approximately in the centre of the body. Kent describes the endoplast as spherical and subcentral. James-Clark (1868) did not observe a nucleus.

My own observations on form *b* indicate that the nucleus is large (up to $\frac{1}{3}-\frac{1}{2}$ of the diameter in fixed specimens) and lies anteriorly, close to the surface, and to one side, in the plane passing through the peristome and the two flagella. It is visible in the living animal in figure 20, plate 26, and in permanent preparations in figures 26–28, plate 26. In permanent preparations, fixed with Schaudinn's fluid and stained with iron haematoxylin by the slow method and orange G, the distinction between a central mass and an outer zone is clear (see figure 28, plate 26). In some cases an intensely staining body was visible within and to one side of the central mass (see figure 28, plate 26).

In a description of a marine species of *Bicoeca*, von Prowazek (1903) states that the nucleus is embraced by two sausage-shaped bodies forming a kind of life-belt about the nucleus. These he observed in preparations fixed with Flemming's fluid and stained with iron haematoxylin. He asserts that these bodies, which he compares with Hertwig's chromidia, but which Grassé (1926) compares with the parabasal apparatus, divide independently of and before the division of the nucleus. Some fifty specimens of form *b*, which had been fixed with Schaudinn's fluid and stained with iron haematoxylin, were examined, but in no case was any such structure found. [It may be objected that Schaudinn's fluid is unsatisfactory as a fixative for parabasals—as in the case of *Trichonympha*, for example. Those of *Bodo edax*, however, are satisfactorily fixed by sublimate alcohol (Kühn, 1915). It will be seen later that specimens of a marine species, *B. maris* n.sp. fixed with Champy's fluid, showed no parabasal apparatus comparable with von Prowazek's chromidia.] Lemmermann (1914) remarks briefly that there is a single basal granule united to the nucleus by a rhizoplast, but gives no authority for this statement. Internal evidence suggests that he is describing von Prowazek's figures. Grassé (1926) has suggested that the bodies described by von Prowazek were in fact the parabasal apparatus, and accordingly he includes the Bicoecinae along with the Herpetomonadinae, Bodoninae, Polymastiginae, Hypermastiginae and Distomatinae in the Protomastigina Senn. All these families are characterized by the presence of a parabasal, almost invariably in association with the blepharoplast (or basal granule).

Examination of preparations of form *b* shows that there is no parabasal present of the form described by von Prowazek under the name chromidia. The anterior and posterior flagella arise from an intensely staining body which is closely applied to the nucleus. This structure appears to be visible in the living animal shown in figures 20 and 21, plate 26. The relations of nucleus and flagella are illustrated in the sketches reproduced in figure 5. For comparison, a figure from von Prowazek (1903) is included. It is clear that my figures are essentially similar to that of von Prowazek; they differ chiefly in the absence of the chromidia. It is evident that the flagellar complex differs considerably from that of the typical bodonids, which possess a large parabasal (as large as the nucleus) and two distinct basal granules (Kühn 1915; Robertson 1927).

(*f*) *Fission*

Division was observed in form *b*, the process lasting about half an hour. When first discovered the animal, which was unusually large, was situated at the mouth of the cup (see figure 6*a*) with its longer diameter placed transversely. It was gently agitating the coiled anterior flagellum, which may already at this stage have been double. The posterior flagellum then contracted, withdrawing the body to the base of the cup (figure 6*b*). Two flagella in addition to the posterior anchoring flagellum were now visible. A constriction then rapidly developed, starting at one side and extending across the body in a direction transverse to the long axis of the cup (figure 23, plate 26: figure 6*c*, *d*). In a few seconds the two halves were completely separated (figure 6*e*, *f*, *g*), and the posterior division product immediately became active and was observed attempting to relax the posterior flagellum and uncoil its anterior flagellum. This was prevented by the presence of the anterior individual, which remained immobile with one flagellum visible, and that tightly coiled. The anterior individual gradually changed its shape, becoming first oval (figure 6*f*), then

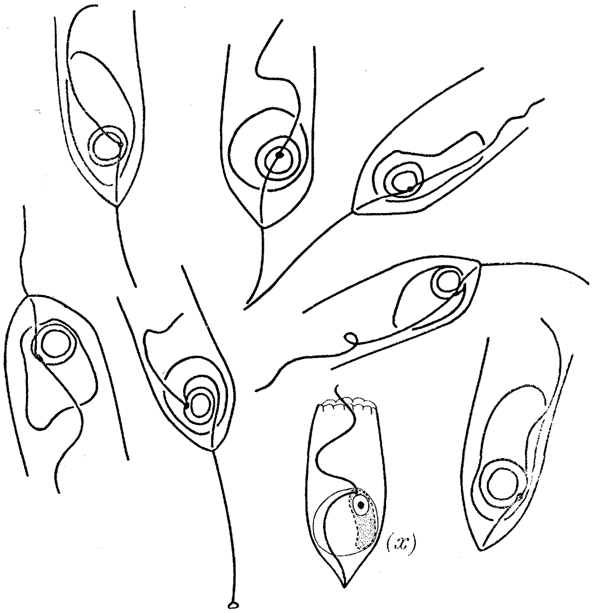

FIGURE 5. Sketches of form *b* showing the relation of nucleus, basal granule and flagella in specimens fixed in Schaudinn and stained with iron haematoxylin and orange G. (*x*) is a figure taken from von Prowazek: the stippled, sausage-shaped object is one of his 'chromidia' seen in side view.

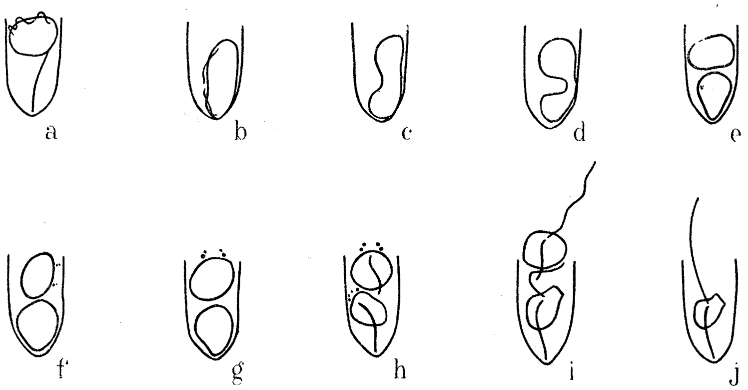

FIGURE 6. Stages in the division of form *b* (see also figures 23–25, plate 26).

shifting to the mouth of the cup and rounding off once more (figure 24, plate 26). In this position it was observed hesitantly uncoiling its flagellum. A few seconds later the second flagellum was seen, loosely trailing behind, and immediately afterwards the anterior flagellum was fully uncoiled and the animal moved out of the house.

The partner remaining behind (figure 25, plate 26) extended immediately, displaying a typical peristomial process of the *b* type and feeding in the typical manner. It was, however, unusually restless (perhaps owing to the continuous intense illumination necessary for photographic work) and shortly afterwards disintegrated. When fully extended it reached to about the middle of the cup, but its movements were too frequent for an exposure to be made.

These observations agree in most respects with those of Kent on *B. lacustris*. He also describes the cleavage furrow making its way across the middle of the body, and increasing in depth; but, according to him, the anterior division product leaves the cup immediately, and the posterior portion takes some little time to assume the form of a typical individual. He insists that the anterior product adopts the form and habits of a free-swimming monad, altogether unlike the parent and most nearly resembling some representative of Dujardin's genus *Heteromita*. This agrees with Penard's account of the sessile form when leaving the house as a biflagellate monad. Kent's observation of loricae containing spore-like bodies has not been repeated. It was frequently observed that the house contains a little detritus passively displaced by the movements of the animal (see figure 1 *b*), but there was never any indication of spore formation.

The observations recorded here also accord with Stein's figures of fission in *Bicoeca lacustris*, although the apparent loss of the anterior part of the house which he figures in one case was not observed.

Both Senn (1900) and Lemmermann (1914) question the occurrence of transverse fission, and it is conceivable that division is in fact longitudinal (parallel to the antero-posterior axis), rotation in the house giving the appearance of transverse fission.

4. The relationship between forms *a* and *b*

In the light of the observations on the forms *a* and *b* recorded here, it is suggested that James-Clark originally confused two species; the one, *B. lacustris*, corresponding to type *a*, the other corresponding to type *b*. The alternative to this assumption is that the two forms are indeed younger and older stages of the same organism, and that development involves not only a change in the shape of the house and the length of the pedicel, but also a change in the conformation of the peristomial process and its relationship to the flagellum. It must be supposed that this is converted from being a lip-like expansion of an incipient collar surrounding the base of the flagellum (*B. lacustris* James-Clark, *B. exilis* Penard) to a short, laterally placed, columnar process at the top of which the cytosome opens. No parallel case of metamorphosis such as this has been described in any other free-living protomonad.

Štolc (1887) redescribed the forms *a* and *b* and was the first to suggest that they are two species; he gave to *b* the name *B. vacillans*. Francé (1897) states, however, that *B. vacillans* is *B. lacustris* James-Clark, and it is clear that he regarded *B. vacillans* as the alleged older form described by James-Clark.* Štolc's figures (two of which are reproduced in figure 7) indicate clearly most of the differences between the two forms, including the contraction of the mouth of the cup on withdrawal in form *a*, but his delineation of the peristome is incorrect in both *a* and *b*. The posterior flagellum is continued forward in his figures beyond the insertion of the anterior flagellum and then curves backwards to join the peristome—Štolc having interpreted the contour of the peristome as a continuation of the posterior flagellum. He gives diagrams of ingestion and vacuole formation in the peristome. During division both products are shown with an anterior flagellum before fission is complete, and from his figures it appears that the original anchoring flagellum is retained by the more anterior division product, while the posterior one migrates to the mouth of the cup before developing a posterior flagellum. Štolc also gives a drawing of a newly attached flagellate (younger than those in figure 4 of this paper) without stalk or house-rudiment.

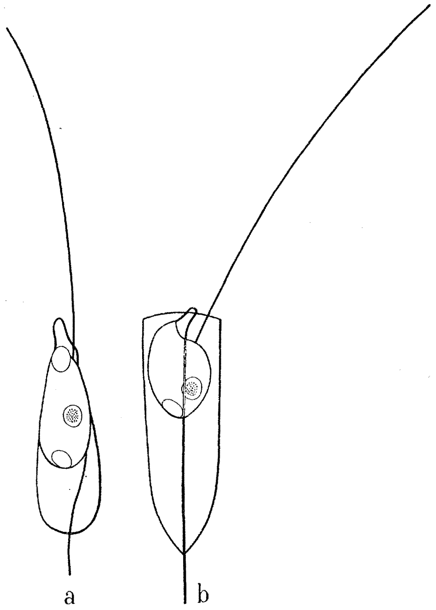

FIGURE 7. (*a*) *B. lacustris* James-Clark. (*b*) *B. vacillans* Štolc. Redrawn from Štolc (1887).

Against the view that *b* passes through a stage *a* in the course of development is my observation that immediately after division the individual remaining attached in the house has the typical peristome of *b*. Are we then to assume that the liberated

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* Perhaps because of Štolc's paper being in Czech, this suggestion has never, to my knowledge, been discussed since it was made. Francé's comment is tacit: *B. vacillans* (= *B. lacustris* James-Clark).

sister individual settles down and develops not into *b* but into *a*? Moreover, recently settled individuals (figure 4) have the long stalk characteristic of *b* rather than of *a* and possess a typical peristome before the house is complete.

Until the life history $a \to b$ has been confirmed, it seems advisable to place the forms *a* and *b* in separate species. *a* appears undoubtedly to be James-Clark's *B. lacustris*; *b* is indubitably *B. vacillans* Štolc.

The structure of the so-called peristome is different in each species of *Bicoeca*. We have already noted the differences between forms *a* and *b*; *B. exilis* Penard is in turn different from these and, as we shall see later, a marine species of the genus differs from all three fresh-water forms in this respect. On the basis of the structure of the peristome, form *b* might be referred to the colonial genus *Poteriodendron*; it differs from Stein's figures of *P. petiolatum* only in that the 'posterior contractile filament' is not terminal, as represented by Stein, but is a flagellum arising at the base of the anterior flagellum. Since, however, this would mean creating as many new genera as there are species of *Bicoeca* (inasmuch as the peristome is different in each species) it is proposed instead to revive Štolc's species, *B. vacillans*. For the sake of comparison, the characters of the two species are given side by side in table 1.

TABLE I. CHARACTERS OF *BICOECA LACUSTRIS* JAMES-CLARK, *B. VACILLANS* ŠTOLC AND *B. MARIS* N.SP.

	Species		
Character	*B. lacustris* James-Clark	*B. vacillans* Štolc	*B. maris* n.sp.
Shape of body	Pear-shaped	Ellipsoidal to sub-spherical	Truncately ellipsoidal
Shape of peristome	Leaf-like	Columnar	A blunt hillock to one side of the truncate anterior end
Shape of cup	Oval; rim closely embracing body; when body is withdrawn rim contracts	Cylindrical, tapering posteriorly	Cylindrical, rounded posteriorly
Texture of cup	Readily visible in life	Readily visible in life	With difficulty visible in life
Stalk	Absent or extremely short	As long as or longer than the cup	Absent
Carriage of anterior flagellum when retracted	Neatly coiled	Neatly coiled	Irregularly coiled
Insertion of posterior flagellum in cup	Terminal, at the point where the long axis passes through the base of the cup	As in *B. lacustris*	In many specimens subterminal, to one side of the long axis
Contractile vacuole(s)	One, situated posteriorly	One, situated posteriorly	Not observed

5. *Bicoeca kepneri* Reynolds

A form closely resembling *a* has been described as a new species, *B. kepneri*, by Reynolds (1927). He differentiates this form from *B. lacustris* on the grounds: (1) that James-Clark's form showed a preference for *Zygnema* filaments whereas his form was attached to *Oedogonium*; (2) *Bicoeca lacustris* is tinted yellow (James-Clark) while *B. kepneri* is greyish-white; (3) the lorica of *B. lacustris* is 5–10 μ longer than that of *B. kepneri*; (4) *B. kepneri* has but a single contractile vacuole while *B. lacustris* has two (see p. 457); (5) the anterior end of *B. lacustris* is extended into a large lip while that of *B. kepneri* is developed into a 'thin sheet of protoplasm' (the difference is scarcely obvious); (6) the mouth of the lorica is circular in *B. lacustris*, but is extended beneath the peristomial protoplasmic sheet to form a 'peristomial flap' in *B. kepneri*; (7) *B. lacustris* has a definite cytostome and cytopyge while *B. kepneri* shows neither. With regard to the last point it is not clear what Reynolds understands by a definite cytostome, since he describes the ingestion of food particles at one point only, that is, between the sheet of protoplasm and the base of the flagellum.

Reynolds observes that Bütschli's account of *B. lacustris* only differs from *B. kepneri* in that he does not describe the 'peristomial flap', and that he records a tendency to form colonies. Of the differences between *B. lacustris* and *B. kepneri* only (6), in my opinion, is worthy of serious consideration. According to Reynolds, Stein's figures suggest the relation between lorica and peristome described by him, but Stein 'fails to point out the fact that the protoplasmic sheet is actually attached to the extended wall of the test. Indeed he shows it distinctly unattached in one of his drawings.' This is misleading. Stein does not suggest in his brief legend that the cup itself is drawn out into a lip-like process, even though his drawing gives this impression. The process is labelled peristome, in each case, as if it were a single, and not a double, structure. Quite what the drawing to which Reynolds alludes is supposed to represent is not clear, but even here Stein marks the reflected lip as the peristome, whereas Reynolds would interpret it as part of the cup.

Unfortunately I did not see Reynolds's paper until my supply of *B. lacustris* was exhausted; certainly I never observed any one-sided extension of the cup and always supposed that the continuation of the wall of the cup along the peristome in Stein's figure was due to an error. In view of the considerable distance between the retracted body and the constricted mouth of the cup (seen in figure 15, plate 26) it is difficult to imagine that a protoplasmic membrane connecting the two should have escaped notice. It would have been instructive had Reynolds given diagrams of some of the older loricae, which he describes as so rigid that they are vacated by their tenants.

Assuming that type *a* is that most correctly styled *B. lacustris*, it is apparent that Reynolds's form is very closely related to this; the difference between *B. lacustris* and *B. kepneri* is much less than that between *B. lacustris* and *B. vacillans*. In my experience the rim of the cup can only be distinguished with certainty in *B. lacustris* when the body is retracted. Until I have an opportunity of re-examining type *a* I do not feel inclined to accept *B. kepneri* as a distinct species.

Reynolds's observations on the relation between nucleus and flagella in fixed specimens are essentially in agreement with those on *B. vacillans* and on a new species, *B. maris* (see below), recorded here. He finds that the two flagella arise from the nucleus at an angle 'of 40–80° of arc from each other'. In some specimens they appear to arise from basal granules in or near the region of the nucleus surrounding the karyosome. His figures of fixed specimens are strikingly similar to those in figures 26–28, plate 26, and lend support to the view (to be discussed later, p. 470) that the structure of the nucleo-flagellar complex in the Bicoecidae justifies the separation of this family from the Bodonidae.

Several other points in Reynolds's account are worthy of attention. He states, for example, that the free-swimming division-product has only a very short posterior flagellum, scarcely projecting from the body. Settling is said to occur after an hour or so. The posterior flagellum then lengthens and secretes round itself a sheath (the peduncle); the posterior flagellum is thus supposed to run the entire length of the stalk. Of this I have certainly seen no evidence in *B. vacillans*, where admittedly the stalk is considerably longer than in *B. lacustris* (where it may be absent) or in *B. kepneri*. If the stalk were hollow in this way one might expect the posterior flagellum to disappear into the stalk during contraction. This does not happen in *B. vacillans*; on the contrary, the posterior flagellum is thrown into a coil when the body is withdrawn.

6. *Bicoeca maris* n.sp.

The species of *Bicoeca* to be described here was found in a culture of *Uronema marinum* Dujardin in peptone and sea water. It differs in many important respects from other species hitherto described, and since it was present in comparatively large numbers it has been possible to verify many points in the structure of the genus which could not be sufficiently investigated in *Bicoeca lacustris* and *B. vacillans*. The appearance of the organism is shown in figure 8 and figures 29–34, plate 26. The house is without a stalk and is much more tenuous than that of *B. lacustris* or *B. vacillans*. The body is broad anteriorly and rounded posteriorly and lies about halfway along the length of the cup. There is no lip as in *B. lacustris* or columnar peristome as in *B. vacillans*, but the truncated anterior end is often raised at one side into a blunt hillock, as in figure 8 and figures 29 and 30, plate 26. The form of the front end is not constant but varies in different individuals and in the same individual in time.

The two flagella may appear to be continuous (figures 29 and 30, plate 26) and certainly arise together. This is clear in newly settled individuals and in what I suppose to be the free-swimming phase (figure 32, plate 26). Both flagella are remarkably stout and conspicuous. Contraction of the posterior flagellum withdraws the body to the base of the cup as in other species. The anterior flagellum, however, behaves in a manner entirely different from that of other species. It is not regularly coiled on retraction, nor does uncoiling proceed as in *B. lacustris* and *B. vacillans*. It is usually carried partly flexed (see figure 29, plate 26), that part which is visible being stationary. No contractile vacuole has been observed. Occasionally a highly refractive body about one-third the diameter of the cell has been seen in the neighbourhood of the insertion of the flagella (see figure 8) and has been presumed to be the nucleus. The ingestion of food has not been observed.

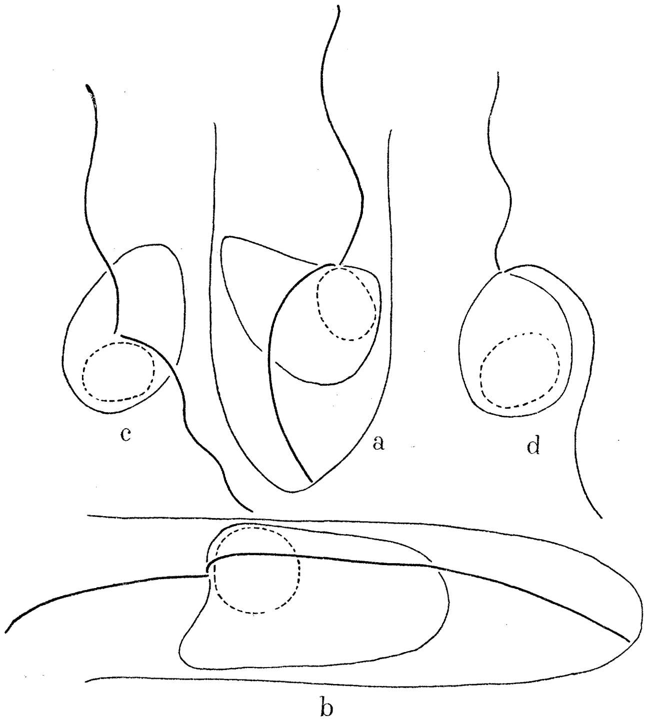

FIGURE 8

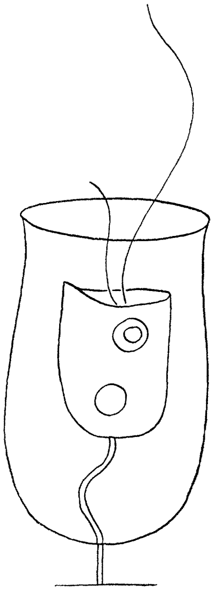

FIGURE 9

FIGURE 8. (*a*) and (*b*) Sketches of *B. maris* n.sp. showing range in shape of body and cup; outline of nucleus marked with broken line. Note somewhat lateral insertion of posterior flagellum in wall of cup and slight development of peristome. (*c*) and (*d*) Free-swimming individuals supposed to have been set free from *B. maris*.

FIGURE 9. *B. pocillum* Kent, redrawn from Kent (1880–1).

It has not been possible to identify this form with any species of marine *Bicoeca* hitherto described. *B. gracilipes* James-Clark, found by that observer on *Sertularia*, has a peristome resembling that of *Bicoeca lacustris*; the body is oval, and the animal lives in a slender calyx with a long stalk. *B. tenuis* Kent, from filamentous algae and *Sertularia*, has a relatively narrow, shortly stalked house, quite different from the form described here. There is, however, a marked resemblance between the peristome of *Bicoeca pocillum* Kent, found by Kent on hydroids and polyzoans, and that of the marine form with which we are here concerned. Kent states that the house is cup-like or subcylindrical, and the pedicel short, rarely half as high as the house. The body is described as subovate or calceolate, rounded posteriorly, the anterior margin excavate, produced on one side as a broad, flattened lip-like process; one of his figures is shown in figure 9 of this paper. He shows, however, as in all species of *Bicoeca* described by him, two anterior flagella.

Reference has already been made (see p. 460) to the description given by von Prowazek (1903) of the relations between nucleus and flagella in an unnamed marine species of *Bicoeca*. His figure of a fixed preparation shows a non-pedicellate calyx, the rim of which is slightly crenate (see figure 5*x*). I have not observed this in any of my specimens, but nevertheless believe it possible that von Prowazek's form may be identical with the form described here.

In permanent preparations, fixed with Champy's fluid and with Schaudinn's fluid (without acetic acid) and stained with Heidenhain's iron haematoxylin and orange G, the house is clearly defined (see figure 31, plate 26) and in no case stalked. Several fixed and stained specimens showed what had already been seen in the living forms, namely, that the posterior flagellum is, in many cases, not attached to the base of the cup, but is inserted somewhat laterally (figure 8). The Champy-fixed specimens retained the form of the organism in life (see figure 34, plate 26).

A careful examination of some fifty specimens revealed no constant structure corresponding to von Prowazek's chromidia. In two or three cases the nucleus lies in a region of protoplasm which, under the conditions of fixation and washing adopted (24 hr. fixation in Champy's fluid, 24 hr. washing in running tap water) retained some of the osmium and appeared to differ from the surrounding and more vacuolated protoplasm. In the majority of cases, however, no trace of von Prowazek's sausage-shaped bodies forming a girdle round the nucleus was visible. The nucleus, as in *B. vacillans* (figure 28, plate 26), has a distinct karyosome, represented in von Prowazek's figure (compare figure 5*x* and figures 31, 33, and 34, plate 26).

As in the case of *B. vacillans* no trace of a parabasal comparable to that of the Bodonidae could be found. In most cases where the details could be seen with certainty the two flagella appear to spring from a single basal granule closely applied to, or in the immediate neighbourhood of, the nucleus. In one or two cases the anterior flagellum appeared to be connected with the karyosome (figure 33, plate 26), and in others a common axial filament appeared to run some little distance over the surface of the nucleus to terminate in a granule not closely applied to the nucleus.

It can be said with certainty, however, that there is no chromidium as described by von Prowazek, and that there is no parabasal comparable to that of the Bodonidae. Comparing this form with the preparations of *B. vacillans*, it was found that no suggestion of a posterior prolongation of a common axial filament was visible in the latter. Since there was no trace of a second anterior flagellum in the form described here, it is proposed to regard it as a new species, in spite of the resemblance, in certain respects, to *B. pocillum* Kent.

It is proposed to call this species *B. maris*. The diagnosis is as follows: peristome but slightly developed; house not stalked, visible with difficulty in life; anterior flagellum loosely and irregularly coiled on retraction; no contractile vacuole; body 5 μ long; house 10 μ long, 5 μ wide; in sea water. For the sake of comparison, the characters of *B. maris* are summarized along with those of *B. lacustris* and *B. vacillans* in table 1.

7. The position of the Bicoecidae in the Protomonadina Blochmann

It was stated initially that the most satisfactory definition of the Bicoecidae Stein is that given by Doflein and Reichenow (1929): 'Gehäusebildende kleine Formen mit zwei Geisseln, einer langen am Vorderende inserierenden, nach vorn ragenden Hauptgeissel und einer nach hinten gerichteten, zum Haftorganell ausgebildeten Schleppgeissel (Stielgeissel)...Neben der Geisselbasis ein rüsselförmiger, manchmal kragenartiger Plasmafortsatz....' Recently, however, Kudo (1939) has extended the family Bicosoecidae Poche (1913) to include an unfortunate collection of profoundly dissimilar genera: *Bicosoeca* (*sic*) James-Clark, *Salpingoeca* James-Clark, *Codonoeca* James-Clark, *Diplosigopsis* Francé, *Histiona* Voigt, *Poteriodendron* Stein and *Lagenoeca* Kent. Such a procedure is only excused by the vagueness of current ideas on the affinities of the genus *Bicoeca*.

The Bicoecidae have been regarded as closely related to the Craspedomonadinae on the one hand, and to the Bodonidae on the other. Klebs (1893) regarded them as a link between the Protomastiginea bearing one flagellum and the Craspedomonadaceae, and Francé (1897) included them in his book on the craspedomonads. Štolc (1887) and Lauterborn (1899) appear to have been the first to make a frank comparison of the anchoring filament with a trailing flagellum comparable to that of the Heteromastigoda Bütschli. Senn (1900) raised the question whether it is better to regard the family as derived from the Oicomonadaceae or from the Bodonaceae; in the latter case the formation of collar or peristome in the Bicoecidae must be regarded as a parallel development to collar formation in the Craspedomonadaceae. He concludes, however, that until all details of structure have been cleared up, the family must be regarded as transitional to the craspedomonads. Von Prowazek (1903) remarks that 'die Bicoecinen oder Bicoecaceaen scheinen...durch das Vorhandensein von zwei Geisseln (der sogenannte Stiel ist nur eine modifizierte Schleppgeissel) mehr mit den Monadaceaen die auch eine Nebengeissel besitzen, als mit den Oikomonaden verwandt zu sein'. Hartmann and Chagas (1910) omit the family Bicoecaceae from their classification of the Protomonadina, transferring its genera to the family Bodonaceae. This they do on the authority of Lauterborn and von Prowazek (see above). Supposing that the passage from von Prowazek quoted above is that on which their decision is based (I am unable to find any other reference to the subject in von Prowazek's paper), it is incorrect to say as they do: 'die Bicosöcaceen sind nach... von Prowazek Bodonaceen, da der sogenannte Stiel nur eine umgewandelte Schleppgeissel darstellt....' Lemmermann (1914) includes the Bicoecaceae in a list of forms with a single flagellum, although he describes the contractile filament as a *Schleppgeissel*, obviously thinking in terms of bodonid organization. Nevertheless he includes in the Bicoecaceae the genus *Histiona* Voigt, which lacks an anchoring flagellum. Penard (1921) figures *Bicoeca exilis* leaving its house as a *Bodo*-like flagellate; on the other hand what I have supposed to be the free-swimming phase of *Bicoeca maris* is not particularly *Bodo*-like (figure 8 and figure 32, plate 26). Doflein and Reichenow (1929) remark that owing to the presence of a trailing flagellum used as an organ of attachment many authors group the Bicoecidae with the Bodonidae. Kudo (1939), however, comments on the nature of the anchoring, contractile filament as follows: 'protoplasmic body anchored to base by a cytoplasmic filament (flagellum?)'.

In my opinion the Bicoecidae are not to be regarded as particularly closely related either to the Craspedomonadinae or to the Bodonidae. The connexion between nucleus and flagella in the Bicoecidae recalls the condition depicted by Burck (1909) in a craspedomonad, *Salpingoeca amphorideum* James-Clark: the single flagellum terminates in a blepharoplast, closely applied to the nucleus. In the related genus *Codonosiga*, however, the blepharoplast is not in contact with the nucleus.

While it is true that in certain species of *Bicoeca* the lip occasionally resembles a rudimentary collar (as in *B. exilis* Penard), the peristomial process in *B. vacillans* or the small hillock of protoplasm in *B. maris* cannot be compared with such a structure. It cannot be held, therefore, that the genus as a whole foreshadows craspedomonad organization, any more than do various species of *Monas*.

Again, the carriage and movement of the anterior flagellum in the Bicoecidae offer no similarity to the condition in the Craspedomonadinae, and in any case the anchoring filament present in certain craspedomonads is not a flagellum. It will be remembered that Grassé excludes the Craspedomonadinae altogether from the Protomastigina on the grounds that the mode of division in this family is unique.

If we accept Grassé's view that the structure of the nucleo-flagellar complex is of fundamental classificatory importance, it is impossible to group together the families Bicoecidae and Bodonidae, since the organization of this complex in the Bicoecidae differs considerably, as we have seen, from that in the Bodonidae. Moreover, should it be shown in the future that the presence of an accessory anterior flagellum is a constant feature in certain members of the family, this would provide yet another reason for keeping separate the families Bicoecidae and Bodonidae.

At the moment, therefore, it seems inadvisable to attempt to group the Bicoecidae with any other family of the Protomonadina.

I am deeply indebted to Miss M. Mare who supplied me with the original culture of *Uronema marinum* containing the new marine species of *Bicoeca*.

I wish to express my gratitude to Mr Clifford Dobell, F.R.S., for his many kindnesses and invaluable criticism, and to Dr A. Bishop, Dr M. Robertson and Professor E. G. Pringsheim for the help in various ways which they have afforded me.

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DESCRIPTION OF PLATE 26

FIGURES 10–18 and 30–33 were taken with a 2 mm. apochromatic objective, × 95, n.a. 1·32, and a periplanatic eyepiece, × 10; figures 19–29 and 34 were taken with the same objective and a × 20 eyepiece. The final magnifications are given below. To facilitate reproduction the deposit of silver on the print has been strengthened, where necessary, with a soft graphite pencil (4 B). The features visible in the original photographs are shown in the drawings to the right of the photographs. *a.f.* anterior flagellum; *p.f.* posterior flagellum; *c.* cup; *n.* nucleus; *p.* peristome.

FIGURES 10–15. Type *a* (*Bicoeca lacustris* James-Clark). Magnification × 730.

FIGURE 10. Shows the anterior flagellum, the lip, and the ovoid house embracing the posterior end of the body.

FIGURE 11. Shows the lip in a different position, food vacuoles, and the shape of the house.

FIGURE 12. Shows the lip and several food-vacuoles.

FIGURE 13. Shows the base of the house, and the posterior flagellum running forward over the body to its anterior insertion.

FIGURE 14. The same; the organism has shifted; body not in focus.

FIGURE 15. Shows the body retracted and the mouth of the house constricted.

FIGURES 16–28. Type *b* (*Bicoeca vacillans* Štolc). Figures 16–18, × 730; figures 19–28, × 1460.

FIGURE 16. Shows the anterior flagellum (stationary portion) and the truncated peristome.

FIGURE 17. Shows a recently formed food-vacuole below the surface of the peristome; the anterior flagellum and part of the house are visible.

FIGURE 18. The house and the posterior flagellum are visible (note the slight spiral twist of the incompletely extended posterior flagellum). The peristome is seen as a short, solid column.

FIGURE 19. A large food vacuole is visible. Note the co-linearity of the anterior and posterior flagella.

FIGURE 20. The nucleus is visible at the anterior end of the posterior flagellum. At this point a darker spot may be basal granule + parabasal. Observe the irregular border of the peristome (on the right).

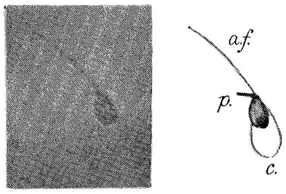
FIGURE 21. The course of the posterior flagellum is shown particularly clearly. Note the conspicuous particle near the anterior end of the flagellum.

FIGURE 22. In this individual the peristome is drawn out into a point as in Stein's figures of *Poteriodendron petiolatum*.

FIGURE 23. Division is just complete: the anterior flagellum of the upper division product lies coiled and to the right. It is visible in optical section as three dots.

FIGURE 24. The anterior division product has rounded off and is preparing to leave the house; the anterior flagellum is still coiled.

FIGURE 25. The anterior division product has departed, leaving the sister flagellate behind (contracted at the base of the house).



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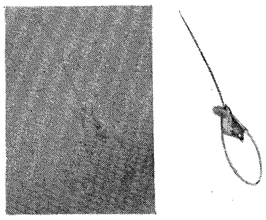

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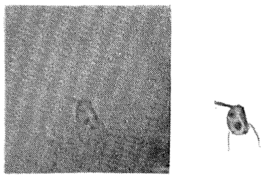

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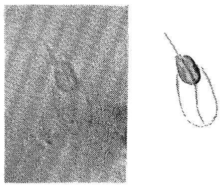

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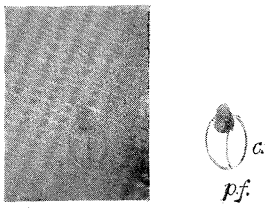

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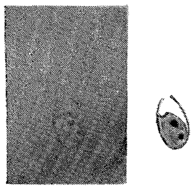

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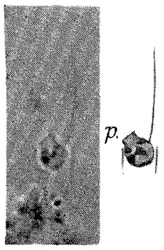

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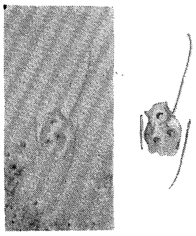

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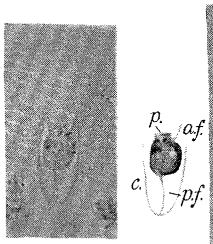

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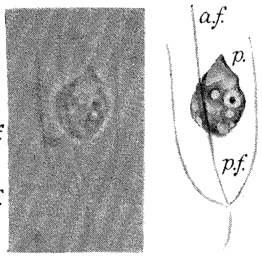

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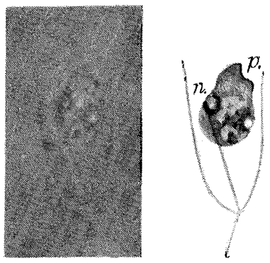

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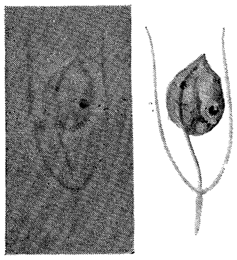

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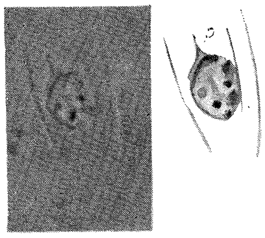

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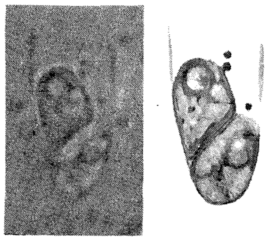

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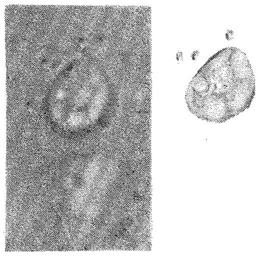

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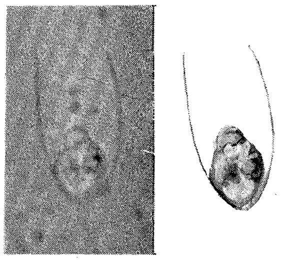

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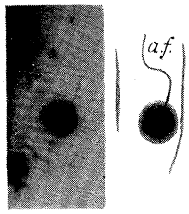

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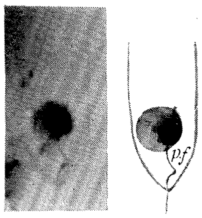

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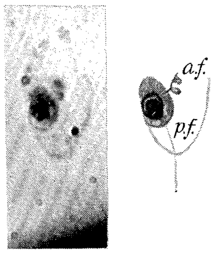

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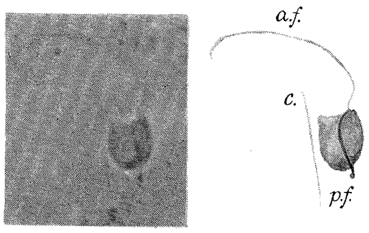

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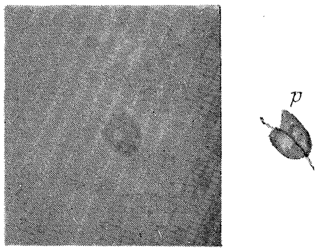

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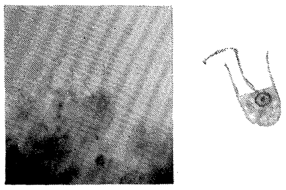

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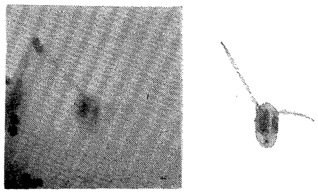

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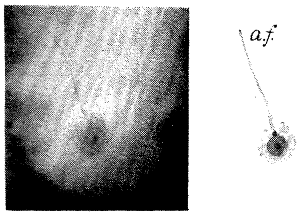

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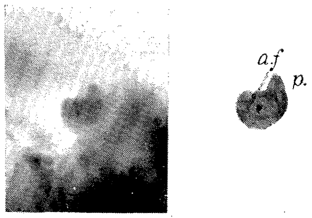

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Figures 26, 27. These are two photographs, at slightly different levels of focus, of the same individual (fixed with Schaudinn's fluid, stained with iron haematoxylin and orange G).

Figure 26. Shows the posterior end of the anterior flagellum and the anterior end of the posterior flagellum continuous across the nucleus.

Figure 27. Shows the posterior anchoring flagellum and the posterior end of the anterior flagellum.

Figure 28. A permanent preparation fixed with Schaudinn's fluid and stained with iron haematoxylin and orange G. The nucleus is visible. Note the central karyosome, containing a densely staining body, and the outer zone. Both anterior and posterior flagella are visible.

Figures 29–34. *Bicoeca maris* n.sp. Magnification × 1000. Figures 31–34, fixed and stained specimens.

Figure 29. General view of flagellate; note carriage of anterior flagellum.

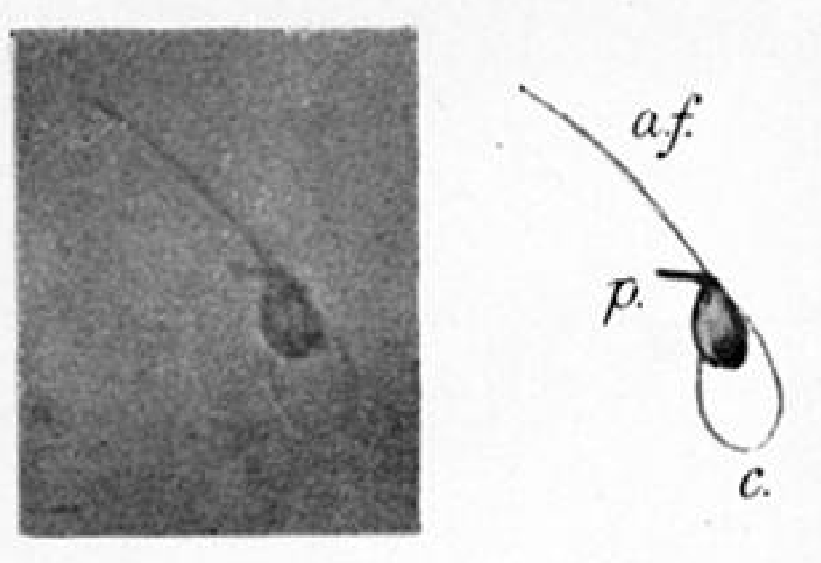
Figure 30. Shows apparent continuity of anterior and posterior flagella; peristome characteristic.

Figure 31. Shape of cup and insertion of anterior flagellum shown.

Figure 32. Supposed free-swimming phase.

Figure 33. Newly settled individual; cup not yet secreted; basal granule clear and rhizoplast to karyosome suggested.

Figure 34. Newly settled individual; cup not yet secreted; anterior flagellum, basal granule and nucleus clear; peristomial eminence shown.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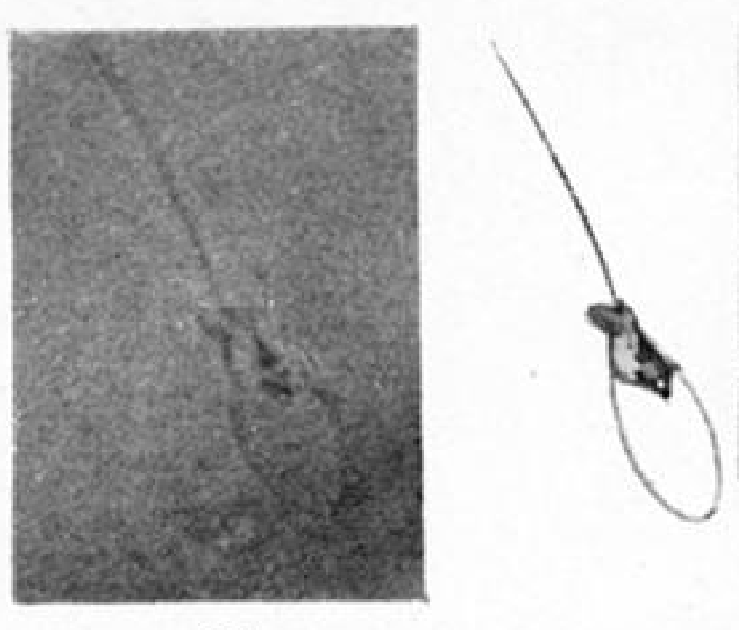
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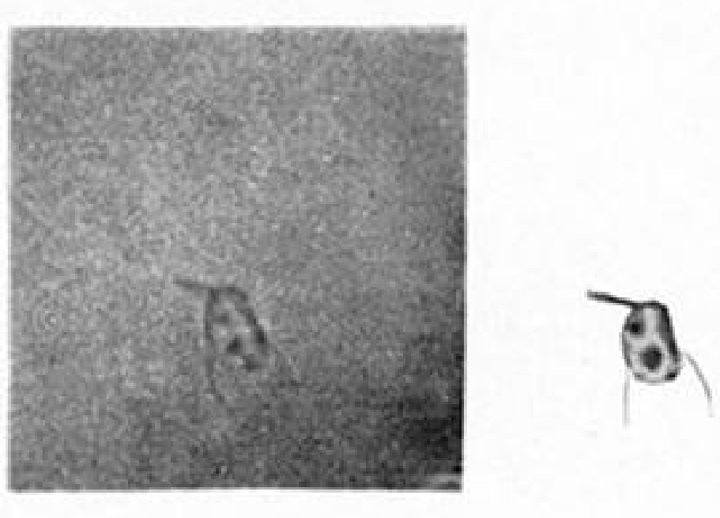
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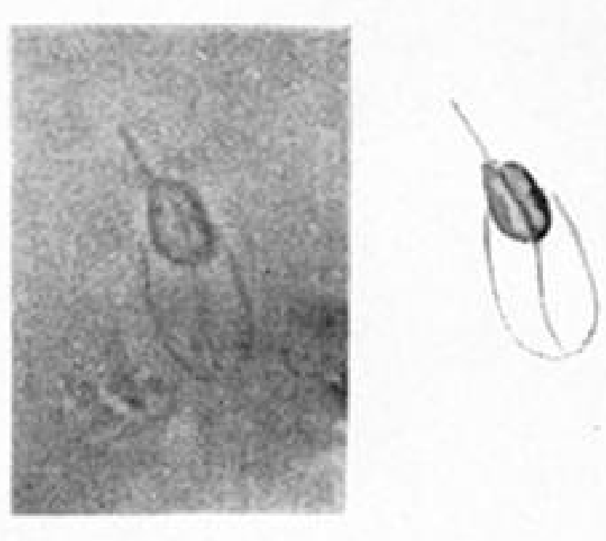
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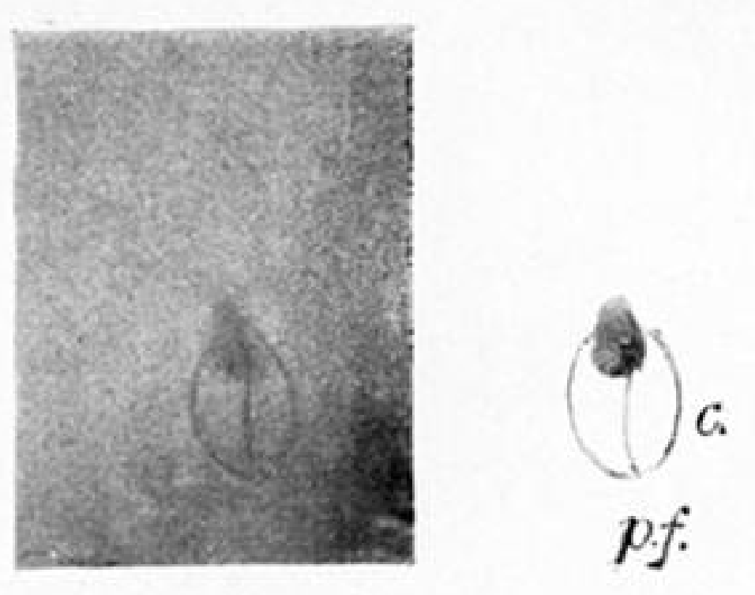
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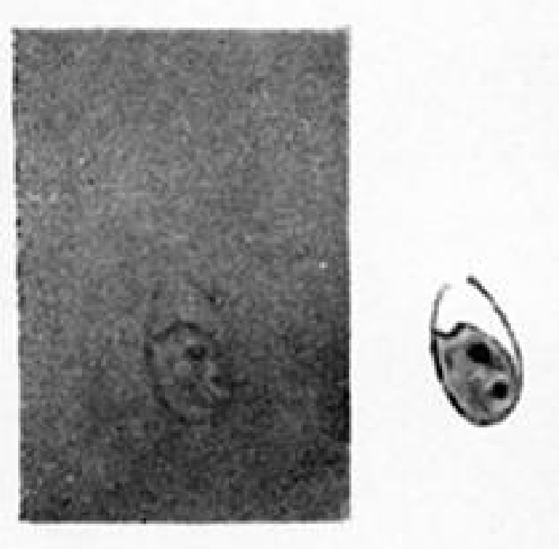
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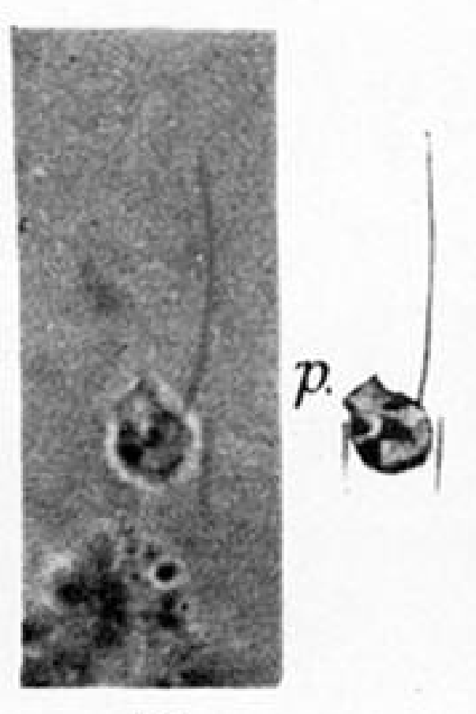
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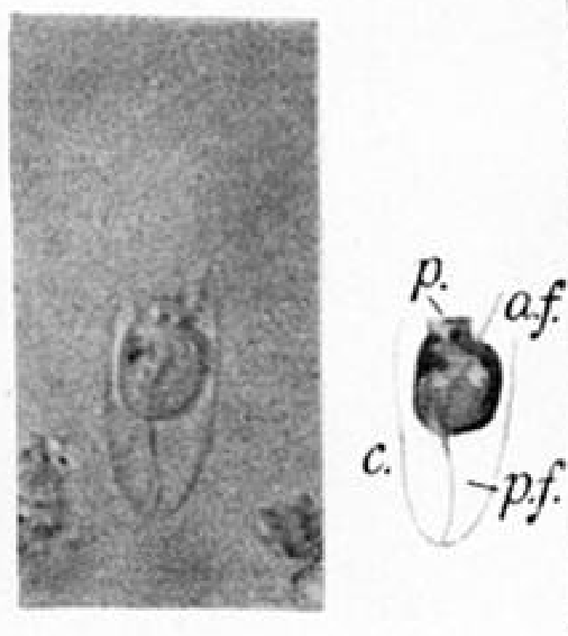
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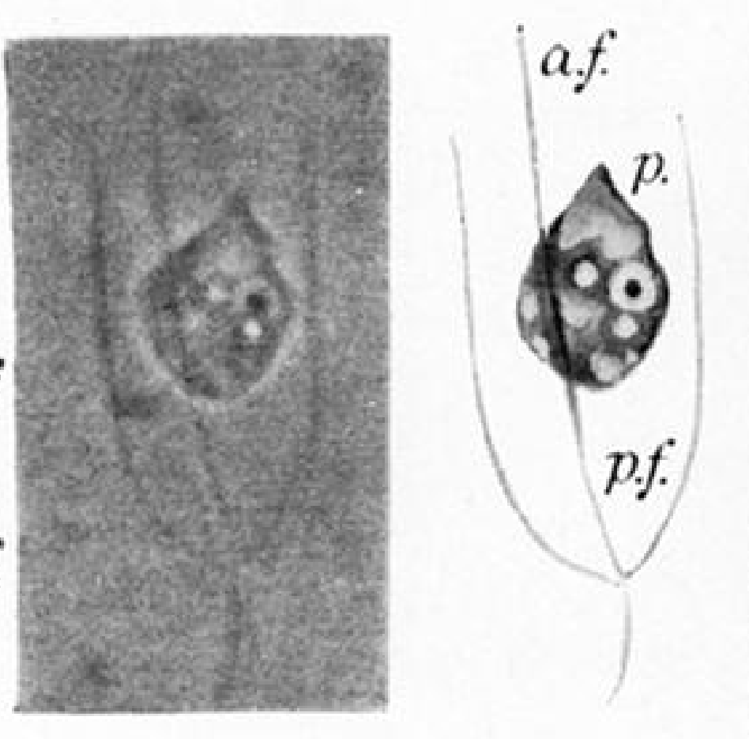
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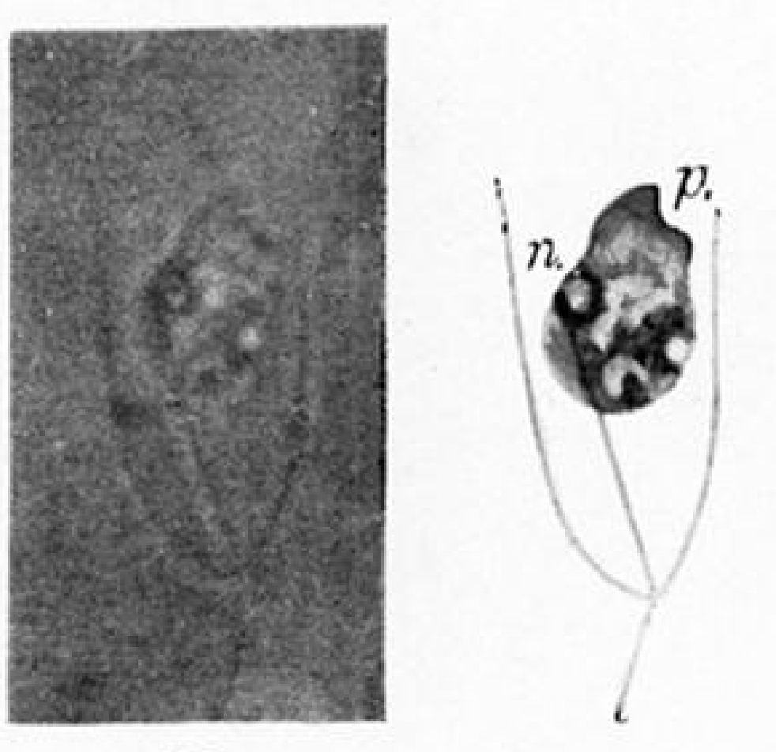
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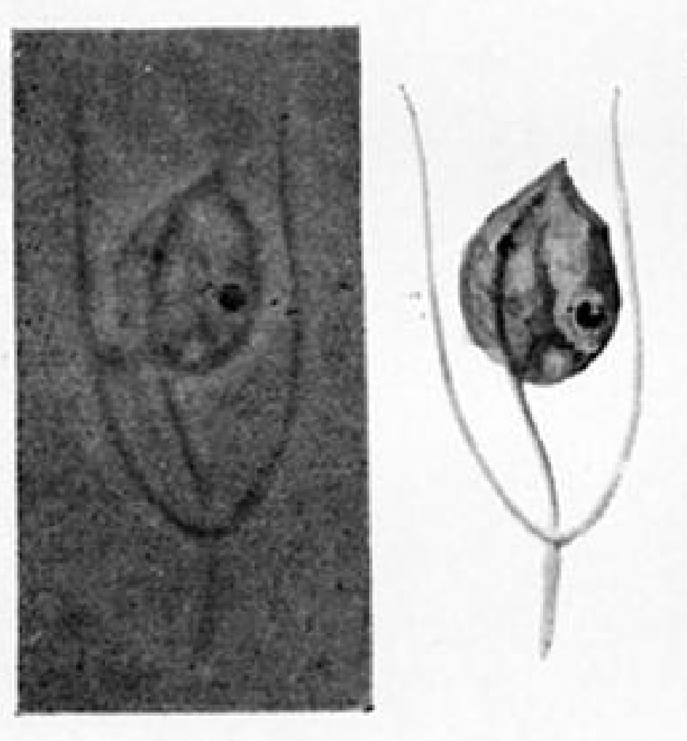
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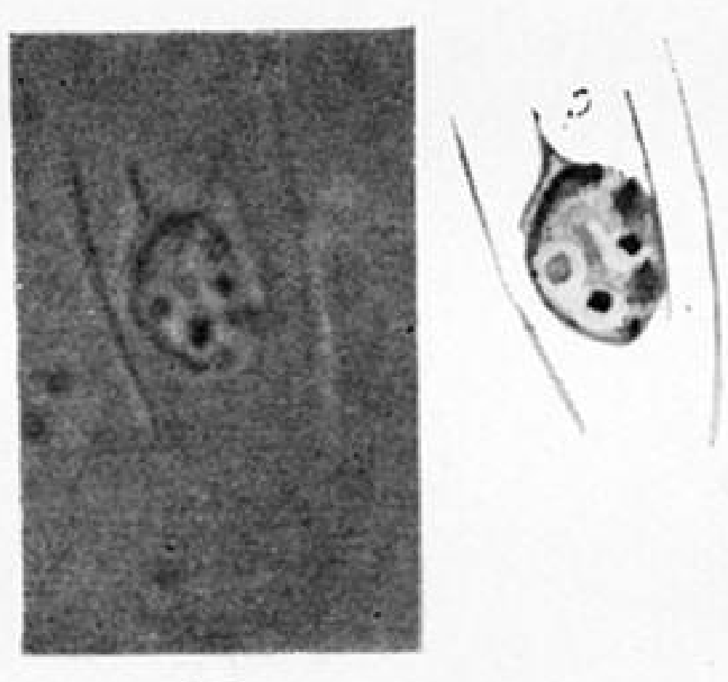
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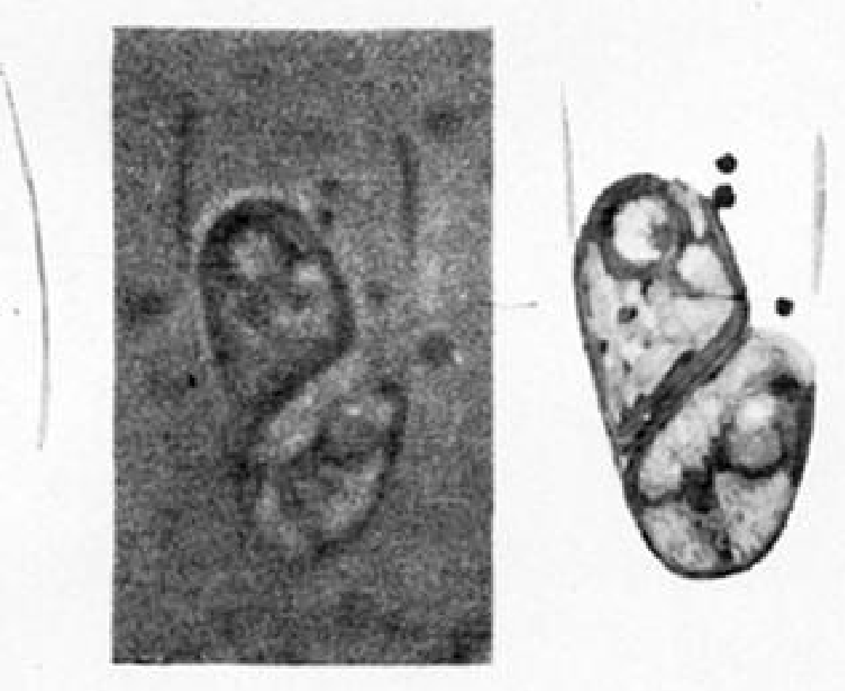
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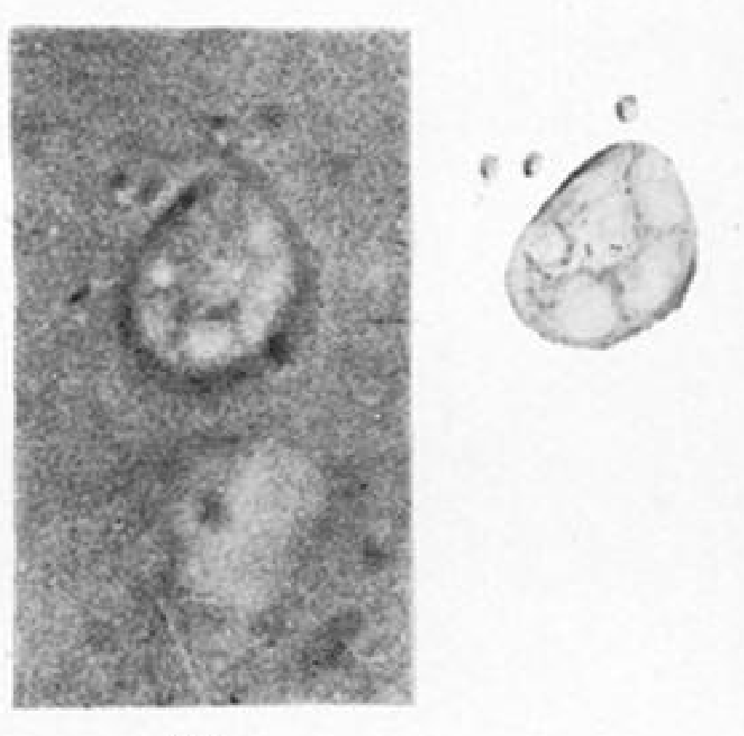
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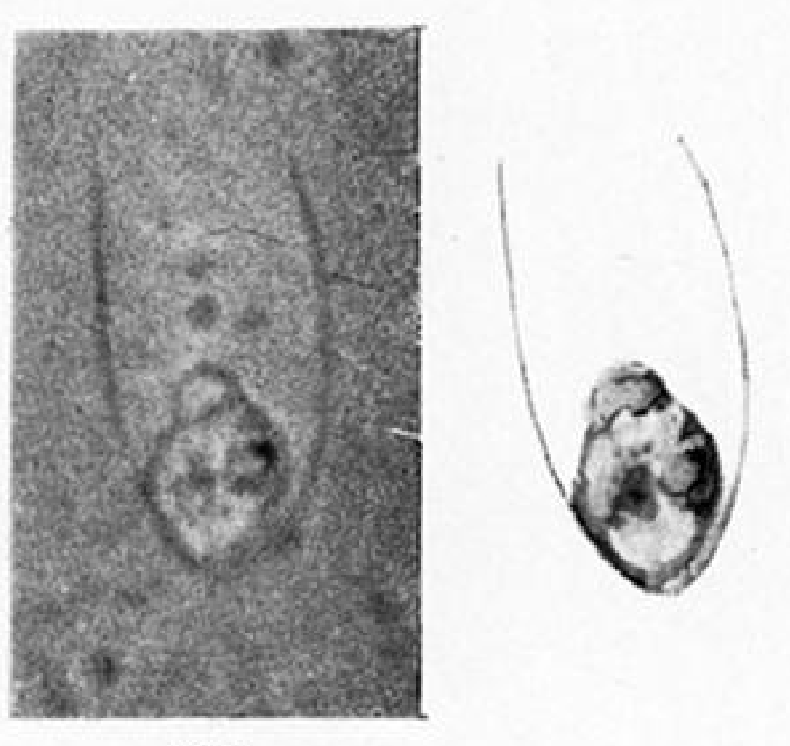
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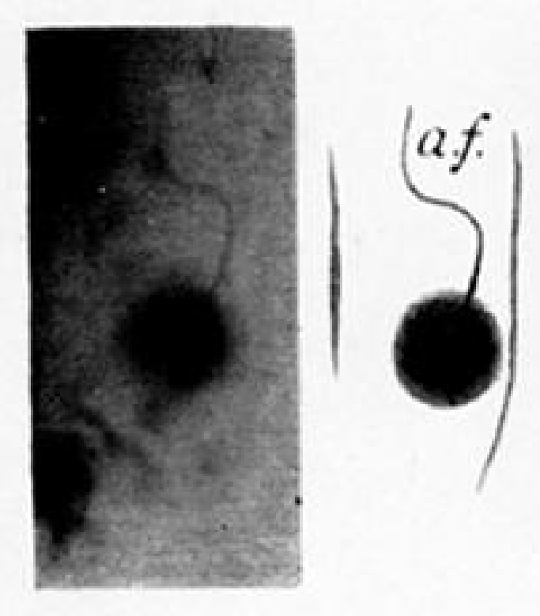
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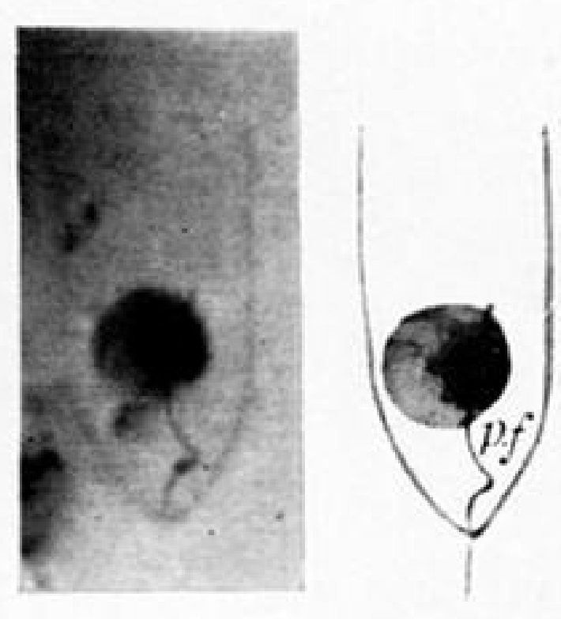
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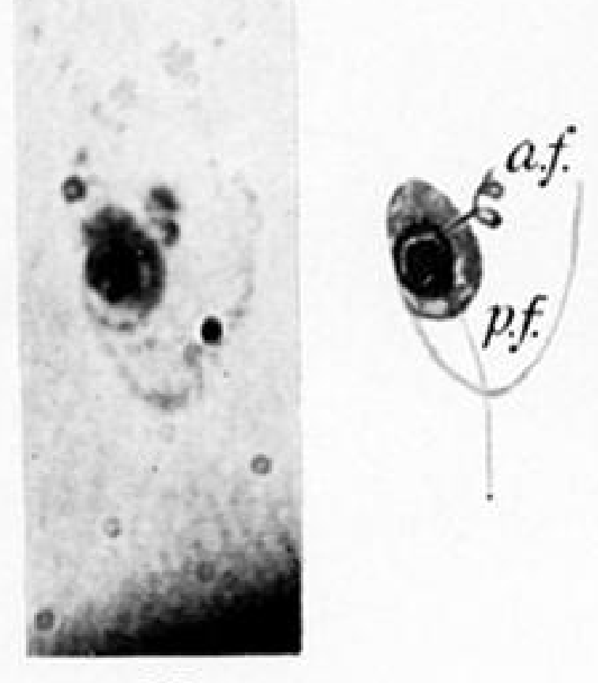
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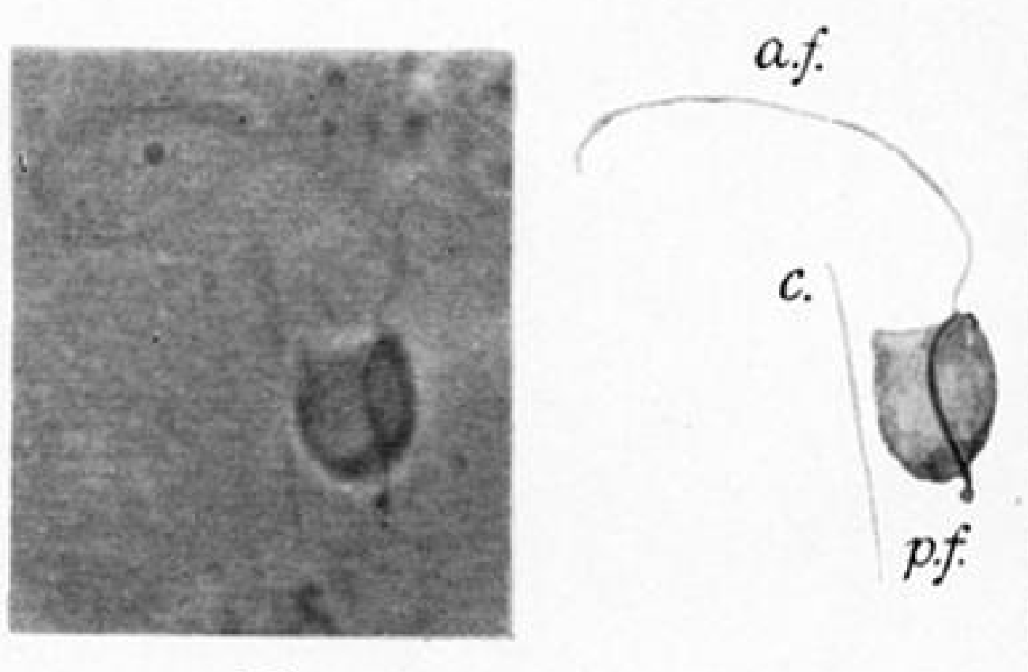
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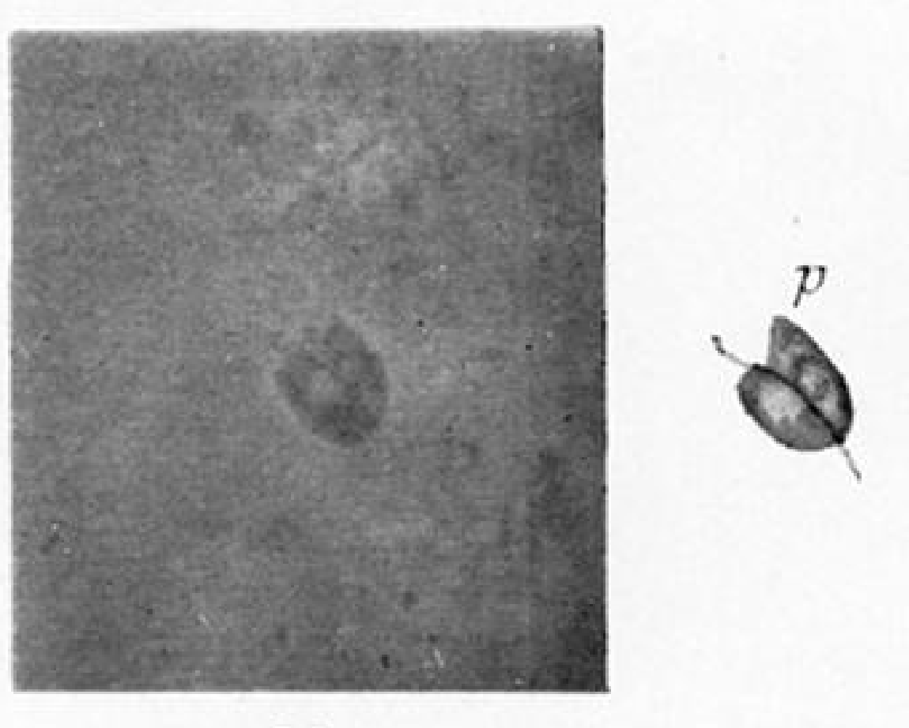
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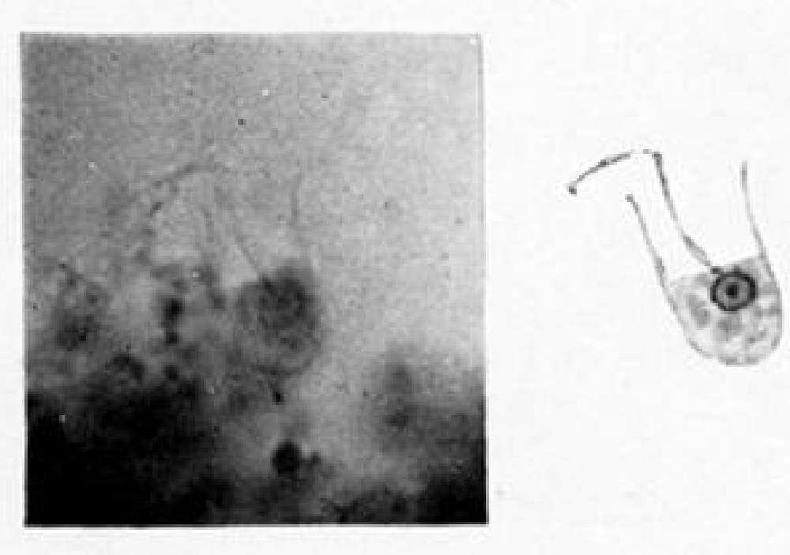
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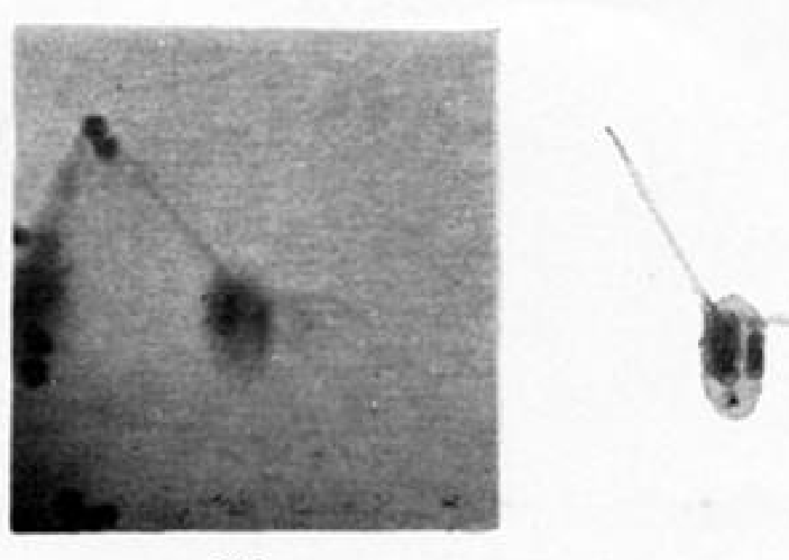
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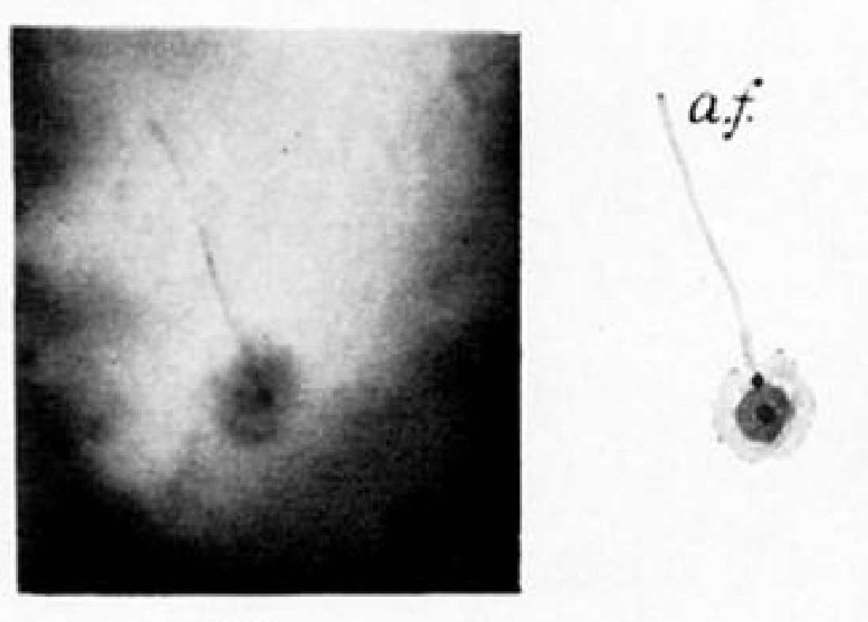
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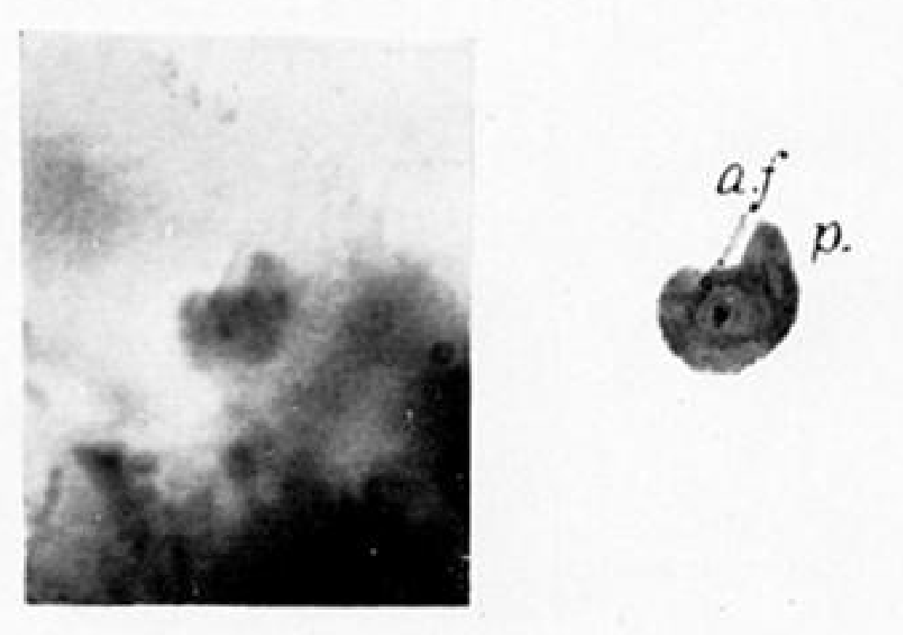
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Description of Plate 26

Figures 10–18 and 30–33 were taken with a 2 mm. apochromatic objective, × 95, n.a. 1·32, and a periplanatic eyepiece, × 10; figures 19–29 and 34 were taken with the same objective and a × 20 eyepiece. The final magnifications are given below. To facilitate reproduction the deposit of silver on the print has been strengthened, where necessary, with a soft graphite pencil (4 B). The features visible in the original photographs are shown in the drawings to the right of the photographs. *a.f.* anterior flagellum; *p.f.* posterior flagellum; *c.* cup; *n.* nucleus; *p.* peristome.

Figures 10–15. Type *a* (*Bicoeca lacustris* James-Clark). Magnification × 730.

Figure 10. Shows the anterior flagellum, the lip, and the ovoid house embracing the posterior end of the body.

Figure 11. Shows the lip in a different position, food vacuoles, and the shape of the house.

Figure 12. Shows the lip and several food-vacuoles.

Figure 13. Shows the base of the house, and the posterior flagellum running forward over the body to its anterior insertion.

Figure 14. The same; the organism has shifted; body not in focus.

Figure 15. Shows the body retracted and the mouth of the house constricted.

Figures 16–28. Type *b* (*Bicoeca vacillans* Štolc). Figures 16–18, × 730; figures 19–28, × 1460.

Figure 16. Shows the anterior flagellum (stationary portion) and the truncated peristome.

Figure 17. Shows a recently formed food-vacuole below the surface of the peristome; the anterior flagellum and part of the house are visible.

Figure 18. The house and the posterior flagellum are visible (note the slight spiral twist of the incompletely extended posterior flagellum). The peristome is seen as a short, solid column.

Figure 19. A large food vacuole is visible. Note the co-linearity of the anterior and posterior flagella.

Figure 20. The nucleus is visible at the anterior end of the posterior flagellum. At this point a darker spot may be basal granule + parabasal. Observe the irregular border of the peristome (on the right).

Figure 21. The course of the posterior flagellum is shown particularly clearly. Note the conspicuous particle near the anterior end of the flagellum.

Figure 22. In this individual the peristome is drawn out into a point as in Stein's figures of *Poteriodendron petiolatum*.

Figure 23. Division is just complete: the anterior flagellum of the upper division product lies coiled and to the right. It is visible in optical section as three dots.

Figure 24. The anterior division product has rounded off and is preparing to leave the house; the anterior flagellum is still coiled.

Figure 25. The anterior division product has departed, leaving the sister flagellate behind (contracted at the base of the house).

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Figure 32. Supposed free-swimming phase.

Figure 33. Newly settled individual; cup not yet secreted; basal granule clear and rhizoplast to karyosome suggested.

Figure 34. Newly settled individual; cup not yet secreted; anterior flagellum, basal granule and nucleus clear; peristomial eminence shown.