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THE

MONTHLY MICROSCOPICAL JOURNAL.

DECEMBER 1, 1874.

I.—*Continued Researches into the Life History of the Monads.* By W. H. Dallinger, F.R.M.S., and J. Drysdale, M.D., F.R.M.S.

(*Read before the* Royal Microscopical Society, *Nov.* 4, 1874.)

Plates LXXXIII., LXXXIV., and LXXXV.

The prosecution of our inquiries as to the developmental history of the minute monad-forms found in macerations of fish was continued during the past summer. Our methods were precisely the same as those previously described; so also was our mode of work, everything being mutually accepted as a correct interpretation.

Prolonged work with infusions has led us to make observations

DESCRIPTION OF PLATES LXXXIII., LXXXIV., AND LXXXV.

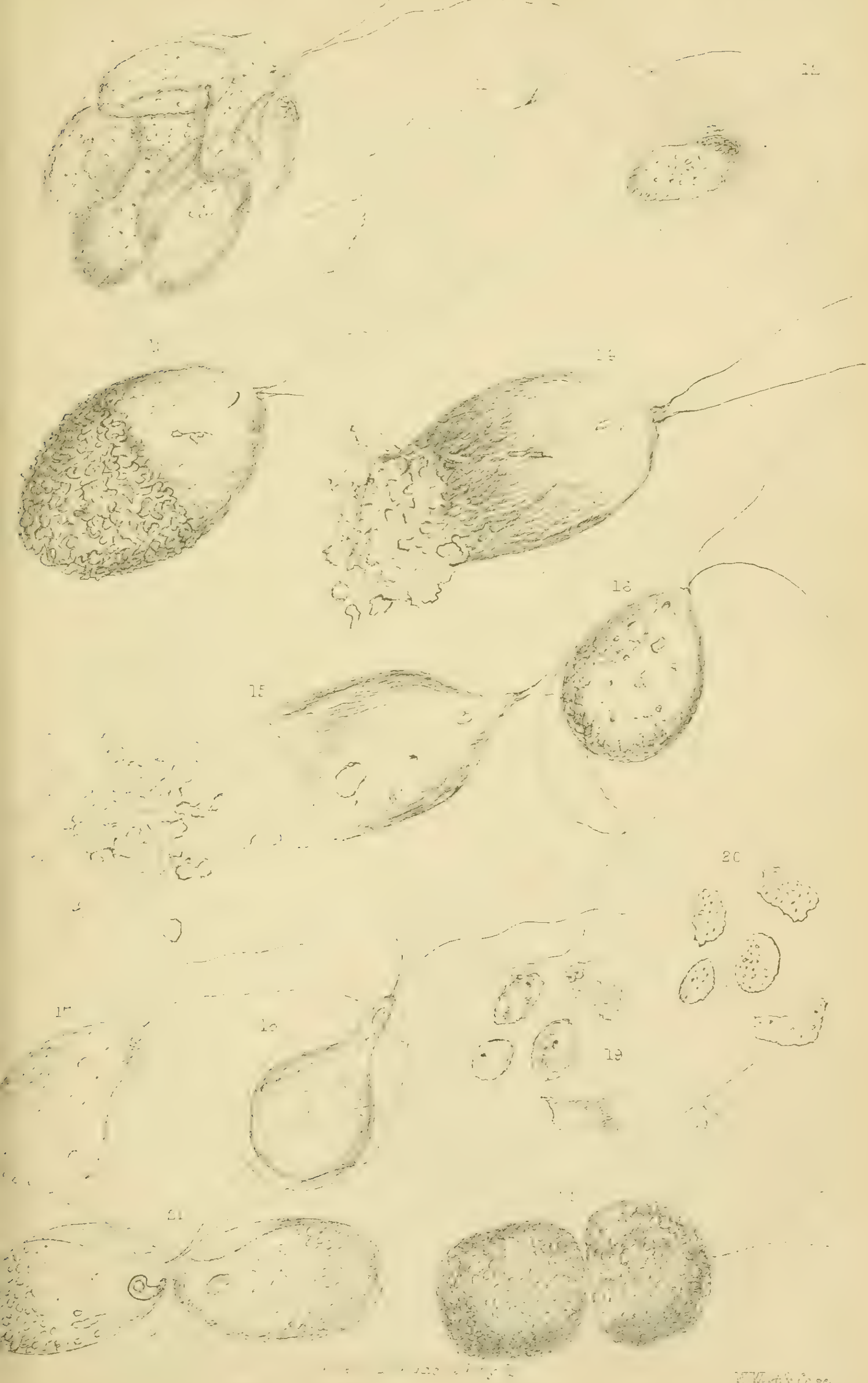
Fig. 1.—Typical specimen of the monad described.
" 2.—Shows the different positions taken by the enlarged bases of the flagella when the latter are in motion.
" 3.—The peculiar structure *a*, *b*, intimately connected with the bases of the flagella *c*, indicates a probable organ of locomotion; of which *b* may be muscular.
" 4.—The earliest condition of change of state, showing hyaline investment more clearly.
" 5.—First constriction within the hyaline.
" 6.—Constriction more developed.
" 7.—The first division into two complete; but the forms are still within the hyaline.
" 8.—Transverse constriction ensues in each of the preceding.
" 9.—Division into four has taken place, and the flagella of some of the enclosed ones are protruding.
" 10.—Further multiplication has ensued, and the first of the new forms is escaping from the hyaline investment.
" 11.—The hyaline envelope after all have escaped.
" 12.—The same when one or more has aborted.
" 13.—A specimen of the granular form from which parthenogenetic elements are emitted.
" 14 and 15.—The emission of the above.
" 16, 17, and 18.—The condition of the monad after emission.
" 19 and 20.—The germinal points seen in the granules of sarcode emitted, as discovered in the process of development. × 10,000 diam.
" 21.—Sexual contact.
" 22.—The earliest result of the blending.
" 23.—The still condition which follows.
" 24 and 25.—The cyst bursting and emitting a cloudy mass containing germs.
" 26 and 27.—Represent the "clubbed" condition.

concerning them which, although without explanation or apparent bearing at present, seem to us of sufficient importance for note. Our first maceration was a cod's head; it was freely exposed to the air, but excluded from the light. For two months nothing at all remarkable presented itself. Abundance of *Bacteria termo*, *B. lineola*, and Amœbæ were found. But at the expiration of the twelfth week the form to be described in this paper gradually appeared—survived for three months and two weeks, to the almost complete exclusion eventually of other forms—and then was supplanted by other monads, some of which have been described by us in former papers.

This maceration was made from ordinary water supplied by the company on the Cheshire side of the Mersey. The same year, in the same place, another cod's head, and the head of a salmon were macerated in separate vessels. It was later in the year, and the production of vital forms was slower; yet in the course of four months the same phenomena as those described above took place; the only difference being that the form that we are about to describe did not persist so long.

In the autumn of the same year another cod's head maceration was made in Liverpool from the ordinary water supplied to the town. This up to the spring of the following year showed no trace of the form in question, nor indeed of any monad, but swarmed persistently with gigantic specimens of the *Spirillum volutans*. After this several other macerations were made, in the same place, and the form we desired appeared, but no spirilla could be discovered. While a maceration of salmon's head made in April, 1873, under the same circumstances at the same place (viz. on the Lancashire side of the Mersey), was found in April, 1874, to swarm with the peculiar monad form in question; but another infusion of herring made at Rock Ferry (on the Cheshire side) late in the summer of 1873 has not yet shown the monad we hoped for. What determines their appearance or non-appearance we have no data even to surmise; but it is a subject which is securing our attention.

Another incident in our last summer's work may be mentioned. We always work from a small quantity of the large vessel of decaying matter which we can keep at hand. During the early summer the intense and continued heat evaporated all the fluid from the salmon's head infusion without our knowledge. The form at which we were working had been in it in great profusion. It was growing less abundant in our small working tank, and we feared that we must wait another year to finish our inquiries. But we led a forlorn hope, and took the hard, porous, dried, papier-maché-like mass which formed the dry residuum of the infusion, and determined to put it into an exhausted maceration of the same



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The life-history of Monads.

kind at Rock Ferry, which at the time showed only very feeble signs of *any* life, and certainly no monads. We watched the result; and, to our great surprise, in three days the required monad appeared in remarkable vigour and daily increasing abundance, enabling us to complete our researches into its cycle of development. Whilst at the same time another, and remarkable form, whose history we have since completed, and which had only very feebly shown itself before the drying up of our infusion, now showed great vigour, and eventually survived and predominated, evidently very much at the expense of the former.

This may be accounted for in two ways at least. First, the germs—which we have proved to exist in the development of this form—gave origin to new monads when the caked mass was broken up by solution and set them free in normal conditions; and second, we are strongly inclined to believe that hundreds of millions of the adult forms were only *desiccated* by the drying up, and were resuscitated when the fluid was restored; an opinion which subsequent experiment has done much to confirm.

With reference to the immediately asserted, and eventually absolutely secured ascendency of the *new* form above referred to, after the remoistening of the dried maceration, it is evident that some new conditions had arisen in consequence of the drying up of the pabulum, and its subsequent remoistening, which in the struggle for existence made it the fittest to survive.

The form we now describe has occupied our attention for at least three years, but some points of difficulty each year presented themselves, and we have delayed any reference to it until we had learned as much concerning it as we deemed possible. It is in fact the form incidentally referred to in our first paper,* and drawn, in various positions, at *a*, *a*, &c., Fig. 1, Pl. XXIV., vol. x., of the 'Monthly Microscopical Journal.'

It is a form possessed of more distinctive and distinguishable structure than any other so low in the scale of life with which we are acquainted. Its most marked peculiarities may be summarized with the aid of Fig. 1. The sarcode is invested with a distinct hyaline envelope, perfectly structureless to our best appliances, and sharply distinguishable from the protoplasm of the body; two flagella, inserted into what appears like a special organ of locomotion; a large central disk or nucleus-like body, *a*; numerous protoplasmic granules, *b*, the function of which we shall shortly explain; a pair of "snapping" eye-spots, *c*;† and occasionally some remarkable club-like appendages to the anterior part of the body, the nature of which we have failed to ascertain; and to which we shall again refer.

The body is oval, the pair of flagella with which it is furnished

* 'M. M. J.,' vol. x., p. 53.
† Ibid., vol. xi., p. 8.

being placed anteriorly. The average length of the long diameter of the body is the 1100th of an inch. The flagella are about twice the length of the body, very fine, and intensely rapid and graceful in their movements. They are inserted into a couple of pear-shaped bodies, with their thickest ends in contact with the investing membrane. They are shown as they generally present themselves in Fig. 1, *d*, but they also assume the conditions drawn in Fig. 2, being intimately connected with the motion of the flagella; this may be distinctly seen when the motion of the monad becomes slower. *a*, *b*, *c*, and *d* show some of the positions assumed, and their relations to the movements of the flagella.

The motion of this monad when in complete activity is extremely graceful, almost swallow-like; but there is no question left upon our minds that it is wholly accomplished by means of the flagella. They are usually thrown out in the manner of a swimmer's arms, and made to meet at the posterior end of the monad; but they can also be used in all directions, either singly or together, giving either a rolling forward motion, or a gyrating horizontal motion, or even a longitudinal revolution. They can also move backwards, by uniting the flagella and making a sculling motion.

To attempt to give anatomical explanation of their movements as produced by what appears to be a mere mass of structureless sarcode would be waste of space. But we are constrained to indicate what was seen twice by both of us, and three times by one, as indicating something that suggests structure. We were observing once with the $\frac{1}{50}$th, and once with the $\frac{1}{25}$th, when we perceived by careful focussing what is drawn in Fig. 3, where the rod *a* seemed to run longitudinally through the monad as if for support; the bulbous part *b* was closely connected with the knobs *c*, which give actual support to the flagella.

The posterior part of the sarcode is always filled with granular masses of protoplasm to nearly the extent of half the body, as seen in Fig. 1. These, as we shall subsequently see, play an important part in the life history of the creature. Immediately above this granular mass is situated a nucleus-like body; it is without structure, and large in proportion to the size of the monad, always occupying the same position, *a*, Fig. 1. Beside these peculiar features this creature possessed almost constantly the snapping eye-spots which we have shown to belong to other monads, and have fully described in earlier communications,* but the function of which we have failed to discover.

We may now consider the phenomena attending the developmental history of this form, which is divisible into three chief features.

(1.) By continuous observation on the normal form, with a

* 'M. M. J.,' vol. xi., p. 8.

power of from 1200 to 10,000 diameters, the fine hyaline investment in the initial stages of development is perceived more clearly, enveloping the monad, but no change of shape or motion ensues, Fig. 4. In about forty minutes to an hour a line suddenly appears across the short diameter of the oval, which soon develops into a very marked constriction, as seen in Fig. 5. This constriction continues rapidly to increase within the hyaline membrane, which throughout the process preserves its normal form, until it reaches the condition drawn in Fig. 6. During the whole of this time the motion of the monad is unaffected; and in about two hours from the first* a total division takes place. Just before division, however, in some way not made out, two short cilia appear in the place of the future flagella, as seen in *a*, Fig. 6; but directly actual division takes place the separated monad turns over, and occupies the position seen in *a*, Fig. 7. After swimming freely in this condition for not less than ten minutes an indentation may be observed in the long axis of the divided bodies within the hyaline, and in from seven to twenty minutes a constriction longwise ensues,† as seen in Fig. 8, where *a* and *b* show the lines of constriction. After this the divided bodies remain within the hyaline envelope, sometimes dividing into eight and even into sixteen, although rarely, and swim about with an elegance and ease certainly not surpassed by the pregnant *Volvox globator*. Generally this compound mass is dependent for motion on the original flagella of the original monad, which persist throughout; but at times, determined by conditions we have not discovered, the flagella of each new form protrude beyond the hyaline envelope, as seen in Fig. 9, but these always move in concert, and apparently obey a common impulse. After swimming in this way for a length of time, varying from ten to one hundred minutes, or more, one of the forms within the hyaline investment protrudes itself, as seen in Fig. 10, and shortly escapes a perfect monad like its parent. This is repeated in each case until in the majority of instances all escape, leaving the fragment of a pellicle or sac behind with the old flagella attached, as drawn in Fig. 11. But in many cases there appears to be incapacity to throw off the last one or two, and it remains apparently dead, as seen in Fig. 12. This is the usual method of increase, and goes on with great rapidity; the multiple forms in a fresh field, always bearing a large proportion to the other forms. This process does not terminate with the first generation so produced, but may be continued for many generations in succession with no congress of any kind and no visible modifications.

(2.) But the attentive and patient observer will soon find

* Sometimes it is much quicker, and at other times much slower than this.

† This is not invariable: sometimes the constrictions are all along the short diameter.

himself arrested by another kind of phenomenon. Some of the normal forms become *extremely* granular at their posterior or non-flagellate end, so that the granules give the protruding effect of an acorn cup. These swim with great freedom, and are generally larger than the other forms. One of them is represented at Fig. 13. Suddenly, and without warning, these swiftly moving bodies shoot out almost the whole mass of granules, and deposit them, as seen in Figs. 14 and 15, leaving the monad almost entirely destitute of granules, and with the hyaline membrane still retaining its shape, but the sarcode within much altered in form and position. This is shown in Fig. 15; but also other modifications attending the emission are drawn at Figs. 16, 17, and 18. At certain stages of development thousands of these granular forms are visible in every "dip" of the fluid. At first the extruded granules seem to have no significance; and they were for a long time a source of great perplexity to us. But we confined our attention at length wholly to these for some time, and by the use of our best appliances were enabled to discover their nature. When deposited, the granules are amorphous, more or less agglomerated, and perfectly transparent. Watching them attentively with the highest available powers of the $\frac{1}{50}$ we at length saw spots, or minute points or dots, appear in the granules, as seen in Fig. 19. These under constant observation increased, and in one of them, as many as seventeen were counted. In this condition they are drawn at Fig. 20. They remained like this for from two to three hours, only slightly increasing in size. At the expiration of this time a vibratory motion of the internal points was perceived, which very rapidly increased, and in the course of forty minutes intense internal activity was visible, the minute dots within the sarcode moving upon each other in all directions. This lasted from ten to fifty minutes, when they all escaped and at once swam freely as minute bacterial-like bodies, but no trace of any organs of locomotion could be discovered. After they began to move they rapidly increased in size, so that in from four and a half to five hours they were of normal size, and endowed with all the powers of the original monad. This was seen again and again, in all its stages, and the new forms were followed up to the condition of multiple fission, as before described.

Other phenomena presented themselves, but nothing that we could explain or correlate; and we were for two years inclined to think that this must be the entire process of development. But commencing again with fresh working power, we were this last summer enabled to find what gives completeness to this history.

(3.) We had occasionally seen during the whole period of our researches on this form a coming together of two of the monads; but from its infrequency and occasional abortiveness, as well as from the prominence of other phenomena, we did not with any continued intensity follow it up. This past summer we made it a specific object, and by dint of close application found that, in comparison with other phenomena, very occasionally two of the monads, at times in no way distinguishable from each other, met and touched each other at their anterior ends, swimming freely together, as seen in Fig. 21. The normal flagella rapidly disappeared, and the bodies melted into each other; another stalked double flagellum appearing at one end in a manner never in any way understood by us. The nuclear bodies *a*, *b*, Fig. 21, blended also into one; the whole thing in this stage being shown at Fig. 22, where also an intensely granular state peculiar to this condition is shown. This body preserved its freedom of motion for a long time —occasionally for ten or twelve hours—but during this time it lost slowly the line of juncture, and became oblong and then rounded; after which its motion was more sluggish, and it eventually became quite still. Fig. 23 represents it in this condition. It remained in this state sometimes as long as twenty-four hours; but generally, from four to six hours was the time occupied before any changed ensued. The uncertainty, however, made constant watching absolutely necessary. The whole sac showed as the first symptom of change a slight vibration or wave-like motion, and then, with no further premonition, its edges broke up and a cloudy mass poured out, in which with competent powers it was comparatively easy to detect myriads of minute points. Fig. 24 depicts this; and by following up rigorously these emitted points, we found that after a short period of inactivity they became motile, and rapidly grew, acquiring flagella, and becoming perfect monads of the parent type. Not only so, but these very forms were persistently followed, and were seen to increase by multiple fission, and to deposit granules as before described. At times the globular condition was not taken, but the emission took place in the condition shown at Fig. 25. It will be seen that this, and another form which we hope to describe in a subsequent number, gave us more trouble and perplexity than any we had worked at. But after working the whole life cycle out it now appears to us that this monad primarily multiplies sexually by the congress of the genetic elements. This, however, is comparatively a very rare occurrence, and serves for many (probably) hundreds of generations. But a kind of parthenogenesis, or internal budding, follows—resulting in the emission of the sarcodic granules which contain minute monad-germs—this being by far the more frequent and rapid mode of increase; while at the same time multiple fission is taking place in all directions.

Thus we have the minute germ sexually produced; the bud produced in large quantities within the unfertilized form, both of which *grow* to the parent size; and the perfect series of monads produced directly by multiple fission.

From the peculiar manner in which the parthenogenetic products are deposited—in a clear investing sarcode—the capacity for desiccation so remarkably shown by this monad may be understood on the principle pointed out by Mr. Henry Davis.*

There is one condition of this monad which, in spite of most constant and assiduous research, has defied all our attempts to discover its meaning. We have called it the "clubbed" stage, for in this special condition the monad was vested with one or two peculiar knobbed stalks either supplanting or associated with the flagella. The ordinary clubbed condition is shown at B, Fig. 26, where *b*, *c* appear to have taken the place of the ordinary flagella. Almost as frequently the condition seen at A is assumed where there is one flagellum and one knob; but instances have often occurred in which both flagella and two knobs exist together as at *c*.

We have endeavoured for three years to find the meaning of this, but have entirely failed. We persisted in our efforts, because, so far as we could discover, this anatomical phase seemed to coincide with certain stages of development. But wider and closer observation has enabled us to abandon this idea. Our first impression was that this phenomenon had a sexual significance, and this arose from the fact that we had frequently observed copulating forms, as at *c*, Fig. 21, in which one of the monads was clubbed. But from the large number of cases subsequently watched with all conceivable care, in which no such a phenomenon presented itself, we are obliged to abandon this also. That it is without significance in the creature's development we are unwilling to think; the more because of its occurrence each year, and with greater or less persistence throughout, as well as on account of the occasionally observed method of its production. In Fig. 27 the mode of origin is shown. At first two disks were seen within the sarcode, as in *a*, *b*, A; these would slowly push out, as in *c*, *d*, B, and the stalks would appear, and eventually they would be wholly and permanently thrown out, as in *e*, *f*, C.

But in spite of this we have failed to correlate it with any step in the developmental history, which appears complete without it; and we can only record the facts, and hope that some more fortunate workers may be able to interpret them.

In the course of our work on this and other forms we have been more than ever strongly impressed with the danger of hasty conclusions. It animates our diaries to comment from time to time on the probable meaning of certain observed phenomena—to speculate on their relation to what we had fully ascertained and what we had yet to discover. At times, indeed, our inferences, *when*

* 'M. M. J.,' vol. ix., pp. 206–209.

made, seemed inevitable. But nothing is more interesting to us than to see how facts slowly and unceasingly pursued and ascertained and collated, showed the inutility of our surmises. In investigations of this kind we are convinced that sequences must be made *by the facts themselves.* Inference, however plausible, may vitiate a whole train of observation; and, amongst other things, we are bound to perceive the liability there must be to infer heterogeny if observations be not long continued, and every transitional step in the process be not demonstrated with the severest accuracy.

To complete our work on this form we conducted a series of heating experiments in precisely the same way as before. It will suffice, therefore, to give the results of one series, which may be taken as typical.

Six slides were taken: a drop of the fluid put on and covered with a thin cover. This was carefully examined, and if found to contain what was needed was allowed slowly to evaporate. The whole selected six were next slowly heated up to 250° Fahr., kept at this heat for ten minutes, and then allowed slowly to cool. When cold, they were carefully remoistened with distilled water—the water flowing readily under the cover by capillarity—and they were again examined and reported upon.

Before they were put into the heating apparatus in each case it was discovered that the elements required were there.

On examination after heating, and immediately after fresh moistening, nothing was visible but a baked amorphous mass. Two hours after this no motion of any sort was visible, save in two, where, with $\frac{1}{25}$th, excessively minute points were seen to be in a state of activity, which was translatory and not Brownian.

Twelve hours after minute bodies—almost certainly known to us as the very earliest motile form of the monad above described after development from the germ—were seen in four of the fields. These in two of the instances were traced up to full-sized monads of the form and with the developmental history of the form at which we were working; whilst the other two on the second day had many of the same in full maturity and complete action. The other two were wanting in this form.

From this it is clear that whilst in one condition this monad can survive desiccation, in another—the true sexual-germ-state—it can survive a temperature of 250° Fahr.

We now heated another set of six under precisely similar conditions up to 300° Fahr. But in this whilst some forms with which we were acquainted survived by means of their germs, this form was *wholly destroyed*, and not the trace of one in any form could be discovered in any of the slides.
