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THE FURTHER AND FINAL RESEARCHES OF JOSEPH JACKSON LISTER UPON THE REPRODUCTIVE PROCESSES OF POLYSTOMELLA CRISPA (LINNÉ)

(An Unpublished Paper Completed and Edited from His Note-Books)

(With Seven Plates)

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INTRODUCTORY NOTE

For over 30 years Lister's work upon the reproductive processes of the megalospheric form of *Polystomella crispa* (Linn.) by means of flagellispores has been familiar to protozoologists, and especially to students, both in text-books and in the lectures of university professors, and it recurs incessantly in examination papers. For over 30 years it has been well known that his equally, if not more, important work on the reproductive processes of the microspheric form by what may not improperly be called viviparity had been completed, but with the exception of the short postscript to his paper published in 1895 it has not been available to protozoologists. The reason for this is difficult to fathom for anyone who did not know him intimately. We know that his nervous sensibility was such as to reach at times a pathological condition, and he could never be persuaded to publish anything that he took it into his head to keep to himself. I suppose that, so far as the Foraminifera were concerned, I was his most intimate friend and fellow-worker, but, though we frequently visited each other and continually corresponded, he never showed me any of these preparations, photographs, or lantern slides.

I esteemed it therefore as a great privilege that I was allowed, after his death, to sort and arrange the whole of his microscopical materials and preparations, and the papers and note-books relating to them, and having found the whole of his material, his slides and his own unpublished paper upon it, I was permitted by the late Mrs. Lister, herself a noteworthy zoologist, to give to the world of science the information that it had been awaiting for 30 years.

When the last and the youngest of the men that he taught have died; when the problems attaching to Astroclera have been solved;

when his teaching in the Zoological Schools of Cambridge have become a mere tradition; when his patient, laborious work upon the geology, ethnology, and ornithology of the South Seas has become but a brick in the vast edifice of human knowledge; indeed so long as men shall devote labor and research to the science of protozoology, the name of Joseph Jackson Lister, like that of his illustrious uncle, Lord Lister, and of Harvey, Jenner, Leeuwenhoek, Redi, and Schwann, will live in the hearts and on the lips of men, and the discovery which will spring to the mind when his name is mentioned will be that of the reproductive processes of the reticularian Rhizopods, especially those of *Polystomella,* and the meaning and significance of dimorphism.

Those of us who were privileged to know him, and especially those of us who in our researches have followed in his footsteps, know how delicate and polite was his use of the results of his amazing industry, patience, and almost universal interests—industry and interests pursued and recorded indefatigably in the face of physical difficulties beneath which a lesser man would have early succumbed. How much more profound must be the appreciation of one who, like myself, has been privileged to examine his laboratory note-books and the mass of valuable papers that he left behind him at his early death—left in a condition of such exquisite perfection that the examiner is never once checked by the reflection: "If only he were here to explain exactly what he meant by *that.*"

I should hesitate, for fear of being accused of extravagance of speech, to describe the note-books of Lister, were it not that they lie before me as I write and that Mrs. Lister has presented them to form part of the Heron-Allen and Earland library and collections at the Natural History Museum (London), where they will be always available, for the instruction and emulation of future generations of protozoologists. He made notes, not merely for his own use in the kind of personal cryptogram which we are all apt to adopt in recording our own observations, but for the guidance of any research-workers that should come after him. Every sketch or drawing that he made was as highly finished as though it had been prepared for publication, and the systematic dating of his notes enables us to follow his work step by step, and, for practically the whole of his working life, day by day.

It was in the course of the examination that I have been privileged to make, that I came across his own manuscript record of his work at Plymouth, extending from June 1 to August 9, 1894, a

record of such vital interest and importance that no apology is needed for publishing it *in extenso*. It is the record of his observations upon the reproductive processes of the microspheric form of *Polystomella crispa* (Linn.), and I have been able to compare this manuscript with his original laboratory note-books, and with the records of his later work in 1895, and in 1904-5.

Lister's researches upon this organism appear to have commenced in March-May, 1893, and it was during this period that he observed the reproductive processes of the megalospheric form by means of flagellispores, which observations he recorded, with a masterly study of the dimorphism and nuclear conditions of the species, in his world-famous paper read in June, 1894, and published in the Philosophical Transactions of the Royal Society of Great Britain in 1895.[1] By one of those coincidences that are curiously far from uncommon in science, Fritz Schaudinn was pursuing an identical line of inquiry at the same time, and the same results were arrived at and published almost simultaneously by both of these great men though working quite independently and unknown to each other.[2]

But when Lister's Philosophical Transactions paper was virtually on the press, or at least awaiting publication, he was again at Plymouth, checking his former observations, and making further discoveries which may well be described as epoch-making. Let him tell us the story in his own words, but first let us consider for a moment the organisms in question: they are:

(a). *Polystomella crispa* (Linn.): one of the commonest known species, and one of practically world-wide distribution.

(b). *Polystomella macella* (Fichtel & Moll): a depressed and closely allied species, found associated with *P. crispa* but somewhat rarer north and south of the sub-tropical areas. I have recorded it myself from Selsey, Torbay, Clare Island, Galway, St. Mawes, and St. Andrews and the North Sea, so it may well have been among Lister's material: he had no time to be an accurate systematist.

Lister does not seem to have recorded observations upon

(c). *Polystomella striato-punctata* (Fichtel & Moll) until 1904. He was again at Plymouth in June-July, 1904, as he says in his note-book, "hoping to make some progress in the life-history of the Foraminifera." He records his observations upon the reproduction of the

[1] Lister, J. J., Contributions to the life-history of the Foraminifera. Phil. Trans., Vol. 186 B., p. 401, 1895.

[2] Schaudinn, F., Die Fortpflanzung der Foraminiferen und eine neue Art der Kernvermehrung. Biol. Centralbl., Bd. 14, No. 4, February, 1894.

megalospheric form of *P. striato-punctata* by flagellispores on June 29 and July 1. There is no mention of the reproduction of the microspheric form by the processes we are now describing, though it is of world-wide distribution, and nearly always found with *P. crispa,* and it was the first Foraminifer ever figured—by Hooke in 1665 [1] and by Leeuwenhoek in 1702.[2]

He was there again in the same months in 1905, but added nothing of moment to his previous records, but records the fact that in several of his dishes left behind in 1904, Foraminifera and other organisms were still alive.

He printed a highly condensed abstract of these later observations as a postscript, dated August 3, 1894, to his Philosophical Transactions paper, and this postscript, slightly elaborated, appears in this still contracted form in his later works, viz: in Lankester's Treatise on Zoology in 1903,[3] his address as president of Section D at the York Meeting of the British Association in 1906,[4] and in his Evening Discourse at the Royal Institution in 1907.[5] But, for some reason which we shall never know, but which was doubtless connected with his state of health, he never published his paper. No apology is needed therefore for giving to the scientific world his own description of his researches, and their results. It is as follows: [6]

LISTER'S NOTES

July 7, 1894. Plymouth.—For the last three weeks or so, I have kept *Polystomella* in tall glass jars,[7] the water in which has been renewed frequently by a jet playing through a muslin cover over the mouth of the jar.[8] The Polystomellas crawl up the sides from the

[1] Hooke, R., Micrographia, p. 80, pl. v, fig. x, London, 1665.

[2] Van Leeuwenhoek, A., Sevende Verfolg der Brieven, etc., p. 195, pl. (opp. p. 191), fig. 7, *a, b, c,* Delft, 1702.

[3] Lister, J. J., The Protozoa, Sect. 1. The Foraminifera, in E. Ray Lankester "A treatise on zoology," Pt. 1, 2nd Fasc., pp. 47-149, 1903.

[4] Lister, J. J., The life history of the Foraminifera. Brit. Assoc., York, 1906, Section D, Presidential Address.

[5] Lister, J J., The Foraminifera. Proc. Roy. Inst. Great Britain, Evening Meeting, February 15, 1907, p. 489, London, 1909.

[6] I have carefully compared this manuscript statement with Lister's laboratory note-books, and the further details to be derived from these are of such value that I have transcribed such parts of his notes as bear upon his statement, in the foot-notes.

[7] The *Polystomella* were dredged in 5 fms. on *Zostera* grass, inside Drake Island in Plymouth Sound, and the experiments commenced on June 17.

[8] When this spraying was not in progress the jars stood on the sill of a window in the sun. J. J. L.

bottom and may be clearly seen when in bright light, with a black background. Usually one or two of the terminal chambers contain little protoplasm and appear empty. In the ordinary condition their pseudopodia are inconspicuous, but they may generally be detected with a pocket lens, extending in sheaves from the shell,[1] and with a microscope they have the usual appearance of delicate straight threads with granules.

In some 50 cases I have seen examples in the *reproductive phase*. The first sign of this phase is seen in the character of the pseudopodia.[2] Instead of being disposed as above described, the pseudopodia are limited to a circular or oval area immediately about the shell, the center of the area being the mouth of the shell, which is nearly always flat against the glass. This area is covered completely by a close web of radiating and interlacing pseudopodia, and its limits are fairly sharply defined. The pseudopodia are so thick as to intercept the light, giving rise to the appearance of a semi-transparent milky halo about the shell. This may be called the "premonitory halo." It is readily seen by the naked eye.

The animals are generally found in this condition in the early morning.

In nearly all the cases that I have observed the halo has been established by 6: 30 a. m.[3]

After the animal has remained in this condition for some hours, the protoplasm begins to leave the shell, the strands of the pseudopodia, especially the radiating ones, become thicker, and the protoplasm withdraws itself, first from the peripheral ends of the outer whorl of chambers, being massed in the terminal chambers. Gradually the protoplasm leaves the shell, passing through the direct communications between the chambers, and also, as is seen in specimens preserved at this stage, through the canals which exist in the walls separating the chambers from one another. The protoplasm is generally brown, owing to the presence of brown granules.[4] As the protoplasm emerges into the area of the halo, this becomes streaked with brown, at first in

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[1] When they are observed immediately after the jet of water has been playing into the jar, a long sheaf of the pseudopodia is seen pointing towards the current set up in the water. After the water has become still, they are shorter and point in various directions. J. J. L.

[2] This was first observed on June 21, 10: 30 a. m.

[3] While these observations were in progress, Lister frequently remained all night in the Laboratory of the Marine Biological Association.

[4] 1: 30 p. m.

thin radiating streaks, which become thicker and fuse with one another until the area is, to a greater or less extent, filled with the dark brown mass.[1]

Specimens which are removed from the wall of the jar while surrounded by the premonitory halo, and placed on cover-slips with a small drop of water, will generally send out fresh pseudopodia and attach themselves to the cover-slip. They may then be placed over holes in filter paper through which a current of water flows, and the hole be completely filled with water. In this way the animal is immersed in circulating water. In some cases the pseudopodia thrown out are of the short reticulated character of those forming the halo, and these indicate that the process is going on uninterruptedly; but it frequently happens that though the animal attaches itself to the glass, the pseudopodia are of the long, little anastomosing character of the ordinary condition. In this case the protoplasm remains in the shell—the animal having, owing to the disturbance, returned to the ordinary state. If however the reproductive phase is continued, the process may be observed under the microscope.

When the protoplasm has emerged from the shell, the whole mass undergoes amoeboid changes of shape,[2] and under the microscope may be seen to be in a turmoil of movement,[3] the protoplasm coursing along in broad interlacing streams. The streams may be seen to pursue a definite course, the protoplasm in any one part of the mass moving in the same direction for many minutes without interruption.

When newly emerged, the brown granules are uniformly scattered through the protoplasm. Gradually a mottled arrangement is produced owing to the appearance of clear spaces (regions) free from brown granules. As the process continues these clear spaces (regions) become larger and more defined, and they are then seen to be more stationary than the remainder of the protoplasm, the streams of granules flowing past them. They are not however entirely stationary.

In one instance the area free from brown granules first became evident one and a half hours after the protoplasm had emerged from the shell.

Gradually the streaming movements of the protoplasm become less, as the clear regions attain greater prominence, and in about half an hour after their appearance the whole mass becomes broken up into

[1] 1:55 p. m.

[2] The mass which is at first diffuse, gradually draws together into a more compact mass, the pseudopodia being almost entirely withdrawn leaving branching lines of fine granules marking the positions they had occupied. J. J. L.

[3] 2:30 p. m.

rounded spheres, some 50 μ in diameter, whose center consists of clear granular protoplasm (in which I thought I detected a radiate arrangement) the peripheral part being dark with the coarse brown granules.[1]

In some cases part of the protoplasm remains in the terminal chambers of the shell and divides into spheres in this position. This, however, is not usual.

The spheres form at first a compact mass. Shortly, each becomes surrounded by a close felt of very delicate anastomosing pseudopodia, which when seen with a simple lens has the appearance of a mass of white granules[2] and I supposed at first that a deposit of lime granules had taken place about the group of spheres. They gradually draw apart from one another, so that each can be seen as a distinctly isolated mass.

I have killed and stained a number of specimens at different stages of this process. Those in the stage before the protoplasm has left the shell, as well as those at the beginning of the later stage, have the central chambers still filled with protoplasm. In all these specimens it is obvious that it is a *microspheric* individual that is undergoing the process. Again, the specimens mentioned above which, having shown a "premonitory halo," returned to the vegetative condition, on being removed to a cover-slip, are found on being decalcified and stained, to belong also to the *microspheric* form. Altogether I suppose I have some 15 specimens whose central chambers are still filled with protoplasm and hence furnished evidence as to the form to which they belong.

In a batch of specimens of Polystomella (some 200-odd) megalospheric and microspheric specimens were nine to one. This is good evidence that the reproductive phase I am dealing with is that of the microspheric form.

The specimens killed in the first stage present, when stained, the appearance I have often seen, the many nuclei being of irregular shapes, and surrounded by numbers of "stained strands." In some cases no definite nuclei can be detected, and only few of the strands. When nuclei are present they do not extend into the terminal chambers of the shells.

In specimens whose protoplasm has begun to emerge, faintly stained round nuclei 10 μ in diameter are found in the clear protoplasm of the terminal chambers, while the innermost protoplasm still has the diffused flush and contains strands of stained matter.

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[1] 2:40 p. m.

[2] 4:30 p. m.

In some cases the protoplasm immediately surrounding these nuclei has a yellowish red color, as though, perhaps, it contained material which was passing in towards the nucleus. The nuclei 10 μ in diameter are found in the later stages now described. They acquire stronger staining powers as the sphere stage is approached.

Continued July 21.—The duration of the stage in which the protoplasm remains in the condition of closely aggregated spheres, and which I call stage iii, varies from two to eight hours. The average duration in a number of cases is about four hours. The most marked change which can be seen in the living condition during this period is in the disposition of the brown granules in the spheres. At first the center of the spheres is clear, the granules lying at their periphery, while in the later part of the stage the granules occupy the sphere leaving only a clear layer at the periphery.

After stage iii the development may pursue one of two courses:

1. In by far the greater number of cases that I have watched the spheres lose their sharply defined outline and gradually fuse with one another into one or a few lumps.[1] Sometimes long pseudopodia are thrown out during the process of fusion but this does not always occur. The lumps so found generally divide, forming smaller lumps of varying size which move apart by means of pseudopodia, and also exhibit amoeboid changes of form. It frequently occurs that one of these lumps attaches itself to the empty shell, spreading over part of the exterior and interior.[2]

The protoplasm remains in this condition for weeks. The smaller lumps appear gradually to break up into granules, losing their definite outline and apparently dying. The large lumps may retain their sharply defined outline for weeks, the movement of the protoplasm becoming gradually more sluggish, and the volume of the mass apparently decreasing. What their ultimate fate may be I have not seen—but it appears probable that it is the same as that of the smaller divisions (lumps) into which the protoplasm divided—gradually disintegrating.[3]

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[1] 7 : 30-9 : 30 p. m.

[2] 11 : 30 p. m.

[3] These conditions lasted until July 1, many other specimens being kept under observation. On this date Lister tabulates the stages of the process as follows: Stage 1. Premonitory halo formed but protoplasm still in shell. Stage 2. Protoplasm emerged from shell but still in one mass. Stage 3. Protoplasm divided up into isolated spheres. Stage 4. Spheres fused to form a common mass sending out pseudopodia. Stage 5. The mass divided up into amoeboid lumps with pseudopodia. Lister's preparations of shells in all of these stages are in our collection at South Kensington.

2. In some ten cases (out of say 150 which I have now seen) the spheres have separated after some hours, sending out long and abundant pseudopodia, and moving rapidly away from one another.

Within 24 hours a second chamber is added to the sphere,[1] and a calcareous shell is developed.[2] In this condition they are readily recognized as young megalospheric individuals.[3]

July 22.—After writing the above yesterday it occurred to me that the first of the two processes described above was an abnormal one—the result of the impurity of the water. I therefore changed the water

[1] This was first observed at 7: 10 p. m. on July 2. Lister's note (note-book, vol. ii, p. 91) reads "The empty shell is now surrounded by a host of small bodies. These all possess a globular mass containing yellow protoplasm. In many cases a second mass shaped like the second chamber of a megalospheric form, and more transparent than the globular mass is present. In other cases two transparent ½-oval masses are present. Some of them have extended pseudopodia." On July 3, at 9 a. m. these second chambers had highly accentuated themselves. (See drawing note-book iii, p. 27.) All the stages were observed on this day in another specimen between 9 a. m. and 9: 40 p. m. (drawing in note-book, vol. ii, p. 92). This had acquired its second chamber at 8: 30 a. m. on July 4.

[2] This was first observed at 12: 20 a. m. on July 5. At 9: 10 a. m. the former specimen had its young "with a rough shell-hyaline material outside this." (Note-book, vol. ii, p. 99.)

[3] On July 7 (the day Lister began the account we are studying) at 10: 15 a. m. he writes (note-book, vol. ii, p. 101) "The specimen which yesterday morning at 10: 30 a. m. was in stage 3, and whose spheres then separated, I have now transferred to picric with several of the spheres attached. They are young megalospheric forms with a second chamber formed." These observations were continued and repeated day after day with the same patient observations and accurate records. On July 11 Lister was able to construct a table, founded upon 23 specimens which had been observed, at the times passed in the stages, the average being: Stage 1, 3 hours. Stage 2, 2 hours. Stage 3, 7 hours. (On the 12th he observed the same phenomena in *Rotalia beccarii* (Linn.) of which he made a beautiful drawing (note-book, vol. ii, p. 106).) The average for 12 specimens watched on July 13 was: Stage 1, 4 hours. Stage 2, 2 hours. Stage 3, 8 hours. (The young Rotalia (66 specimens) gave an average of stage 1, 3 hours, 20 minutes. Stage 2, 1 hour, 30 minutes. Stage 3, 4 hours, 20 minutes. The observations went on as before, thereby confirming the accuracy of his previous records up to the 21st; on the 22nd he made the discovery as to the water which has been recorded in his own words, which now follow. When making dredgings at Plymouth, while this paper was awaiting publication (in April, 1929), we had the good fortune to find, in a dredging from inside Drake Island (the locality from which Lister obtained his material) a very large number of young Polystomellae, in exactly the condition here discribed—*i. e.*, a megalospheric chamber, followed by one or two succeeding chambers. See our paper, "The Foraminifera of the Plymouth District," E. Heron-Allen and A. Earland, Journ. Roy. Micro. Soc., 1930, vol. 50, p. 194.

in two of the jars, putting instead of the aquarium water, water from beyond the Breakwater which I had in a bottle.

Today six individuals have passed through the reproductive phase and all have pursued the second course—giving rise to young megalospheric individuals. Those (4) in which the protoplasm separated in the afternoon have already (9:35 p. m.) added a second chamber to the megalosphere, while those which have separated since 7 o'clock consist only of a spherical body, with abundant ray-like pseudopodia.

These six individuals pursued the course described above up to the end of stage iii—the most noticeable feature about them being the large area covered by the protoplasm in the second and third stages—filling the area of the halo.

This clears up the process in a most satisfactory manner.[1]

To the abstract of the above given in his later works he merely adds: "The whole of the protoplasm of the parent is used up in the formation of the brood of young, the shell being left empty. The process from the first appearance of the halo to the dispersal of the young is complete in about 12 hours. . . . . Each of the spheres was, in fact, a megalosphere. The microspheric parent has given rise to, indeed it has become, a brood of megalospheric young."

Lister was an expert micro-photographer, and in April, 1895, he obtained fresh material from Plymouth, and repeated his observations in his own laboratory, at Cambridge. He heads his notes: "Polystomella material started in dishes, April 30. Several microspheric individuals have reproduced in the manner seen at Plymouth last summer. In a few cases the fusion has occurred, but many have formed normal young." His observations, like those of 1894, were made by the "hanging drop" method in the use of which he was an expert. His notes at this time relate to the flagellispore method of reproduction by the megalospheric specimens, but from May 22 to 24 he made a wonderful series of micro-photographs, 24 in number from a single microspheric individual of which 15 were made into lantern slides, which slides Mrs. Lister has presented to our collection. A selection of these together with certain of the photographs (which are now being published for the first time) are now available, for all time, for the use of students of Protozoology. In all, 20 photographs are here reproduced. They may be tabulated as follows:

[1] On July 25 he writes "There is reason to believe that the aquarium water is affected by the asphalt lining of the tanks." He tested this with further Polystomellae on the 26th in "outside water" between 8:30 a. m. and 7 p. m. with brilliantly successful results. His notes on Polystomella cease, for this time, here.

Figure	Series	May 22, 1895	Lantern slide, Heron-Allen and Earland Collection	
1	E. 1	1:00 p. m.	12/32	The "premoni-
2	E. 2	2:25 "	.....	tory halo."
3	E. 3	4:25 "	12/33	Stage ii.
4	E. 4	4:40 "	12/34	"
5	E. 5	5:20 "	12/35	"
6	E. 6	6:00 "	12/36	"
7	E. 7	6:30 "	12/37	"
8	E. 8	7:05 "	.....	Stage iii.
9	E. 9	8:15 "	.....	"
10	E. 10	8:55 "	12/38	"
11	E. 11	9:30 " [a]	12/39	"
12	E. 12	9:30 " [b]	12/40	"
13	E. 13	10:55 "	12/41	"
14	E. 14	11:15 "	12/42	Final stage.
15	E. 15	11:25 "	12/43	"
16	E. 16	11:30 "	12/44	"
17	E. 17	11:55 "	12/45	"
		May 23, 1895		
18	E. 19	0:40 a. m.	.....	"
		May 24, 1895 [c]		
19	E. 19	11:50 [c] "	12/49	"
20	F. 1 & 2			

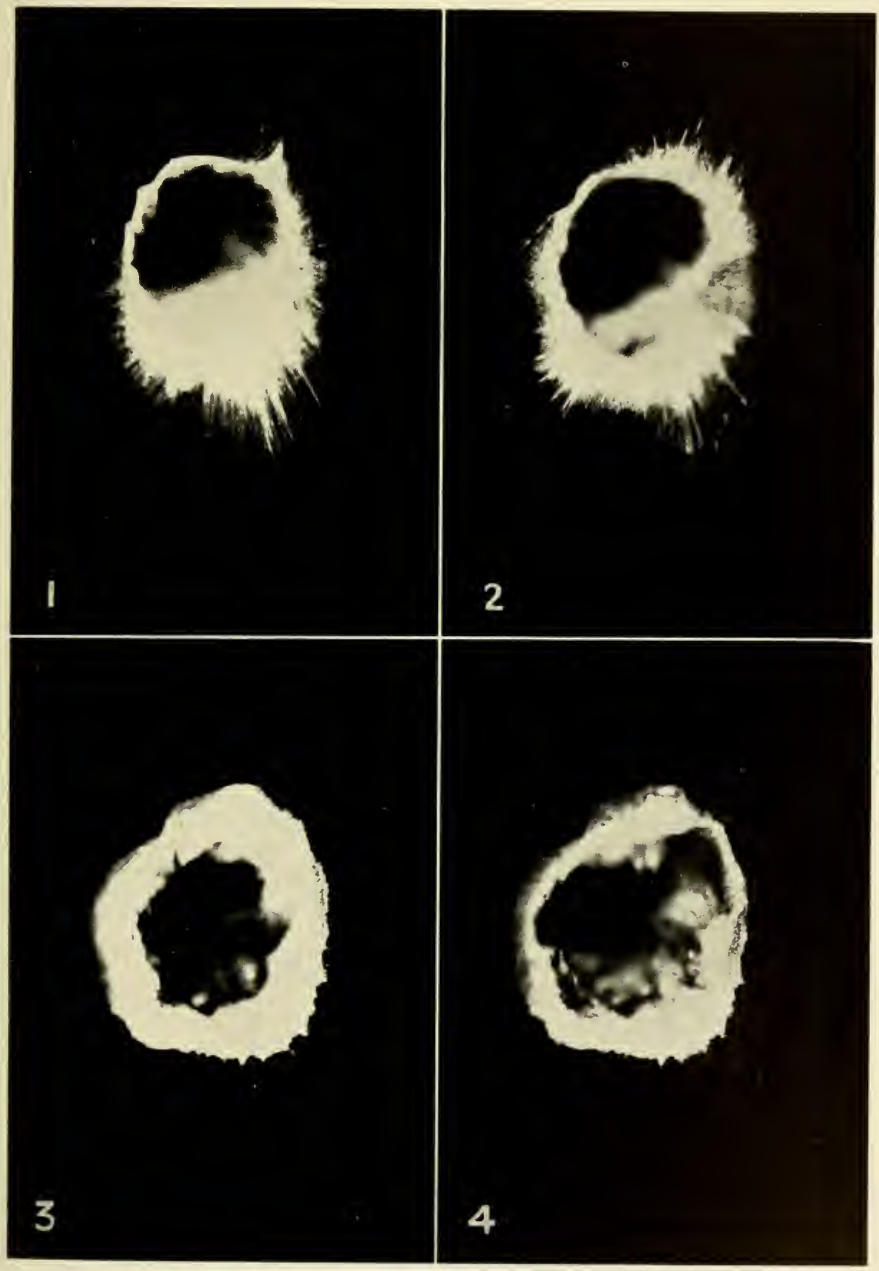
[a] Deep view.

[b] Nearer view.

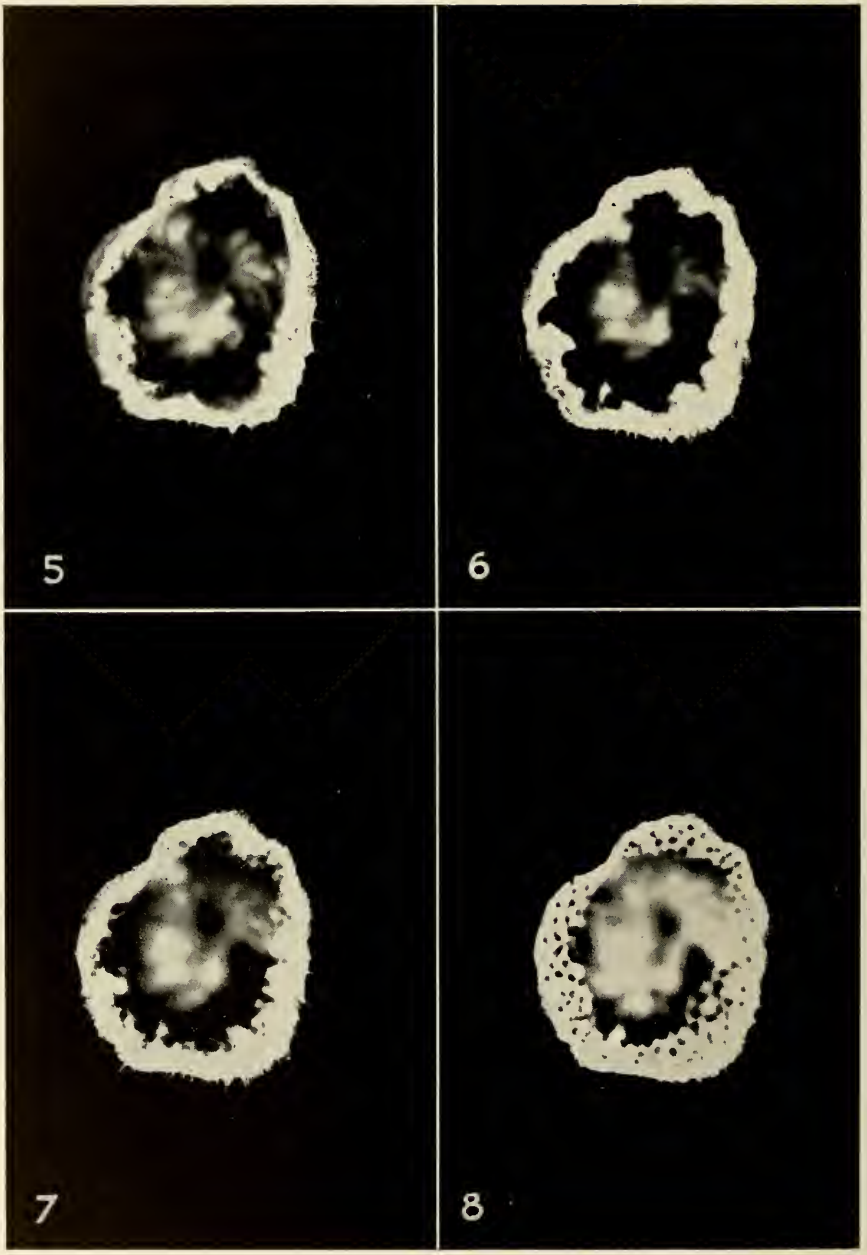
[c] There is something wrong here. J. J. L. dated this slide May 23, 1895, 11:50 a. m. but it obviously belongs here as a second chamber is in process of formation. I think it should have been dated May 24. After E. 18 (which is not reproduced) the *slides* are not numbered, but his register of *photographs* gives the numbers 19 *et seq.*

The last of these, figure 20, is one of the two slides in the collection, showing different magnifications of the same object, which are registered as Ser. F. 1 & 2 but no dates or times are given. They are from another specimen and represent the post-final stage (probably 25-26 May) when a second chamber has been added. They are registered in the Heron-Allen and Earland Lantern-slide Collection as 12/46-47.

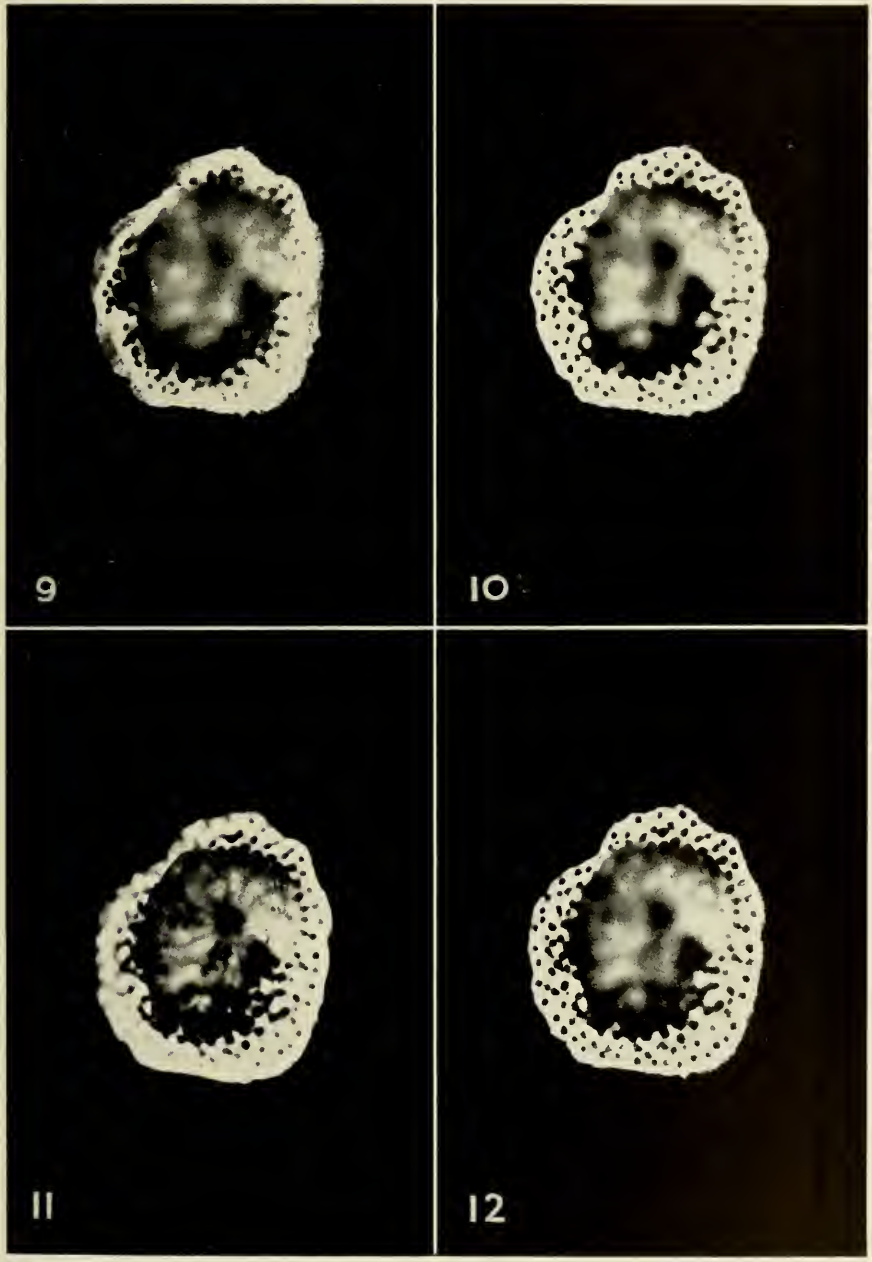
In conclusion I may be allowed to pay a tribute of warm gratitude to Mrs. Lister, whose early death occurred shortly afterwards, for the public spirit which led her to present the Lister Collections in general, and these priceless note-books, preparations (there are nearly 450 of *P. crispa* alone in our collection at South Kensington), and lantern slides, to the nation for the use of future generations of students. I desire, also, to express my gratitude to Dr. J. A. Cushman for correcting the proofs of this paper.



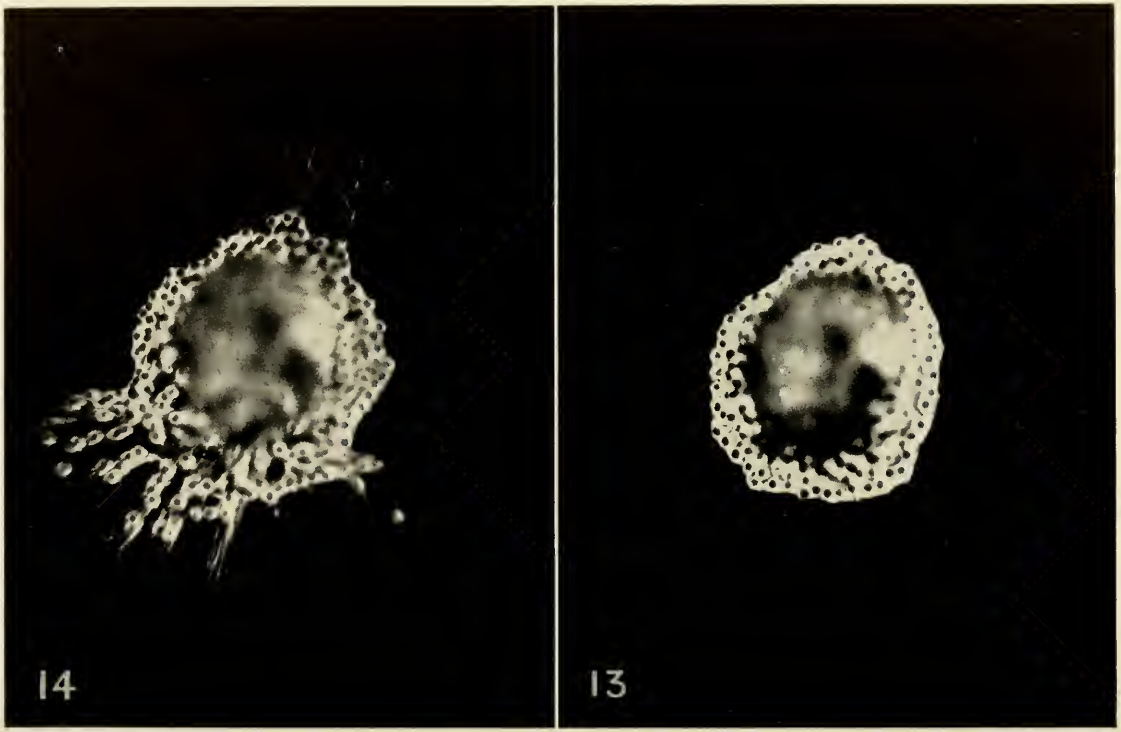
For explanation, see page 11.



For explanation, see page 11.



For explanation, see page 11.



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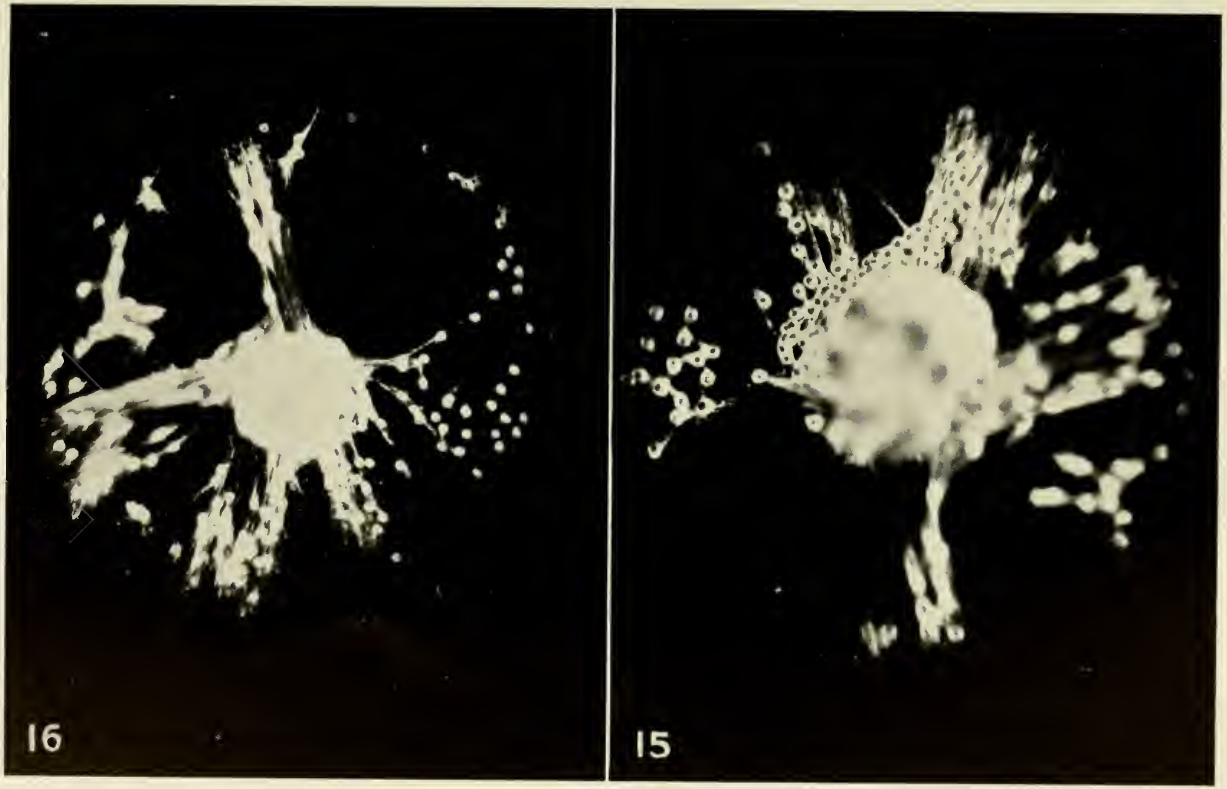
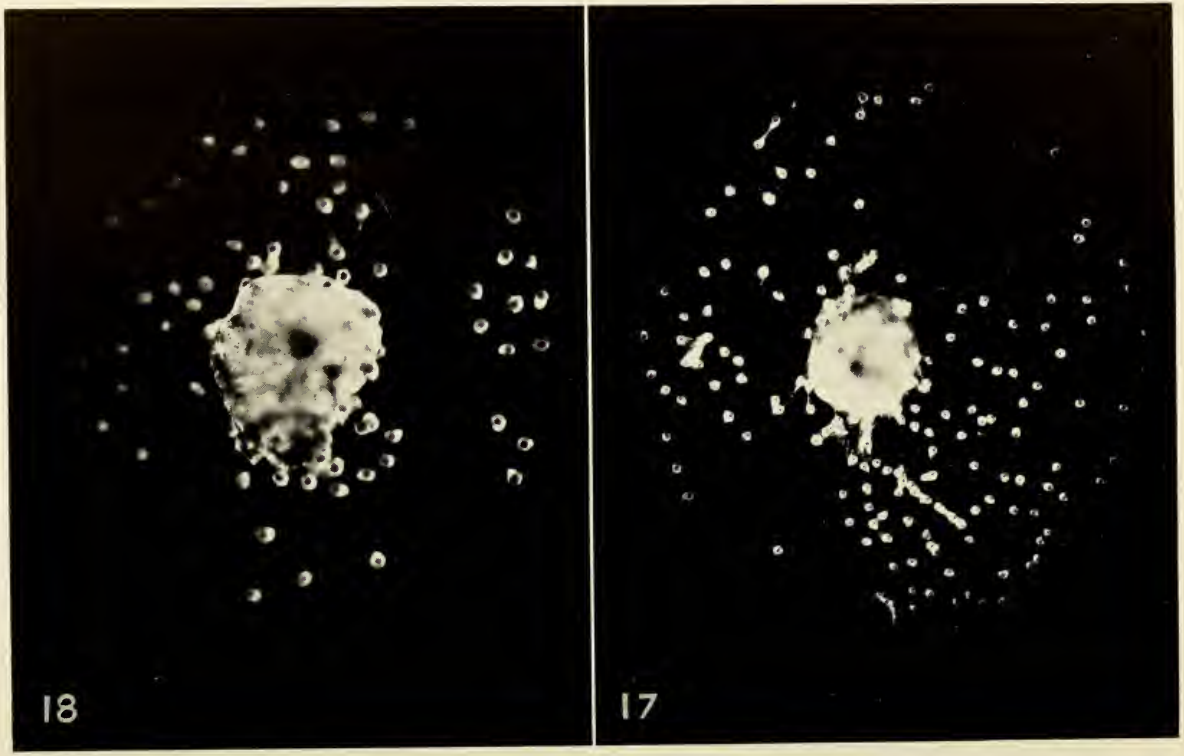


For explanation, see page 11.



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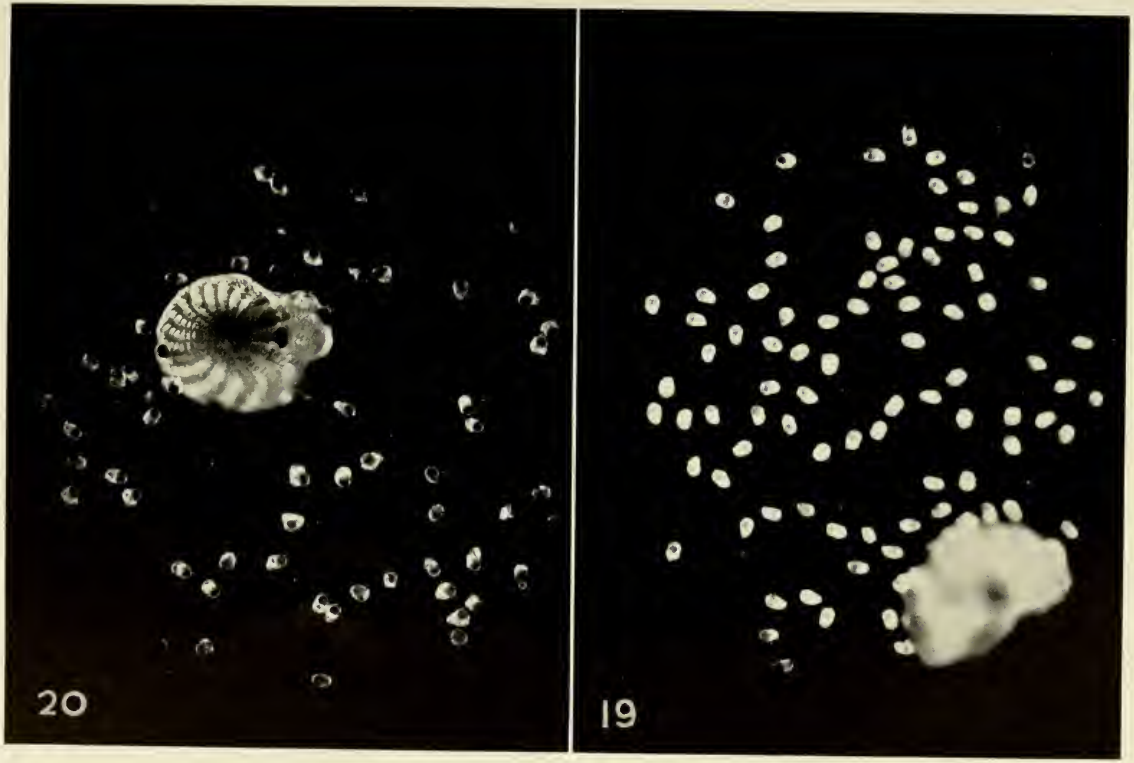

For explanation, see page 11.