Zoology. — *On the structure, life-history and development of Hedrocystis pellucida* HERTW. & LESS. By H. R. HOOGENRAAD. (Communicated by Prof. J. F. VAN BEMMELEN.)

(Communicated at the meeting of February 26, 1927).

1. *Collection and conservation of Material.*

Those Heliozoa, whose protoplasmic body is enclosed in a homogeneous, spherical skeleton, generally provided with a stalk, and perforated by outlets for the pseudopodia, were in 1874 by R. HERTWIG and E. LESSER united in the group of the *Desmothoraca*. This group contains a very small number of genera, only one of which, the genus *Clathrulina*, has become more accurately known, and of this moreover but one single species *C. elegans* CIENK. It is true that SCHAUDINN in 1896 mentioned a second genus *Orbulinella* ENTZ Sr., as being rescribed with sufficient precision, but the author himself of this genus argues in favour of the view, that it occupies a separate position in the systematic arrangement, in the neighbourhood of the Foraminifera. In the same way PENARD, who however did not know the animal from personal observation, presumes that *Orbulinella* stands nearer to the Thecamoebic Rhizopods than to the Heliozoa.

The species belonging to the genera *Elaster* and *Choanocystis* until now have only been observed by their discoverers, and moreover in a very restricted number of widely spread specimens, so they must be considered as quite insufficiently known and therefore of very doubtful value for systematic arrangement.

Somewhat better stands the case for the genus *Hedriocystis*, which HERTWIG and LESSER proposed in 1874 for a species *H. pellucida*, discovered by them in the neighbourhood of Bonn. Later on PENARD described a second species *H. reticulata*, and afterwards BROWN distinguished a third one: *H. spinifera*.

Yet just like those named above the representatives of this genus are so rare and consequently so incompletely studied, that older investigators (ARCHER, SCHAUDINN, BÜTSCHLI), who were only acquainted with the species *H. pellucida*, considered even this to be a doubtful form, which possibly should be united with *Clathrulina*. As the more recent observations have not added much of importance to these older statements, the only form of the whole group *Desmothoraca*, that might be considered as characterized with sufficient accuracy, remained the species *Clathrulina elegans*.

In September 1926 I was able to collect material from the so called Wisselsche Veen near Epe o/d Veluwe, a locality, which for many years I have highly valued as a rich emporium for Rhizopods and Heliozoa, amongst which were several of the rarest and most remarkable forms ever known. Of those that I have already mentioned on former occasions, I wish to refer to *Penardia mutabilis, Vampyrella lateritia, Hyalodiscus rubicundus, Nuclearia caulescens, Quadrula symmetrica, Heleopera petricola, Cryptodifflugia compressa, Paulinella chromatophora, Raphidiophrys elegans* and *viridis, Acanthocystis aculeata* and *turfacea, Clathrulina elegans, Clathrella Foreli.*

In the same way the spoils of this years collecting proved again rich in interesting forms, among which *Biomyxa vagans, Raphidiophrys pallida, Plagiophrys scutiformis, Gromia nigricans, Difflugia oviformis, Lieberkühnia Wageneri,* were new for the locality, the two latter moreover for the dutch fauna in general.

But what chiefly attracted my attention was the frequent occurrence of a great many specimens of one of the above-mentioned species of Heliozoa, namely *Hedriocystis pellucida* HERTW. & LESS. Since the discoverers, who observed it about 1870 in the neighbourhood of Bonn, this animal had been found by LEVANDER in Finland (1892), and by PENARD in a few localities near Geneva, about 1900, but nearly always in scanty numbers. PENARD is the only one, who gives a somewhat detailed description of its structure and life-habits, but its development has hitherto remained unknown.

The sample of water, in which the animals occurred, was taken from a shallow marshy pool, recently called into existence by the removal of the superficial layer of peat. I studied the animals in the usual coverglass-preparations, but always added a few algae and a little detritus to the liquor, with the view of keeping them as much as possible in natural conditions.

As experience proved, when the evaporated liquor was regularly replaced by distilled water, the animals kept alive for days and even for weeks in the same preparation, and went on propagating. In this way they could be studied at a magnification of 400—800 diameters.

2. *Structure of the protoplasmic body and the shell.*

The protoplasmic body of *Hedriocystis pellucida* (Fig. 1) is, in the same way as that of *Clathrulina elegans,* enveloped by a nearly spherical shell, which is fixed to the fragments of detritus lying in the water, by means of a long and thin stalk. The animals born in my preparations, often fixed this stalk on the coverglass or the slide.

On the surface of the shell conical projections are to be seen, either blunt or pointed, provided at the tip with exceedingly minute openings by which the pseudopodia emerge. I have never succeeded in observing these pores directly, but owing to a circumstance to be described later, I have been able to calculate their width at a diameter of $\pm$ 2 μ. By the presence of these protuberances the shell in optic sections has the appearance of a more or less regular polygon with 4, 5, 6 or 7 sides and with prominent angles ;

by elevating the object-lens to a higher level, the eminences on the surface of the shell assume the aspect of sharply defined, dark crescenticform lines, which give a very characteristic appearance to the animal.

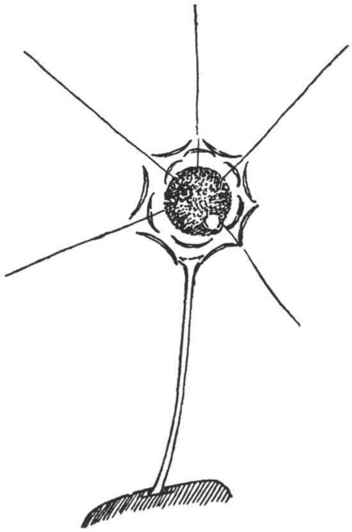

Fig. 1. *Hedriocystis pellucida* HERTW. et LESS. A specimen of the type. In the protoplasmic body at the left topside one sees the nucleus; at the right bottom-side a contractile vacuole. × 800.

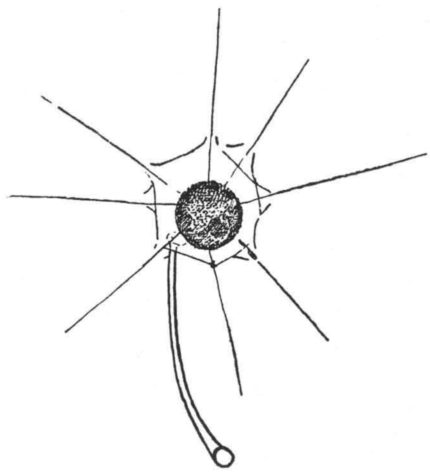

Fig. 2. *Hedriocystis pellucida*. A specimen of the deviating form. × 800.

The above-described form represents the type, but besides this my material contains rather a considerable number of specimens of a second form, which though corresponding with the typical one in all other respects, is markedly distinguished from it by the structure of the shell. In this deviating form the thickness of the shell is much less, which makes the contourline of the optic section decidedly slimmer, to such an extent as to reduce it to a hardly visible line. In the second place the protuberances are less pronounced, so much so, that in high-level observation they never produce the above-described effect. The specimens showing this deviation were always completely colourless, those of the type being of a yellowish-red shade. PENARD considers this shade as a hue of the substance of the shell proper, but according to my view it seems more probable that it is caused by a phenomenon of interference. From a careful comparison of descriptions and illustrations I come to the conclusion, that the discoverers HERTWIG and LESSER have only seen what I have just now described as the deviating form [1]), while the animals observed by PENARD

[1]) They compare the external appearance of the animal to a „Morgensternartige Keule", meaning a mediaeval club, which at its swollen top is provided with spikes. This description corresponds much better indeed with the variety than with the type.

probably represented the type. Transitions between the two forms never came into my observation.

The diameter of my specimens fluctuated between 20 and 25 μ, their dimensions therefore correspond with that of the animals studied by former investigators.

As already remarked by PENARD the stalk is probably solid, not containing a central canal like that of *Clathrulina*. Its length was not in all cases easy to be measured, especially so, when it stood in a more or less oblique position. In the cases, where I was able to take its measure, its length varied between 50 and 90 μ, its thickness is $\pm$ 1 μ. The distal extremity of the stalk is either simply broadened, or split up into a small number of tiny fibres, giving it a more or less rooted appearance, as also sometimes occurs in *Clathrulina*.

As to the material of which the shell and its stalk are composed, nothing can be asserted with certainty; it seems to me to be rather more chitinous than that of *Clathrulina*, which is generally assumed to contain a certain amount of silicon. The protoplasmic body contained in this envelope has an average diameter of no more than 10—12 μ, and is freely suspended, probably by means of the pseudopodia, in the centre of the shell, or a little excentrically. In outward appearance it looks most like that of *Actinophrys sol*. Generally it shows no very distinct shade, but is tinted somewhat blueish-green. Its form is nearly spherical or somewhat flattened in a spheroïdal way.

At its circumference it is sometimes lobed or denticulated in an irregular manner, but habitually it is rather purely rounded. The line of its contour is sharp and dark, which points in the direction of great optic density. Consequently the animals, even when observed with low powers, show a sharply defined appearance, making them immediately conspicuous, when once we have got acquainted with them.

Big food-morsels are generally absent, but small dark granules are always present, though in varying number.

Probably on account of the compact structure of the protoplasm, the nucleus is difficult to be distinguished. In cases where it is visible (Fig. 1, 6), it presents itself as a big, round spot, lying somewhat excentrically and provided with a large light-grey endosome.

Vacuoles seldom occur. Only when an uncommonly big prey has been swallowed (Fig. 6), a vacuole surrounding it can be clearly distinguished. Contractile vacuoles are always present, to the number of two or three. (Fig. 1, 6). They never form prominences on the surface, as in *Actinophrys*; their bulk size is variable and may attain $^1/_3$ of the diameter of the protoplasmic body. Their contractions are regular, with usually short periods; in one case where I was able to observe this process for a considerable time, the interval between two successive contractions amounted to $\pm$ 30 seconds (temperature 18°).

Excretion of undigested food-remains was never observed by me.

The pseudopodia are generally present in restricted numbers, in toto probably never more than 10 to 15, but sometimes only 6 to 8. In the normal condition they are thin, straight, unbranched and rather long, up to ± four times the diameter of the shell; in most cases they start with a sharply defined, unbroadened base from the body of the protoplast. They are therefore different in several respects from the pseudopodia of *Clathrulina elegans,* which broaden considerably towards their base, and moreover are often forked, and sometimes form anastomoses. Eventually however, especially when food is taken in, the pseudopodia of *Hedriocystis* assume various irregular shapes by curving, broadening and by the appearance of vacuoles (Fig. 6). I never was able to observe a real current of granules; what might easily be considered to be such, in reality turned out to be nothing but the sliding movements of a microbe, absorbed as a food-object, and transported in the direction of the protoplasmic body.

3. *Life-history.*

In my specimens the food, conformally to what was observed by PENARD, chiefly consisted of bacteria, only in a few cases a small Flagellate or the swarm spore of some alga was captured. The absorption occurs in the usual way. The pseudopod, with which the prey comes in contact, generally forms a very spacious food-vacuole around it. Inside this the food-morsel becomes slowly moved towards the shell (Fig. 6). During the ingestion the pseudopod remains stretched: the prey, enclosed in its vacuole, glides along it with tolerable speed. It is clear that this movement points to the existence of a protoplasmic current in a centripetal direction.

Small objects speedily disappear into the interior of the protoplasmic body through the pores of the shell, bigger ones on the contrary remain for a long time fixed on its outside, surrounded by a protoplasmic mass, which itself is in communication with the rest of the body. After a certain lapse of time the prey is seen to become smaller and less sharply defined and at last it disappears completely in the protoplasm. In some cases I could observe that the last remnant slipped into the shell and sank into the protoplasmic body. Just as in *Clathrulina* part of the food at least is digested outside the shell.

Under normal circumstances the animals swallow rather a large quantity of food. It is not rare that several pseudopodia at a time are seen to carry bacteria towards the protoplasmic body. Digestion and absorption of the food seem to take place rapidly; occasionally I succeeded in following rather big food-morsels from the moment of their entrance into the protoplast up to that of their disappearance or becoming unrecognizable; the whole of this process lasted a couple of hours. By this rich nutrition the young animals grow rather rapidly: in two or three days they attained the normal size, and shortly afterwards the reproduction sets in.

As far as is known up till now, this latter always occurs by binary fission of the protoplasmic body ; one of the daughter-individuals then escaping from the shell, to form a new specimen, which provides itself with a stalk, while the other remains behind, occupying the old shell. The processes of division and formation of the shell together take less than twelve hours ; after this both animals enter into the period of food-ingestion and growth, then a new division sets in and so on. So the whole of the simple life-history of *Hedriocystis* takes place within three days, of which the greater part is devoted to feeding and growing, a much smaller period to propagation. The latter is — as far as known — purely vegetative, processes of impregnation or sexual differentiation have hitherto remained quite unknown for this animal, as for most Heliozoa in general.

4. *Reproduction.*

The older investigators do not seem to have observed the division. It is true that HERTWIG and LESSER, as well as PENARD, make mention of specimens, in which two protoplasmic bodies were seen inside one shell, and which therefore undoubtedly had just before passed through the act of division, but about this process itself they tell us nothing. I have been able to follow it several times from beginning to end ; as far as I could see, it always takes the same course.

The division (Fig. 3) takes place during activity inside the shell, which

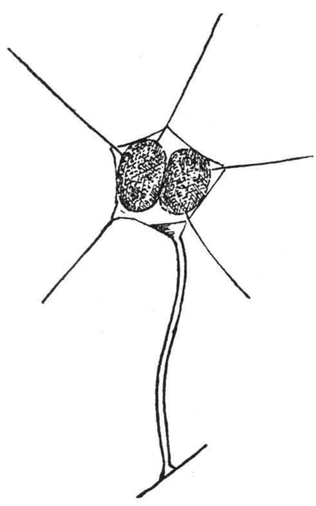

Fig. 3. *Hedriocystis pellucida.* Divided specimen of the deviating form. × 800.

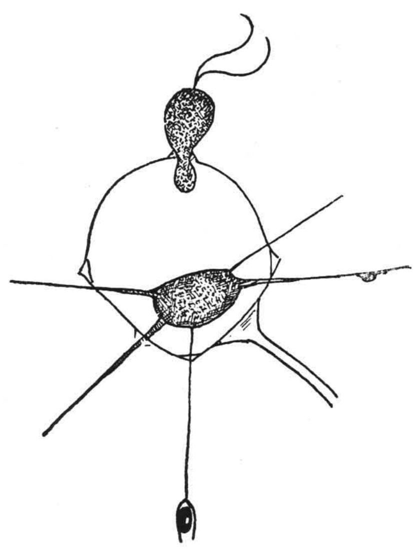

Fig. 4. *Hedriocystis pellucida.* Divided specimen of the deviating form, one of the daughter-individuals leaves the shell as a swarm spore with two flagella. The other animal is taking in food with two of its pseudopodia. × 1200.

means, that the pseudopodia remain protruded. Nor is there the slightest indication of encystment or of a resting stage. I never saw cysts, as described by HERTWIG and LESSER and figured by PENARD; and I am inclined to explain their observations as simply caused by temporary retraction of the pseudopodia, a condition which I have observed more than once. PENARD himself states that the wall of the cyst was "lisse et peu apparente"; HERTWIG and LESSER express themselves in the same sense.

The divisional process proper shows nothing particular; it is completed in a few minutes. The behaviour of the nucleus could not be observed. During the division the capture and absorption of food goes on as usual.

The plane of division generally stands perpendicularly to the stalk, or at least to that part of it, which is in immediate contact with the shell.

After division is complete, the two daughter-individuals generally change their position, and lose their definite orientation inside the shell-cavity. They then assume a broad-elliptic shape, their long axes standing parallel, while they are a little flattened on the side where they are in contact with each other.

For how long the animals remain in this condition, I cannot tell, but I presume it is only for a short time, and certainly no more than 12 hours. At the end of this period one of the two individuals loses its rounded shape and begins to make amoeboïd movements, at first at intervals, afterwards more continually. Shortly afterwards two flagella become visible, arising side by side on the surface of the body and soon they begin to show slow movements. They are exceedingly thin and therefore difficult to be seen, probably also because their optic density is but slightly different from that of water. Shortly after this, the pseudopodia are retracted, and the animal begins to force itself through one of the shell-pores (Fig. 4). At first a small drop of hyaline plasma appears on the external surface of the shell, in the course of time this slowly enlarges by continuous outpouring of plasma through the shell-opening; the part of the body still remaining inside the shell proportionately diminishing in bulk. During this act the animal is continually constricted by the extremely narrow shell-pore, and so has the form of a dumb-bell; the diameter of the constriction amounts to 2 μ; therefore this will probably be the width of the shell-pore. From this extreme constriction, and the fact that its diameter remains unchanged during the whole act of escaping from the shell, we may conclude that the animal does not succeed in enlarging the pore through which it forces itself out; the shell therefore, however thin, must be of a rather rigid texture.

When the last part of the protoplast is still inside the shell, the two flagella have already passed out and their movements, at first slow, grow faster, and under their influence the free part of the animal, still fixed by the shell-pore, is brought into a rapid vibration, Soon afterwards the animal begins to rotate along its longitudinal axis, and thereby the last contact with the shell is broken. The animal then stretches and shortens itself and swims away as a zoöspore with peculiar undulating and rotatory movements. The other half, remaining in the shell, rounds itself and takes up a central position, so assuming the normal state for this animal.

The zoöspore (Fig. 5) has a cylindrical shape with rounded ends, sometimes the posterior pole is a little pointed. Its length is 15 μ, its breadth 3 μ. It is transparent, uncoloured and rather regularly granulated. In its anterior part is a nucleus, somewhat difficult to discern and at the posterior end a small but distinct contractile vacuole. The length of the flagella is probably somewhat greater than that of the spore. The rhytm of the swimming movements is so characteristic, that even with a low power it is easy to distinguish the zoöspore from similar organisms.

After a short time, usually only two or three minutes, the movements become slower, and soon the zoöspore fixes itself, and rounds itself off as a protoplasmic body of $\pm$ 10 μ in diameter.

Fig. 5. *Hedriocystis pellucida.* Swarm spore. Before the nucleus, behind the contractile vacuole. $\times$ 1200.

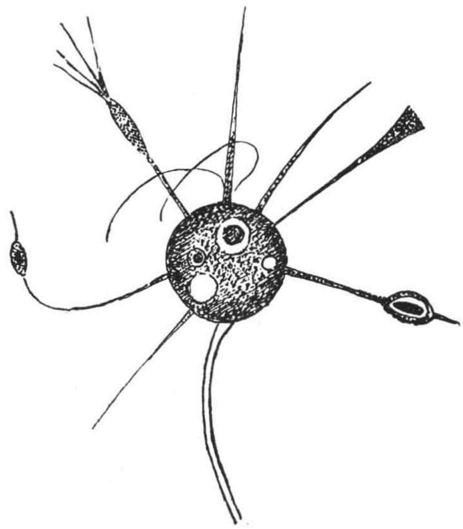

Fig. 6. *Hedriocystis pellucida.* Young specimen before the formation of the shell. At the top two flagella are still visible, at the bottom the outgrowing stalk. Abnormal pseudopodia forms two of the pseudopodia with a captured microbe. In the plasmic body at the top the nucleus, at the bottom, right and left side a contractile vacuole, at the left of the centre a digestion vacuole with a microbe. $\times$ 1500.

The flagella, which, during the free-swimming period, remained invisible, on account of the rapidity of their movements, now become visible again. During a considerable lapse of time, at least a couple of hours, they execute peculiar, pendulating movements, but at last they disappear. What may be their final fate, to become dejected, or retracted, I am not sure ; their extraordinary thinness already necessitates to the greatest exertion to get a look at them, and even then one only succeeds from time to time just for a moment. Almost immediately afterwards the pseudopodia make their appearance, within a minute or so they have attained their normal length. In its general aspect the animal now rather resembles a miniature specimen of *Actinophrys sol* (Fig. 6). During the first period of their existence the pseudopodia appear to be in a very unstable condition; they often show deviations from the normal, straight and thin form which afterwards is typical for them, these consist in enlargements, sinuosities, ramifications and the formation of vacuoles. While the flagella are still present, the taking in of food already begins. Likewise the development of the stalk is a question of a few minutes only. In the same way as described by HERTWIG and LESSER for *Clathrulina* the stalk is formed by a protoplasmic protrusion of the body. The supposition of PENARD, that originally the stalk is nothing but a pseudopodium, as far as I can see may very well be correct. Be this as it may, soon afterwards the stalk is distinguished from a common pseudopodium by its superior thickness and stabile diameter. Originally it stands rather strictly perpendicular to the surface on which the stalk fixed itself, probably in consequence of a thigmotactic stimulus. This may be stated whith special ease when the support on which the organism fixes itself is the coverglass or the slide. The position of the stalk then being vertical, it becomes visible in projection as a sharply drawn ring of very small diameter, either above or under the protoplasmic body. By means of the scale on the micrometric screw the length of the stalk could be very accurately measured. Still easier could this be done by direct measuring, when the stalk was fixed to some object floating in the water, and thereby was occupying a horizontal position. After fixation the stalk elongates considerably just as in *Clathrulina*; after half an hour it attains its definite length. But long afterwards, for at least two hours, the upper part of the stalk, adjoining the protoplasmic body, shows amoeboïd movements in the shape of blunt protuberances, which soon flatten out again. In a few instances I also was able to distinguish a current of granules in this part of the stalk, of the same character as always occur in the body. In the young stalk of *Clathrulina* HERTWIG and LESSER mention also such a granular current. All these facts plead distinctly for a genetic connection between stalk and pseudopodia, though perhaps the assertion that the stalk originally becomes formed as a true pseudopodium may not be quite accurate. In a phylogenetic sense however the view that the stalk of *Clathrulina* and *Hedriocystis* must be derived from a pseudopodium, seems to find support in the above-mentioned facts. A few hours after its formation the stalk begins to change its aspect; it becomes thinner and more transparent, the amoeboïd motility disappears, probably on account of a change of its purely protoplasmic nature to the harder, more chitinous material, of which the definitive stalk consists.

An insoluble problem in this respect is the question, how the connection of stalk and shell is brought about. For though the stalk undoubtedly is formed as a product of the protoplast, it afterwards has lost all ties with it, and passes exclusively into the shell. As far as I can judge, this question is not even completely solved for *Clathrulina*, though here it applies somewhat differently, because in *Clathrulina* the stalk contains a canal. It is true that also this stalk is originally formed as a purely protoplasmic stem, but then its outer layer hardens to a tube corresponding with the skeleton of the protoplasmic body, and, as HERTWIG and LESSER take it, the protoplasmic core then withdraws from the lumen.

In this connection we also may call to memory PENARD's communications, that in *Nuclearia caulescens* PEN., an organism of doubtful affinities but most probably connected with the Heliozoa [1]), both types of stalk seem to occur. One of them corresponds according to PENARD's description with the formation of the stalk in *Hedriocystis*.

About the formation of the shell I can make only a few remarks; nor is there much known about it in *Clathrulina*. As in this latter form the shell is always formed later than the stalk; HERTWIG and LESSER even saw a specimen dividing before the shell was formed, but I never met with this phenomenon.

At the moment the outline of the shell first becomes visible as an extraordinary thin stria, we should expect it to show itself immediately on the surface of the protoplast; this however is not the case, but it is seen from the beginning at the normal distance from this surface. This means that it is separated from it by a space amounting in diameter to that of the protoplast itself. The shell therefore seems to be formed independently of the body, so to say as a coagulum in the empty space. Up till now I cannot give an explanation of this curious appearance.

5. *The function of the zoöspores in Heliozoa.*

As we saw in the foregoing, *Hedriocystis pellucida* exclusively multiplies by fission — at least as far as we know up till now — and this division is followed by the formation of a zoöspore by one of the daughter-individuals. This mode of development likewise occurs in *Mikrogromia socialis* R. HERTW. This animal also splits up into two halves, of which one leaves the shell of the mother-individual, but in this case it may either assume the form of a zoöspore provided with two flagella, or that of an *Actinophrys*-like organism. The remaining history of these stages however is totally unknown.

In *Hedriocystis* the same process repeats itself periodically with one and the same animal, which thereby assumes the character of a mother-organism, producing a whole generation of daughter-individuals by serial division.

[1]) This organism was found by me on former occasions already, in a few specimens in the „Wisselsche Veen".

The division causes the multiplication of individuals, the formation of the zoöspore favours the distribution of these individuals in space.

Both processes: binary division and formation of zoöspores, also occur in *Clathrulina*, though as far as we know the connection between them is less regular.

The alliance between this and *Hedriocystis*, which originally was only inferred from the structure of the shell and the protoplast, therefore finds a new support in development.

So we may state that the group of *Heliozoa desmothoraca* contains at least two forms, *Clathrulina elegans* and *Hedriocystis pellucida*, which in their structure and development are fairly well-known. The rest of the species brought under that heading, remain rather uncertain.

In the group of Heliozoa, apart from *Clathrulina elegans*, zoöspores had already in former days been observed in the case of *Acanthocystis*-species. This mode of reproduction likewise frequently occurs in other groups of Rhizopods, especially with Radiolarians. PASCHER, in his well-known treatise on the connections between Flagellates and Rhizopods, combates, especially on botanical grounds, the opinion of DOFLEIN, that in all departments of Rhizopods the forms with flagellate phases are the most primitive.

Now the systematic place of the Heliozoa as a whole is still rather uncertain, and the same is the case with the different smaller units which compose it, with regard to their mutual relationships; yet we may assume with a fair amount of probability that the *Desmothoraca*, to which *Clathrulina* and *Hedriocystis* belong, with their peculiar perforated and pedunculated shells, represent a less original condition than the naked' *Aphrothoraca*, such as *Actinosphaerium*, and *Actinophrys*. The occurrence of zoöspores in the more highly differentiated types and their absence in the lower constitutes, as regards Heliozoa, an argument in favour of PASCHER's views.

PASCHER, who, in the above-cited study, proposes the thesis, that Flagellates are more primitive organisms, Rhizopods on the contrary more secondarily modified ones, affords a great phyletic value to zoöspores, in the sense of the theory of recapitulation.

Zoöspores should be temporary recollections of more primitive stages of development, through which the organism passed in former periods. Even in relatively high-differentiated forms they always still occur, be it as carriers of the sexual function, or as emigrants for the distribution of the species.

Even if this supposition should prove right, it affords no explanation of the fact, that the zoöspores, as reminiscences of more primitive flagellate organisms, may occur in higher specialised forms, while they have disappeared in less specialised, more original types. Their occurrence with sedentary organisms, as *Clathrulina* and *Hedriocystis*, where nothing is known about a possible sexual function for them, might however, as

PASCHER points out, be brought into connection with a chance of distribution in space, beyond the immediate neighbourhood of the mother-organism.

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