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THE STRUCTURE AND DEVELOPMENT OF THE COLONY IN GONIUM

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Gonium, a simple coenobic plant growing in all our fresh waters and becoming very abundant when conditions are favorable, is an interesting type which illustrates in very simple terms a close approximation to a pure mosaic development. The plant is a simple plate-shaped colony consisting of four, eight, or sixteen cells. The arrangement of these cells is strikingly uniform in the sixteen celled colony and in this respect it is in marked contrast with such forms as the water net. There are no structural variations in Gonium corresponding to the various shaped meshes with from three to six or seven sides which we find in the water net, and as we shall see this relative fixity of type is doubtless correlated with the method of formation of the colonies by a definitely specified series of cell divisions. In its method of development Gonium thus affords an interesting type for comparison with other coenobic plants in which the colonies are formed by the spontaneous aggregation of free swimming zoospores. The forms I have studied seem to agree in all essential respects with the description of the widespread species Gonium pectorale, Müll. I have found it in aquarium jars at Madison and in open pools at Berkeley, Calif. The figures and micro-photographs here given are all from the Californian material.

The structure and development of the flat plate-shaped colonies of Gonium and their relationship to other members of the volvox series have been carefully described by many of the earlier students of the algae (1, 3, 6, 16). The morphogenetic processes by which the solid and hollow globular colonies of Pandorina and Eudorina and the plate-shaped colonies of Gonium and the later discovered Platydorina are developed early attracted attention and the order of cell division and the cell lineage have been accurately worked out.[3]

In my material I do not find that the third divisions tend to be radial, as is described for Eudorina and as Al. Braun[1] thought they must be for Gonium. Cohn's[3] figures of the eight celled colonies whose correctness Braun doubted are good representations of forms, which I find quite commonly. The very young eight celled stage consists simply of two rows of cells and is quite unlike that described for Eudorina. The figures of Bütchli[2] and Migula[14] for the sixteen celled stage are quite inadequate as compared with the earlier one of Cohn.[3] They fail to show the form of the cells accurately and give no correct indication of the apparent difference in size between the central and peripheral cells. They also fail to show that the middle cell on each side is somewhat drawn back toward the center as was noted by Müller[16], Cohn[3] and Al. Braun[1], Oltmann's[17] figure taken from Migula is incorrect in all these particulars. Braun[1] regards the colony as consisting of three concentric series of cells, four, four and eight, thus emphasizing the fact that four of the outer twelve cells are out of alignment with the other eight.

Microphotographs of colonies in a stage of vigorous and rapid growth such as are reproduced in figures 4 to 6 show that the sixteen cells form a square with its corners truncated, giving it a somewhat octagonal outline with a slight depression in the middle of each side. The cells are ovoid or pear shaped (Fig. 19) and bear two cilia at the narrowed end. Part of the cilia are shown in the eight celled colony (Fig. 17). By means of these cilia the organism moves through the water flatwise so that it presents its edge view when observed from above under the microscope. Such an edge view of an eight celled colony is shown in figure 19, and we observe that the cells are noticeably longer than they are wide. The long axis of the cells in the outer row is inclined outward so that the cilia of these cells do not point straight ahead, but obliquely forward.

As the colony swims it rotates edgewise. This mode of locomotion seems extremely awkward since the colony thus offers the greatest resistance to the water. The arrangement of the cells in two series, with four in the interior and twelve in the periphery, is correlated with the presence of the large square intercellular space, which is an almost universal characteristic of the colonies. It is not impossible that the opening so formed has some significance in maintaining the equilibrium of the colony as it moves through the water. The water which is to be displaced does not necessarily all have to flow around the edges of the colony; a portion may pass directly through the opening in the middle and doubtless this favors steadiness of movement.

It has been claimed that the whole colony is imbedded in a gelatinous secretion which is so abundant as to fill all the intercellular spaces, including the central square Migula[14] finds evidence of the thickness of this gelatinous envelope in the observation that the motion of the cilia is limited to the outer one-half or two-thirds of their length. I have not been able to convince myself of the presence of any such abundance of jelly about the colonies in my material. The cell walls are gelatinous and I have frequently observed the motion of the peripheral portion of a cilium while the basal portion remains quiet as if held in some way. The same cilium may, however, a few moments later bend freely from its base. Such observations can be readily made on mature colonies whose cells are dividing. The ciliary motion becomes very weak at this time, as will be noted below. Moore and Goodspeed[15] report that the entire cilium may take part in the stroke, though usually only the peripheral one-half or one-third is used. Of course, the amount of jelly secreted may vary under different environmental conditions.

The most important characteristics of the colony as a whole are to be found in the space-relations between the cells. These relations are on the whole strikingly constant and constitute the fundamental structural features of the plant. If we examine the interrelations of the cells of the colony beginning at either corner in the outer row we find, counting the points of contact of each cell with its neighbor, that we have the simple series, 3, 3, 4, repeated four times (See Figs. 1 to 6). The pairs of cells that make the corners of the square are each in contact with only three cells while the middle cell of the side, which is in the slight depression, is just as regularly in contact with four. Each of the four interior cells is in contact with six of its sister cells and these simple relations bring with them an arrangement of the cell walls involving the formation of the series of curves which Cohn long ago observed and figured and which come out very clearly when the colony is photographed a little out of focus, as shown in figure 13. We see from this that each of the four inner cells is in reality an inequilateral hexagon, that side which is adjacent to the central square being a little longer than the others. The walls of the cells, as the photograph shows, form four sets of parallel curves. The intercellular spaces are in the same fashion shown to be triangles with somewhat unequal sides, showing at once that the cells are arranged as compactly as possible. All of these structural characteristics we see at a glance are just those which would obtain in any system of spherical liquid or semi-liquid globules which are placed in two such series, that is, twelve about four, assuming also a tendency to the greatest possible compactness. The details of the organization of the colony are in accord with the principle of least surfaces, limited by the method of division by which the cells were produced. Every semi-fluid droplet of protöplasm has rounded itself up in cross section as perfectly as is consistent with its adhesion to and pressure from the adjacent droplets.

If we put together a series of equal circles arranged in this fashion we shall find that the four inner circles will not be in contact either with each other (text Fig. 1) or with certain of the peripheral cells (text, Fig. 2). To bring into contact the whole series of cells as we find them in the Gonium colonies the diameters of the inner

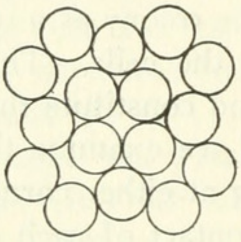

Fig. 1

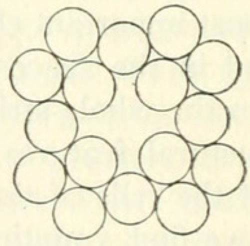

Fig. 2

cells must be increased relatively to those of the outer series. This is apparently accomplished in Gonium by the flattening of the inner cells and by lateral compression of each of the cells in the outer series. This lateral compression of the peripheral cells is especially conspicuous in the young colonies, where the outer cells are frequently (Figs. 1-6) quite oblong.

We have thus a plant of definite form with a specific arrangement of its constituent parts which is strikingly uniform and whose cells show in certain respects the adhesiveness and surface tensions of colloidal droplets of protoplasm. That the cells have also an internal organization is, however, shown by their pear shaped form and the slightly flaring position of the peripheral series (Fig. 19). The constancy in structural features in Gonium as compared with Hydrodictyon is as noted above rather striking and is doubtless due to the mosaic type of development here present.

The only modification in the cell relations which can be regarded as at all normal is that in which the central intercellular square is omitted, two of the four cells of the inner series being brought together so that they are in contact, the other two being proportionately separated. This generally leads to a change of form of the whole colony, in some cases giving it a somewhat rhomboidal outline (Fig. 11). In the case shown in figure 12 the absence of the intercellular square in the center has been compensated in a sense by the formation of another intercellular square at one corner between the inner and outer series of cells. The colony has thus bcome more nearly square like the ordinary type. These cases with rhomboidal central group are rather rare, so few as to make a fraction of one per cent of the colonies to be observed under normal conditions. In them the greater compactness of the central group leads to a correspondingly increased crowding in the outer series. This may lead to the crowding of one cell out of the plane of the others so that it overlaps two or the displaced cell may come to lie squarely in front of or behind its neighbor. How the cilia are placed in such a case I have not been able to determine. I have never seen the sixteen cells arranged to form a perfect rhomboid. The evidence is clear that the colony is in a state of unstable equilibrium owing to the presence of twelve cells in the peripheral series in the space which would be more naturally filled by ten, as shown in text figure 6.

The figures 14 and 15 illustrate divergences from type which may plainly be classified as pathological or monstrous. Figure 15, for example, shows a colony with sixteen cells in a totally aberrant arrangement. This was the only case of the sort which I have observed. Cases in which one or more of the cells have died or have been broken out of the colony in some fashion, are much more common. Such a case is illustrated in figure 14. In such cases the colony shows no tendency to regenerate the missing cells nor to modify its form so as to produce a symmetrical outline. Colonies frequently split in two. This process is shown going on in figure 16. The result is two colonies of eight. Such colonies show no power of regeneration, but they may live and reproduce themselves in an entirely normal fashion. They are to be distinguished from colonies of eight cells formed in ordinary reproduction. Their shape is different, as will be noted.

We may turn now to the problem of the reproduction of the plant in order to determine the method by which such a sixteen celled colony is produced in ontogeny. The cells of the colony are all capable of vegetative reproduction and each one, as a rule, produces a new sixteen celled plate. Division occurs commonly at night from ten to twelve P. M., and the new colonies are set free from the parent cells by the following morning. The general behavior of the plant in these respects is analogous to that of Pandorina, and other related forms. One can watch the process of division readily under the microscope. The colonies generally continue to move about until the division has reached an advanced stage in each cell, but they become very sluggish and can be readily followed. It is impossible, however, in the case of the sixteen celled colonies to obtain satisfactory photographs of these division stages. The connection between the cells apparently becomes very loose. The walls gelatinize and the intercellular connections are broken. As a result the colony becomes warped in various fashions and it is impossible to get any large area of it in a single focus. Figure 10 shows about half of a colony in which the cells are beginning to divide. The colony was sc warped that the other half was badly out of focus. In cell *a* division is just beginning; in cell *b* the first division is complete. Cell c has divided twice and three daughter cells show in the negative, though they have not been brought out in the reproduction. It is obvious at once that the planes of division of the different cells of the colony show no orientation with reference to each other or to the plane of the parent colony. In the case of the four celled colonies conditions are more favorable in this respect and I have obtained a photograph showing the first division of all four of the cells in such a colony. This is shown in figure 22. Division does not begin in all of the cells simultaneously and it progresses quite irregularly, after it has once begun. Here again it is evident that the plane of division is independently determined in each cell.

After the cells are all in division while the motion of the cilia continues weakly the colony may become lodged in such fashion as not to move further, and under these conditions it is easy to make camĕra lucida sketches of the entire sixteen cells of the colony, showing the stage of division which each cell has reached. Text figures 3, 4, and 5 show three successive stages in the reproduction

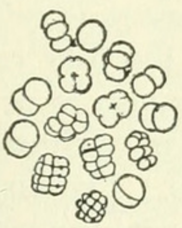

Fig. 3

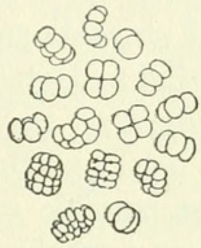

Fig. 4

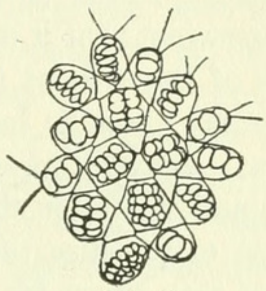

Fig. 5

of the same colony, separated from each other by intervals of about thirty to forty minutes. The drawings were made with camera lucida between ten and eleven thirty p. m. A glance at the first of these sketches shows at once that the planes of division are different for the different cells. The first division may lie at almost any angle to the plane of the colony and in almost any direction from tangential to radial. It is observed at once that the form of the whole has no dominating influence on the orientation of the division planes, although it is entirely conceivable that such influence should be exerted here, if anywhere, since the cells have been in contact with each other and there is every opportunity for cellular interaction. There is no evidence either of any general form—regulating principle at work. Each cell is apparently self-determined as to the plane of its division, that is the plane of division is determined by cellular organization as contrasted with any assumed heredity of form for the whole organism. When once the first division is begun, however, the plane of the future colony is fixed. A glance at the figures shows at once that the subsequent divisions follow the principle of rectangular intersection, the spindle figures, which may be assumed to be present here as in other algae, always lying in the same plane. Each successive plane of division tends to cut that of the preceding division at right angles. No one would question that this is a phenomenon of cellular behavior and is due to the organization of the cell itself, and it works out to produce, as we shall see, a many celled colony of perfectly definite form and organization which is also doubtless fairly adaptive.

The four celled stage consists of equal quadrants which tend at once to round up, leaving a four sided intercellular space between them in the middle. As noted, the colony is already under pressure from the gelatinous cell wall which swells at this stage and forms an envelope which is in contact with the cell mass, although it is so transparent that it does not come out in the photographs. The position of the cells as formed is unstable and this pressure is sufficient in many cases to lead to a slight displacement of the four cells at once, especially as the movement of the cilia tends also to produce unequal strains in the whole mass and thus to lead to readjustments so as to produce the greatest possible compactness. The displacement may go so far as to form a markedly rhomboidal instead of a square group. This condition is shown in a number of young colonies in text figures 3 and 4. It may perpetuate itself throughout the whole life of the colony (Figs. 11 and 12) or it may apparently disappear again later under the conditions of surface tension that develop as the colony grows. It consists in the familiar phenomenon of the separation of two of the cells and the approximation of the other two so that they become slightly flattened on each other in the central region. The next division is at right angles to the second and we thus get a group of eight cells arranged in two rows of four each. This is an interesting stage and is shown in its various appearances in several of the young colonies (text figures 3, 4, and 5). If the colony is under favorable conditions the division may stop at this stage. The cells seem healthy, however, and may grow to normal size as an eight-celled colony (Figs. 17-20) which, however, bears no resemblance in the arrangement of its cells to the normal sixteen-celled colony. I find no tendency whatever in the third division for the new cell walls to assume a position radial to the outline of the colony as is described for Eudorina at this stage and as Braun thought must also be true for Gonium. Such a modification might be expected if there were any tendency here to the regulations which Driesch assumes in his equipotential harmonic systems, since the placing of the third plane of division radially gives in Eudorina a rounded eight-celled group much more nearly resembling the typical sixteen-celled colony of Gonium. The oblong eight-celled colonies have no resemblance in form to the normal colonies and yet they occur abundantly. Their cells grow to normal size and reproduce normally, giving either eight or sixteen-celled colonies, according as the conditions are more or less favorable. I shall discuss this point further a little later. The eight cells as they enlarge are subjected to still further pressure. In rounding up, too, they increase the diameter of the whole colony in one direction more than in the other. The result is that the group becomes curved, as is shown plainly in edge views (text figures 3 and 4). The fourth division occurs at right angles to the third and we get thus the two rows of four cells each divided into two rows and the sixteen-celled colony is thus produced with four cells forming a square or rhomboid in the center and twelve cells forming a peripheral series about them. Such colonies are shown in figures 1 to 9 in successive stages of development.

That the spindle figures always lie in the same planes in the successive divisions may be due to intracellular organization or perhaps, and more probably, in the third and fourth divisions to external stimuli. As noted the cells round up considerably after each division and are thus subjected to pressure from the swollen mother cell wall. This pressure on the edges of the four celled plate may be a stimulus which aids in determining the plane of the next division. At the eight and sixteen celled stage the curved form of the young colonies is good evidence of pressure from the mother cell wall though the latter has become so gelatinized that it is very difficult to make it visible under the microscope. The young sixteen-celled colonies are quite saucer-shaped, as has been observed by the earlier students of the colonies. Kny [10 and 11] has demonstrated the effect of pressures and tensions on the plane of cell division. He concludes that there is a tendency for the cells to divide at right angle to the plain in which pressure is exerted upon them though this tendency may be overcome by his so-called "internal forces." It is certainly impossible as yet to ascribe to pressures and tensions any universally constant effect on cell growth and division, though there can be no question that both may act as determining stimuli in specific cases. With such stimuli present it seems at least unnecessary in the case of Gonium to assume any specific preformation of the germ plasm to determine the plane of cell division in the young colony. The major growth of the colony here is against the pressure of the mother cell wall just as in Hydrodictyon, as I have pointed out, the major growth of the cells is against the pressure of the adjoining cells in the young net.

That the curvature of the young colonies is purely mechanical and is forced upon them by their environment is plain from the fact that a little later when the mother cell wall breaks the plate flattens out immediately. In some cases the mother cell wall may become so distended that this flattening out takes place while the young colony is still enclosed.

In the development of the colonies as just described we have apparently an example of mosaic development. The original parent cell could be laid off into a series of sections, by lines cutting each other at right angles, so that each fragment would represent a cell of the future colony in something near its proper relations to all the others (text figure 7). There might be conceived to be a localized area in the germ cell representing each particular cell of the adult organism. The germ cell has merely been expanded and cut up into pieces, each of which becomes a definitely placed cell of the completed colony.

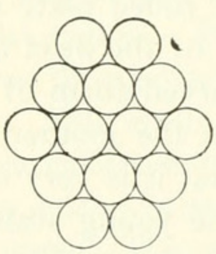

Fig. 6

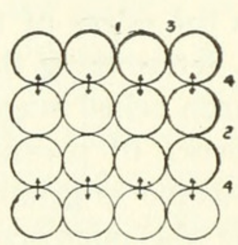

Fig. 7

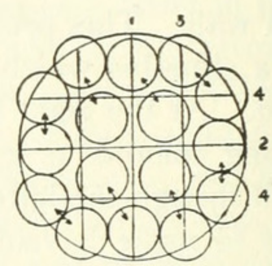

Fig. 8

In text figure 5 I have drawn the outer boundaries of the gelatinous cell walls. These outer layers are apparently denser and more resistant and with the swelling of the inner layers become stretched into figures representing very diagrammatically the arrangement of the cells of the parent colony. The expansion and rounding up of the cell walls leads to their separation everywhere except at the points of protoplasmic continuity between the adjacent cells. Here, although the plasmodesmen have evidently been withdrawn, the pit structure of the cell walls persists as a region of stronger union between the adjacent cells. It is interesting to know that this pit region, or at least the so-called middle lamella which forms the floor of the respective pits, is of about the same size between each pair of cells and appears as a definite disc-like region of connection, from which the cell walls are stretched to form the triangular intercellular spaces which are now very much larger than they were before the swelling of the cell walls occurred. As noted above, this particular colony was one of those whose central group of four formed a rhomboidal rather than a square figure and the point of union of the two cells that are in contact and the wide separation of the other two is conspicuously shown at this stage. It is obvious that a colony of this form is characterized by the greatest possible compactness in the arrangement of its cells. The intercellular spaces are triangular throughout, showing that the globular cell bodies have come into as close relations to each other as possible. Such an arrangement as this, as noted above, would result from surface tension and adhesion between viscous colloidal globules.

The cilia are shown still present with a number of the cells of the colony as they appeared at this stage and in two cases still showing feeble movements. It would seem probable that the connection of these cilia through the cell wall with one of the daughter cells of the new forming colony is maintained, though this is difficult of determination, and it is not impossible that the movements are autonomous and that the cilia have been broken off from connection with the parent cell at this stage. The persistence of the cilia at these late stages in cell division has been observed in other members of the volvox series. The daughter colonies proceed to grow now to the size of the parent and in this process of growth adhesion and surface tension play a part in developing the details of the mature structure as was suggested above. The daughter colonies escape from the mother cell walls during the night and in the morning I find them swimming freely, with no evidence as to their origin. In the case of my material if the plant were studied merely in the day time an increase in the number of colonies would be observed, but with no suggestion as to how they arose.

Since all the cells tend to be of equal diameter and circular in section the production of the mature colony with the definite space relations between its cells requires very considerable readjustments. If division and growth took place without gliding of the cells upon each other we might get a square colony such as is shown in text figure 7. The arrows indicate the pairings resulting from the last division. A comparison of such a diagram as this with any of the photographs of the normal colonies shows at a glance that the readjustments occurring in the formation and growth of the colony tend to a more stable arrangement of the cells and greater compactness. The square intercellular spaces are all replaced by triangular intercellular spaces except in the one case between the cells of the central group of four. The main modifications arise from the crowding in the outer series of twelve since ten is the normal number to form a series about a group of four (text figure 6). If the colony consisted of fourteen cells the crowding and consequent tensions would disappear. In the young colonies, as a matter of fact, the twelve cells of the peripheral row are much compressed laterally in order to maintain connection with the central group of four (Figs. 1-6). In the very young colonies the cells are much flattened upon each other. This may be due to loss of turgor due to a reduction in the amount of osmotically active substances during cell division or it may be due to stronger adhesion between the young cell boundaries. As growth proceeds, the cells tend to round up more and more and this brings to bear a stretching tension on each of the four of the central series, which tends, as noted, to flatten them out, that is, increase their diameter as seen from the face of the colony, at the expense of their vertical diameter. It also tends to draw them apart from each other, and in the vast majority of cases, results in the production of the square intercellular space in the center of the whole colony. In the adult colony, for this reason, the central cells seem larger, but there is no evidence that they really are greater in mass, their apparently increased size being due to the flattening just described. The tensions which are brought to bear on the central cells may be best understood perhaps from such a diagram as is given in text figure 8, in which the large circle and the lines from 1 to 4 represent the mother cell and the successive planes of its division. The small circles represent the daughter cells in the relative positions which they occupy in the adult colony. The inner group of four have maintained approximately their original position while the outer series have been shifted about them. The arrows indicate the pairing of the daughter cells of the last division. This shifting of the outer series around the inner group leads to the greatest compactness with the least possible readjustment of the relations of the individual cells. If the inner cells were shifted with reference to the outer series two of the pairs of sister cells would be widely separated in order to produce the configuration of the adult colony. It is plain that in such a system, the cells all tending to round up, very considerable tensions may be developed and that as noted the central cells will be flattened and the peripheral cells compressed laterally as they are seen to be in the photographs of the young and growing colonies.

The method of reproduction of the cells by simple bipartition with rectangular intersection of the successive planes of division and the surface tensions of the viscous colloidal protoplasmic masses of the cells with their internally determined pear-shaped form and capacity for forming protoplasmic connections give two sets of factors whose interactions determine the shape of the cells and of the intercellular spaces and the shape of the whole colony. The relative diameters of the cells give a suggestion at once of the relations of pressure and surface tension between them. The outlines in the micro-photographs are not perfectly sharp and since the peripheral cells lean outward more or less the photographs show them in more or less oblique optical section while the central cells appear in transverse section. None the less the fairly constant and interesting evidence of lateral compression in the peripheral cells and flattening in the central cells is unquestionably an expression of factors of surface tension and adhesion present in such a system. The tangential or periclinal axes of the central cells are about equal to the radial axes of the peripheral cells. The radial axes of the inner cells are intermediate between the two. The four cells of the outer series which are withdrawn somewhat toward the center of the colony tend to be pear shaped in optical section and seem perhaps to be less compressed laterally at their bases than the other eight of the series.

It is evident that to provide for the pit connections which are seen to be present in the old colonies secondary unions must be established wherever cells are in contact. Sixteen such connections must be established in the ordinary colonies and 17 in the rhomboidal colonies in addition to the eight that may be regarded as persisting between the sister cells in the last division.

That as noted the colonies are under considerable tension between their parts is experimentally demonstrated at every stage in their study. To obtain the photographs it is necessary to kill the organisms in order to bring them to rest. This is a matter of some difficulty since it was immediately found that any shock from poison or by other means which would lead to a contraction of the protoplasmic mass would result at once in breaking up the colony. Extreme dilutions of Flemming's weaker solution were used. Slight changes in the turgidity of the cell, due to a change in the concentration of the medium have the same effect. Any sudden shock leading to further rounding up or contraction is practically certain to break the adhesion and protoplasmic continuity between adjacent cells and the colonies fly apart with a succession of sudden jerks, as can be easily observed under the microscope. Figure 22 shows a colony so broken up.

It is not uncommon to find that in the ordinary course of their existence the continuity between certain cells in the colony may be broken, and thus square or oblong instead of triangular intercellular spaces are produced (Fig. 7). As noted the mature condition shows the cells well rounded (Fig. 8). The walls have become gelatinous and swollen and the plasmodesmen tend to be withdrawn though the pit connections may become more prominent. The colonies sometimes split through the middle, thus producing two eight-celled colonies (Fig. 16). These are, however, different in form from those which result from the interruption of the normal process of reproduction. The eight-celled colonies produced by the interruption of the division of the mother cell vary considerably in their form. The most common type is that shown in figures 17 and 18. Figure 20 shows a very aberrant type seen only once.

These eight-celled colonies indicate most clearly that there is no tendency in Gonium to the process of regeneration. They remain in the form in which they are produced, whether as a result of splitting the parent colony or from dwarfed development in reproduction. The cells of the eight-celled colonies formed by dwarfing undergo rearrangements due to surface tension during their growth analogous to those which take place in the sixteen-celled colonies and as a result they regularly consist of two compact rhomboidal groups of four cells. These two groups may, however, be quite variously placed with reference to each other, as is shown in the figures just referred to. There is no tendency to morphallaxis or regeneration of any sort. The individual cells of Gonium are totipotent and capable of reproducing the whole colony in its perfect form by normal reproduction, but if the process is interrupted the product is not a diminutive model of the adult type, but quite a differently organized individual, as is also true of the half colonies produced by fragmentation. There is no reason in the nature of the case why if the arrangement of the eight cells were controlled by some regulative teleological principle it should not operate to rearrange the eight-celled groups into a form corresponding to that of the normal sixteen-celled colony, only on a smaller scale. This could be accomplished by putting two cells in the center with eight around the periphery, or one in the center with seven around it, or we might have the crossed arrangement found in the eight-celled stages of Eudorina.

The four-celled form of Gonium is generally regarded as a distinct species. The material of this type which I have had for study appeared in a pool in which the sixteen-celled colonies had been very abundant but were beginning to disappear. Eight-celled colonies were also relatively more numerous than they had been before and the conditions suggested strongly that the four-celled colonies might be also degenerate forms of the sixteen-celled type. I was, however, never able to observe the formation of four-celled colonies from the sixteen-celled type. The adhesion between the cells in the four-celled colonies seems very weak and the cells early round up so as to form the characteristic square intercellular space between them (Figs. 21, 22).

We have in Gonium an organism of definite and characteristic structure whose heredity and ontogeny may be expressed in terms of cell organization and simple mechanical interactions of the cells in their growth from the germ cell to the mature condition. The most fundamental feature in the cell organization is that which determines that the successive planes of division shall intersect at right angles, the spindles lying always in the same plane. I have not been able to work out the processes of nuclear and cell division in these minute cells. On the basis of the work of Timberlake and others on nuclear division in the water net and other algal cells we may assume that a centrosome is present here and that the spindle is formed in connection with the divergence of two daughter centrosomes. The intersection of the successive planes of division at right angles implies that, as is generally the case, this divergence extends to a distance of 90 degrees for each of the daughter centrosomes and that the plane in which the divergence occurs is maintained unchanged. either as a result of internal cellular organization or external stimuli. In neither case would any specific representation of the form of the colony in the organization of the germ plasm be implied.

The method of forming the colonies in Gonium stands in marked contrast with that in the water net. We lack here the convincing evidence that the structure of the germ plasm does not represent the space relations of the parts of the adult, which we have in coenobes which are formed by the aggregation of free swimming units, still it seems to me gratuitous to assume in the cells of Gonium any complex specific representation of the structure of the colony as a whole. It is obvious here that the organization of the whole cell which may determine the position of the spindle and the planes of cell division is in no specific sense an *anlage* for the form of the colony and the colloidal qualities of the protoplasm which determine the adhesive and surface tension qualities of the cells are factors in quite another category than the space relations between the cells which they determine. Gonium illustrates clearly the numerous and complex interactions of the most delicate and intensive sort which may arise between cells as a result of their properties as colloidal droplets on the one hand and their fixed method of reproduction by bipartition on the other. These interactions may have much to do in determining the method of formation of such globular colonies as are found in other members of the volvox series.

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