THE EVOLUTION OF CELL TYPES AND CONTACT AND PRESSURE RESPONSES IN PEDIASTRUM

By R. A. Harper

Columbia University

I desire to present at this time an outline of the evolutionary development in the genus *Pediastrum*, noting especially also the relation of the forms of the various cell types which characterize the species to the intercellular biogenetic reactions through which the colonies get their characteristic configurations. We shall find in the subgenera a series of well-marked groups, in each of which the particular initial primitive cell form foreshadows all the types which have appeared in the evolution of this particular series. The differences which characterize the species in many cases pass over into each other by very finely graded variations, so that there has been the greatest possible confusion and uncertainty among systematists as to whether certain types should be considered species, varieties, or mere form races. An orthogenetic trend of development can be recognized in the Diactinia and Tetractinia especially and the forms illustrate such series of continuous variants as Jennings ('16) has produced by selection in *Difflugia corona*.

The genus, as a whole, on the other hand, presents a series of groups, the subgenera, which just as plainly differ by discontinuous characters. In most cases it is necessary to assume a return to the primitive undifferentiated cell type of the simplest species in order to conceive the method of origin of the subgenera.

An orthogenetic trend for the whole genus can perhaps be recognized in the simple tendency to develop spinous projections on the body of the cell, but we need to know more of the relation of such changes of form to the ultimate constitution of the cell before we can be sure that there is any common background for the tendency which has led to the formation of the one-spined, two-spined and more or less deeply lobed, three-spined, and four-spined forms which are recognized as Monactinia, Diactinia, Triactinia, and Tetractinia respectively. It is not obvious on the basis of our present knowledge why an ancestral type which had developed a unispinous form is more likely to have descendants with two- or three- and four-spined cells than with long cylindrical cells like *Hydrodictyon* or spindle-shaped cells like *Scenedesmus*.

In most cases again in the subgenera we are confronted with a series of continuous variations in the configuration of the colonies, which, however, is broken at what appear to be critical points at which a further modification of the form of the cell leads to a quite characteristic change in the symmetry of the whole colony. In some cases, cell forms which have apparently tended to a large degree of asymmetry in the colony, when modified to a certain degree, make the achievement of equal contact and pressure relations and a higher degree of symmetry possible, as in the transition from *Pediastrum simplex* to *P. triangulum* and from *P. Ehrenbergii* to *P. Rotula*. In other cases a more extreme development of a particular cell form may make a new configuration of the colony necessary with a symmetry much more difficult to achieve, as in the transition from *P. asperum* to *P. clathratum*. Throughout, as I have already pointed out ('15), we have the conflict of these orthogenetic tendencies in the evolution of the cell form and the law of cell reproduction by bipartition, giving the geometrically progressing series of cell numbers, 2, 4, 8, 16, 32, etc., with the principle of least surfaces requiring an entirely different series of numbers, 1, 7, 19, 37, 61, etc., for its full expression.

I am presenting elsewhere ('18) the results of a study of the organization, reproduction, and heredity of *Pediastrum asperum*, together with further observations on the variations in a series of seven colonies of *P. Boryanum*. The results there described are assumed in this paper. These two species represent respectively the forms with spines well developed on both peripheral and interior cells of the colony and rather large intercellular spaces, and those with small or no intercellular spaces and the spines little developed on the interior cells. In both species, I have pointed out, the cells seem in some degree directly adapted to the formation of bilaterally symmetrical plate-shaped colonies of sixteen cells. There is a considerable number of species of *Pediastrum* in which the cell form is by no means so obviously adapted to a symmetrical configuration of the colony as a whole, species in which in some cases the lobing of the cells, as noted, is carried to extremes or is of a kind calculated to result in more unstable conditions of equilibrium and a greater tendency to asymmetry in the colonies. This increase in the length of the spines and the correlated large size of the intercellular spaces by favoring floating may be adaptive for species tending to assume the plankton habit of life. These species in their relations to *P. asperum* may be considered as extreme or aberrant, though representing natural and easily conceived modifications of the cell form shown in it and in *P. Boryanum.* Such types illustrate the operation of orthogenetic tendencies in the production of results which are non-adaptive from the standpoint of the organism as it was situated when the tendency first appeared, but may become adaptive under new environmental conditions.

P. asperum apparently represents a climax type viewed from the standpoint of the possibilities of developing a least surface configuration with unit cells derived by bipartition. The deeply four-lobed form of the cells permits the best possible approximation to conformity with the circular outline and the intersection of all boundaries at 120° as found in the corresponding nineteen-unit least surface configuration.

The two-spined series has by far the largest number of species and is unquestionably the most common type, though the single-spined species, *P. simplex,* is at times found in great abundance and in almost pure growths. In general, and in all its variations, the two-spined form of cell seems to be better adapted to the formation of the anomogenous cell group with the bipartition series of cell numbers as contrasted with normal least surface groups. There is general agreement that the delimitation of species must be based on cell form and we have quite a series of types differing primarily in the degree of development and the form of the two spines.

We shall get a clearer understanding of the significance of cell form in such groups if we compare the conditions found in other species of the Diactinia with those in *P. Boryanum* and *P.*

asperum and further with those in representatives of the Anomopedium group, *P. integrum*, the Monactinia, the Triactinia, the Tetractinia, etc. I have not been able to study the reproduction and colony formation in these species and can only compare their adult forms with those I have more fully studied.

A. **Anomopedium.**—*Pediastrum integrum* Näg.

I have seen only a few specimens of *P. integrum.* The individual shown in FIGURE 1 ('18) has but seven cells, the missing cell perhaps lies at some point above or below the other cells of the colony though it can not be made out in the photograph nor was it discovered in the specimen before photographing. The species is figured by Nägeli ('49) as occurring in 4-, 8-, 16-, 32-, etc., celled colonies, all of whose marginal cells have two very rudimentary spines. All the colonies figured by Nägeli, except three of those with four or eight cells, are very irregular and he states that the regularly concentric arrangement of the cells which is common in other species of *Pediastrum* is exceptional in *P. integrum.* He also states that it is common to find the cells in two layers. Braun ('55) does not figure the species.

Nägeli gives the habitat of the species as wet cliffs. Nitardy ('14) reports that he has seen but one specimen. His figure shows

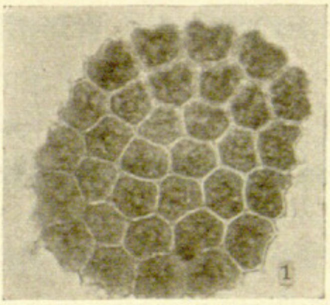


FIG. 1. *Pediastrum integrum* Näg. Perhaps the same as *P. muticum* Borge. Spines more prominent than in the eight-celled colony figured in '18, fig. 1. × about 300.

that it was quite irregular and he notes that it was plainly two-layered. He explains his failure to find more specimens as due to his having been concerned especially with material from lakes, pools, etc., and notes the agreement of most authors that *P. integrum* is found on rocks over which water trickles rather than in the deeper waters of pools, etc. The question at once arises whether the irregular form of the colonies in two layers is not due to environmental conditions which check the vigor of the swarm-spores just as it is checked in agar cultures of *P. Boryanum* with resulting irregularity of the colonies and reduction of the spinous projections. It seems hardly possible that *P. integrum* is only a habitat form of *P. Boryanum* but it would be interesting to grow it in water cultures along with *P. Boryanum* and observe its behavior as to cell shape and the symmetry of the colonies. I have not had the species in numbers sufficient for such experiments. The specimen shown in FIGURE I shows the thirty-two cells in one plane but the arrangement is quite irregular and asymmetrical, though there is a fair approach to the concentric circles. The short papillae seem to be quite reularly directed radially outward in the colonies so far figured, but the tendency to have certain cells out of the plane of the colony is marked and either indicates that the poles of the transverse axes of the cells and the affinities which they represent are relatively less strongly developed or that the cells are unable for environmental reasons to achieve their normal orientation and interrelations in the colony. *P. integrum* may be a species whose colonies regularly fail to achieve their typical development and yet are able to maintain themselves. I am more inclined to believe, however, that it is a primitive type in which the polarities and cell differentiations characteristic of the Monactinia and Diactinia are not fully achieved. Whether or not *P. integrum* is a good species, it may certainly be regarded as representing in the form of its cells a primitive type out of which the better adapted cell forms of the Diactinia have been developed.

B. **Monactinium.**—*Pediastrum simplex* Meyen.

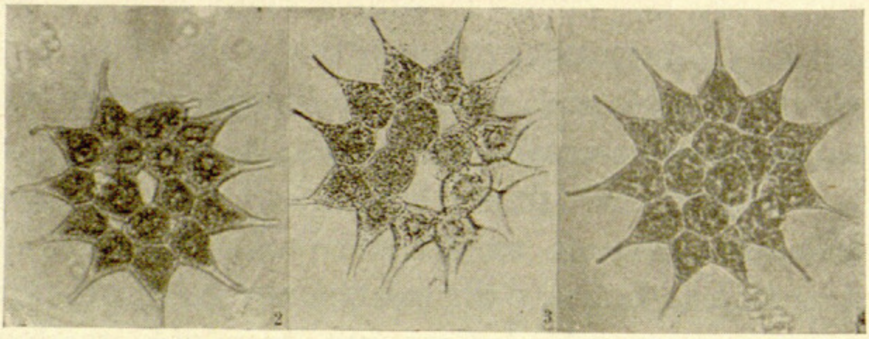
The species of *Pediastrum* whose cells show a single spine are common and widely distributed. The evidence of their variability is well shown in the fact that De-Toni ('89) believes they can all be included in one polymorphic species, *P. simplex*, while various other authors have recognized *P. duodenarium* (Bailey) Rabenh., *P. clathratum* Lemm., *P. triangulum* (Ehrenb.) A. Br., *P. Sturmii* Reinsch, etc. *P. simplex* has been described as including forms both with and without intercellular spaces.

It is impossible to determine from the evidence in the literature as to the independence of these various forms and yet there can be no doubt that in different localities and in different seasons one or another of them may be found in almost pure growths and to the exclusion of the others. It seems clear that a particular type of cell form tends to perpetuate itself, but with much fluctuation. Nitardy ('14) includes all the forms under the name *P. triangulum* (Ehrenb.) A. Br., dropping the name *P. simplex* because it has been used so variously by different authors.

I have photographs of both eight- and sixteen-celled colonies. A comparison of the sixteen-celled colonies of *P. simplex*, as I find it, with those of any species with well-developed two-spined cells suggests at once the greater capacity of the latter to form symmetrical colonies with the bipartition series of cells 4, 8, 16, 32, 64, etc. The two common arrangements in my observation seem to be, first, an irregular group of five in the center and eleven around them (FIG. 2), and, second, an irregular group of four in the center with twelve around them (FIG. 3).

The peripheral cells show their polarity by the regularity with which the spine is turned outward. Whether they are flattened enough to indicate the existence of a second differentiation in a transverse axis, I have not been able to determine. The arrangement of the inner group of cells is, as noted, quite irregular in all the colonies I have seen. Several intercellular spaces are commonly present, but show no constancy as to size, shape, or position. They may be from three- to six-sided. It is generally quite impossible to determine which side of any one of these interior cells tends to be produced into the spine. In two cases, however, I have observed an interior cell with a well-developed spine projecting into an intercellular space. One of these is shown in FIGURE 4. Whether the tendency to form the one-spined form is as fully fixed in *P. simplex* as is the corresponding tendency to form two spines in the Diactinia is not clear. It is possible that the lack of adaptation in the one-spined cell form to the production of symmetrical colonies is correlated with a failure to fix this cell form so firmly in heredity and that with an increased fixity of cell type such symmetrical forms as Nitardy's *P. triangulum* (Ehrenb.) A. Br. become possible. De Wildeman ('93), however, has observed both irregular and symmetrical colonies and includes them all in *P. simplex*. De Wildeman figures likewise only one symmetrical sixteen-celled colony ('93, *pl. 19. f. 9*) against five which are irregular, but the form of the cells in all of them is essentially the same.

Nitardy ('14) has had an abundance of the more symmetrical forms and their variants which have been variously named *simplex*, *duodenarium*, etc., and, as noted, puts them under the name *P. triangulum* (Ehrenb.) A. Br. with two varieties, *angustum* and *latum*. The latter in its cell form (Nitardy, *pl. 8. f. 5*) agrees with the forms I have found and the two varieties seem fairly well marked in the case of his figures 3 and 5, plate 8. In some of his other figures the distinction is not so clear, but the drawing is rather crude and it is hard to judge. In his variety *angustum*



FIGS. 2, 3, and 4. *Pediastrum simplex* Meyen, sixteen-celled colonies showing the cell arrangement 5 + 11 and 4 + 12, × about 175. Figure 4 shows one of the central cells with a well-developed spine, pointing downward, but not very clearly down in the reproduction.

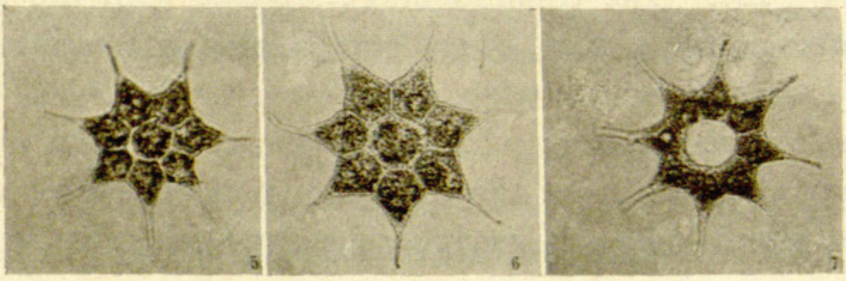
the lobes of the cell are more slender and form large intercellular spaces. The sixteen-celled colonies may have a very definite bilaterally and radially symmetrical arrangement of their cells with four in the center in a square, surrounded by four groups of three (Nitardy, '14, *pl. 7. f. 5*), or two groups of four and two groups of two (Nitardy, '14, *pl. 9. f. 20*), or five in the center, a pentagon surrounded by eleven—four pairs and three (Nitardy, '14. *pl. 5. f. 1*). These symmetrical figures are from his own observations on material from Grünewaldsee near Berlin and are very fine illustrations of the capacity of the swarm-spores of this species to achieve delicately balanced equilibrium relations such as are necessitated by the one-spined cell form. I have not seen these symmetrical forms and have taken from Nitardy ('14) FIGURES 27, *a*, *b*, etc., to illustrate the very interesting bilateral and radial symmetry which these sixteen-celled colonies may show.

My material corresponds more nearly with Nitardy's var. *latum* and Nitardy gives no evidence that his var. *angustum* ever produces dense colonies with small irregular intercellular spaces like the forms of *P. simplex* I have figured. I shall refer to these bilaterally symmetrical colonies and their variants as *P. triangulum* (Ehrenb.) A. Br. (Nitardy, '14, *pl. 4. f. 4, 7, 8; pl. 5. f. 1, 2*; *pl. 6*, etc.) and to the irregular forms I have figured as *P. simplex* (De Wildeman, '93, *pl. 19. f. 14*, and perhaps Nitardy, '14, *pl. 6. f. 3*), leaving unsettled the question whether the one type can arise from the other directly as De Wildeman and others have supposed. Nitardy says he has not seen the forms without intercellular spaces such as De Wildeman has figured and evidently about Berlin the symmetrical form and its variants occur predominantly. It is not impossible, of course, that the irregular forms are merely the expression of a lack of vigor at the swarming period.

The regularity of the peripheral series in *P. simplex* even when the central cells are asymmetrically placed is doubtless due to the fact that the outer series of cells seems to come to rest sooner than those in the interior of the swarming group, as I have noted elsewhere ('18). The colonies of *P. simplex* with the irregular central groups (FIGS. 2, 3, 4) are particularly interesting as illustrating a case in which while symmetrical relations of contact and pressure are apparently impossible for all the members of the cell colony they are none the less quite perfectly achieved for a portion of the colony—the peripheral series—so far as their interrelations are concerned.

The eight-celled colonies of *P. simplex* offer fewer possibilities in the complexity of their intercellular relations and there is also much greater uniformity of type. By far the commonest arrangement is one cell in the center surrounded by seven cells (FIGS. 5 and 6). It is evident here that the single cell can hardly fill a circle made of seven instead of six cells (see FIGS. 5 and 9) and intercellular spaces tend to appear and may sometimes be quite large. In FIGURE 6, however, the central cell seems quite to fill the center of the group of eight. I have never seen a colony of this species with two cells symmetrically placed in the center and surrounded by six cells, as is so commonly the case in the eight-celled colonies of *P. Boryanum.* The markedly oblong form of the body of the central cells in *P. Boryanum* is plainly quite impossible for *P. simplex.*

I have seen a number of colonies in which (FIG. 7) all eight cells were arranged in a very perfect circle about a central rounded space. Meyen ('29) and other authors since have figured such forms. Nitardy has found it in his *P. triangulum* (FIG. 27*c*). There evidently is the tendency here to achieve a symmetrical arrangement of one sort or another—a tendency which is quite independent of the presence or absence of any adaptation in the form of the cells to the production of such symmetrical interrelations. We may assume, as in the other species, that this tendency is based on the effort of the cells in the swarming period to achieve a position in which their contact and pressure relations will be equal and balanced in as many directions as possible or that at least such pressure relations as are achieved shall be as nearly as possible mutually compensatory, as in the ring-shaped colony. The significance of occasionally achieved chance configurations is well illustrated in these cases. The symmetry of the circle is here very perfectly illustrated in FIGURE 7, but the chance



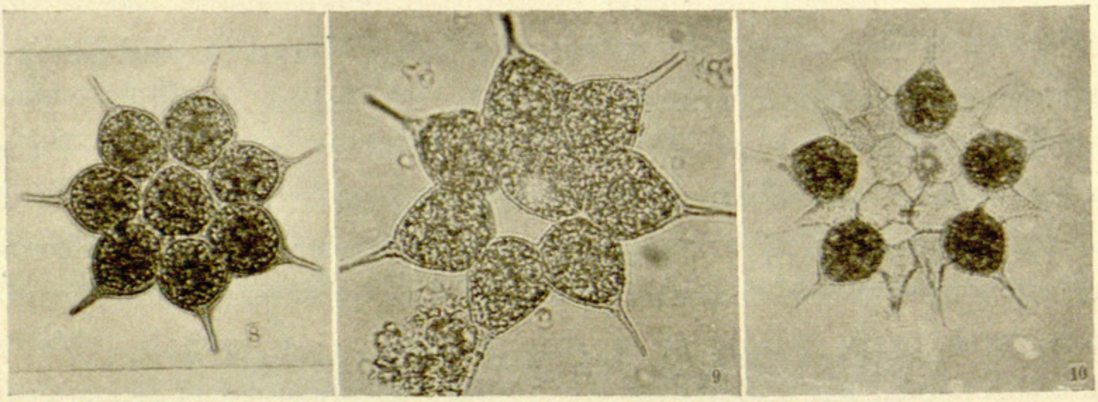
FIGS. 5, 6, and 7. Eight-celled colonies of *Pediastrum simplex* Meyen. 5, central cell does not fill space enclosed by peripheral cells. 6, no intercellular space. 7, ring-shaped colony. × about 150.

that out of a swarm of eight free-swimming cells attempting to achieve interrelations of equal or balanced contact and pressure such a circle will be achieved would seem very remote. The chance for seven about one in a free-swimming group is much greater and affords a sufficiently close approximation to symmetry to make unlikely any very radically different configuration when once it is achieved. A statistical study of the relative abundance of such colonies as are shown in FIGURES 5, 6, and 7 might throw light on the question as to the relative abundance of individuals of the highest vigor as compared with those of high vigor but not the maximum.

It is evident that when in swarming the ring form is by accident once achieved it tends to persist, since it gives, as shown by its contours, the most perfectly symmetrical interrelations possible for the eight *simplex* cells. Just why the cells should tend to find their final resting position in a situation of equal or balanced pressures and contacts instead of unequal or unbalanced pressures and contacts is the same question here as in the case of other coenobes. There are obviously two factors or sets of factors involved in all these adjustments. First, it is plain that during the slow and protracted writhings of the swarm-spores of vigorous colonies the direct physical tendency of such viscid, semi-fluid droplets to adhere and yet as far as possible round up and assume a least surface configuration will have the fullest possible opportunity to come to expression. In the random movements of the swarm-spores these constantly acting physical relations will tend to maintain any accidentally achieved position which is comformable with them and to act as a check on any movement unconformable with them. Results of this sort, however, will be chiefly in evidence in the later stages of colony formation. The general arrangement of the swarm-spores in a plate or ring must be regarded as the result of the interrelations of the cells as free motile organisms involving polarities, tropisms, etc., such as are observed in other morphogenetic processes.

The grouping of eight cells in a ring rather than in a plate of seven about one in the case of *P. simplex*, which we are considering, brings out most clearly the relations of two divergent types of activity. The unconformability of a group of seven units about one—instead of six about one—with the principle of least surfaces as applied to the whole group is what prevents any swarm-spore that accidentally comes into the center of such a group (FIG. 6) from achieving equal contact and pressure relations with all the cells about it and thus leads to its changing its position until in the present case it makes one of a ring of eight (FIG. 7). This is a matter of intercellular reactions involving contact and pressure, polarities, tropisms, etc., the physical unconformability providing for the stimuli. It is obvious that the mere molecular pulls involved in least surface phenomena could never lead directly to such violent changes of group relations, though they may be of final importance in determining the exact contours of the ring when once it is blocked out, as it were, as a result of the intercellular reactions which control the earlier swarming movements.

It is then by no means enough, even when, as here, the inherited cell form is not especially involved, to identify offhand the results of these complex physiological reactions as simply the expression of the physical principle of least surfaces which, at least as at present stated, is based on intermolecular relations. If the facts are as indicated we perhaps have here in the relations of the complex reactions of these simple organisms to the wide-



FIGS. 8, 9, and 10. *Pediastrum simplex* Meyen, of the form known as *P. Sturmii* Reinsch. 8, with small intercellular spaces, × about 200. 9, with a large intercellular space, × about 250. 10, sixteen-celled colony, eleven cells empty, *simplex* type, and five cells about ready to form swarmspores, *Sturmii* type, × about 200.

spread symmetries of form, rounded contour, etc., which are based on the physical principle of least surfaces, a suggestion at least as to the origin of the so-called aesthetic satisfaction of higher organisms in physical symmetry and balance of configuration or artistic composition. This capacity to react to inequalities in contacts and pressures or unbalanced pressures from the environment might be ascribed to a sense of symmetry and classed as one of the fundamental properties of living cells. These ring-shaped colonies of *P. simplex* certainly suggest a notable delicacy of response to pressure and contact stimuli.

Pediastrum Sturmii Reinsch, characterized by plumper, more rounded cells with spines supposed to be solid instead of hollow, may be represented by the form I have shown in FIGURES 8, 9, and 10. In my opinion, these are merely colonies of *P. simplex* approaching the reproductive stage, but I have not so far observed swarm-spore formation in the species. Nitardy ('14, p. 178) regards a warty surface, pentagonal peripheral cells, and the non-tapering form of the spine as important characters of *P. Sturmii.*

FIGURE 10 gives quite convincing evidence on this point. In this colony five of the cells are well advanced toward reproduction while the remaining eleven have remained immature. The mature cells have the form characteristic of *P. Sturmii;* the immature cells are like those of the ordinary colonies of *P. simplex* which have not yet reached the reproductive stage, but it is to be noted that the cells in this colony are much smaller than in the other two. The change in form of the cells as they approach the period of reproduction is very marked. Their rounding up leads to the at least partial withdrawal of material from the lobes and a narrowing of their bases. Failure to recognize these changes may be responsible for confusion as to the real character of *P. Sturmii.* Professor B. M. Davis has kindly shown me, and permits me to refer to, as yet unpublished figures showing the reproduction of *P. simplex* which seem to me not inconsistent with this view.

In FIGURE 11 I have been able to bring out faintly, in my original prints, the curious bristle-like appendages at the ends of the spines, which like the similar structures in plankton diatoms tend to keep the organism afloat (see Petersen, '11, and Zacharias, '03). As shown here, it is clear that the individual setae may be widely divergent or almost parallel. The suggestion that they are movable on their bases or points of insertion in the spines is very obvious. The nodular or pear-shaped swellings at their bases are also very conspicuous in the case of the widely spread group from the spine of cell *a* and may very well be contractile droplets of cytoplasm functioning as motile organs.

This colony is further interesting from the fact that the cell *a* seems relatively large as compared with the cells next to it. The whole colony also shows only fifteen instead of sixteen cells. As Nitardy and others have emphasized, the law of bipartition and the resultant 4-, 8-, 16-, 32-, etc., cell numbers are very firmly fixed in the colonies of *Pediastrum*. It is possible that the sixteenth cell lies above or below the plane of the colony in this case and hence does not appear in the photograph. On the other hand, it may be that cell *a* did not undergo the third division and has remained larger than its fellows.

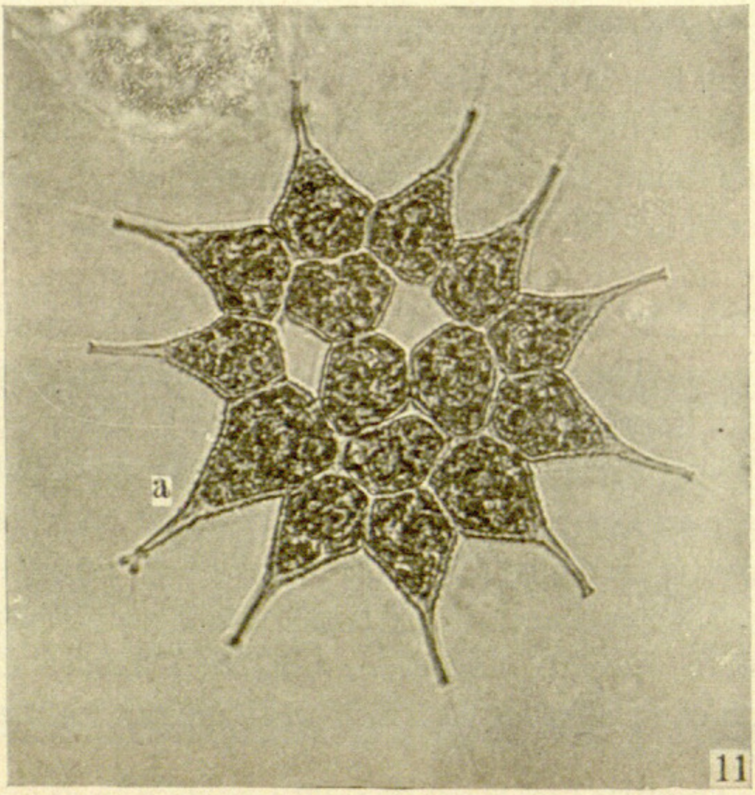


FIG. 11. *Pediastrum simplex* Meyen. Fifteen-celled colony, one cell, *a*, larger than the others; bristles and pear-shaped basal bodies show on some of the spines in the original, but are practically lost in reproduction. × about 400.

Nitardy ('14, p. 183) figures a specimen of *P. Boryanum* with fifteen cells, one of which is much larger than the others and contains a double pyrenoid. There is also a faint line running across the middle of the cell and Nitardy is convinced that the large cell has arisen by fusion of two swarm-spores. He notes that this is the only case of anomaly in cell number which he has observed in twenty years of study of the group. It would seem that the large cell might equally well be due to a failure of one of the cells to complete the third division. The larger size of the cells in the sixteen-celled daughter of a thirty-two-celled colony ('18, FIG. 21) as compared with the thirty-two-celled daughter of the same mother is conspicuous.

C. **Diactinium.**

In the Diactinia we have the largest and most common of the subgenera of *Pediastrum*. The delimitation of species, however, seems in high degree difficult and uncertain. De-Toni ('89) recognizes eight species in the group with eight varieties under *P. Boryanum* (Turp.) Menegh. and seven varieties under *P. duplex* Meyen, many of which are regarded by other authors as good species. Nitardy ('14) believes the whole series can be best regarded as three species with three varieties under *P. Boryanum* (Turp.) Menegh. and three varieties under *P. pertusum* Kütz.

Braun ('55) gives no figure of his *P. pertusum* Kütz. var. *clathratum*, but refers to figures of Meyen ('29), Hassall ('45) and Corda ('39, *pl. 3. f. 18*). Corda's figure of *P. diodon* is certainly unreliable. Meyen's figures, though poor, seem to agree rather better with Lagerheim's figures of his var. *reticulatum*

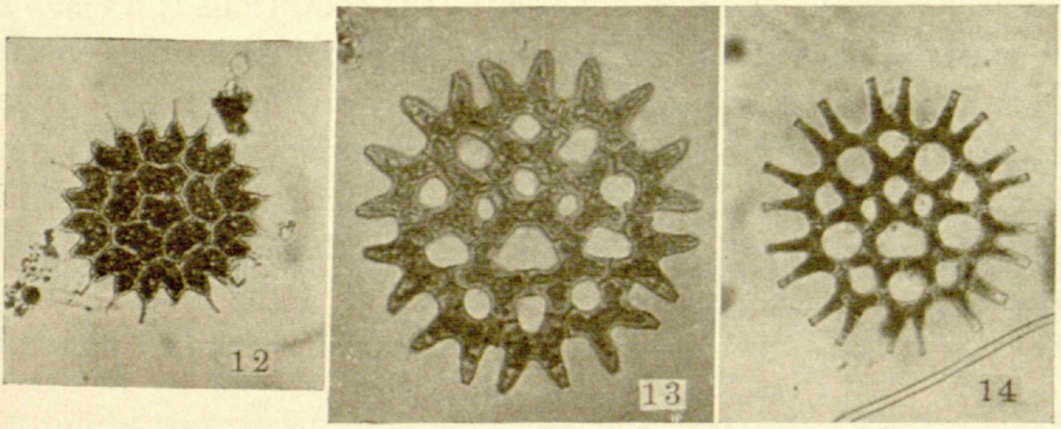


FIG. 12. *Pediastrum Boryanum* (Turp.) Menegh. Sixteen-celled colony typical arrangement, form with slender equal spines, × about 300.

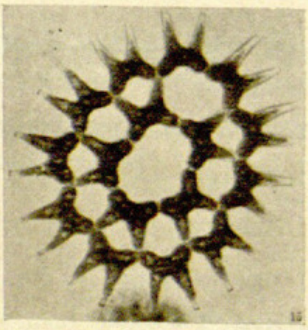
FIG. 13. *P. asperum*, sixteen-celled colony, typical form, × about 425.

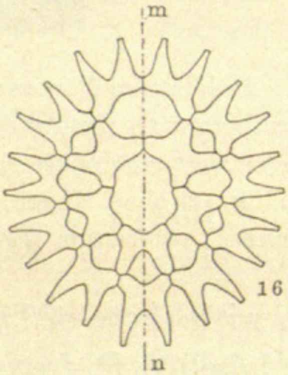
FIG. 14. *P. duplex* Meyen, var. *reticulatum* Lagerh. Intermediate between *P. asperum* and *P. clathratum* (figs. 15–21), × about 300.

('82) than with those of De Wildeman ('00, p. 104, *f. 17* and *18*), which are labelled *P. duplex* var. *reticulatum* Lagerh., and those of Chodat ('01, p. 227 and 228) labelled *P. duplex* Meyen and *P. duplex* f. *genuinum* (A. Br.). Hassall's figure ('45, *pl. 92. f. 4*) is certainly widely different from those of De Wildeman and Chodat. It seems doubtful whether Nägeli ('49), Braun, or Lagerheim had these 5 + 11 forms figured by De Wildeman, Chodat, and Nitardy ('14, *pl. 8. f. 11*). Both types are found in this country and cultures will have to show whether they both can be produced from the same mother colony. Until the question is settled it is certainly more convenient to keep them under the old names of Meyen, Kützing, and Braun. I shall call the type shown in FIGURE 14 *P. duplex* Meyen var. *reticulatum* Lagerh. (Meyen, '29, *pl. 43. f. 16 and 17*; Lagerheim, '82, *pl. 2. f. 1*), and the forms shown in my FIGURES 15–21, *P. clathratum* A. Br., *P. pertusum* Kützing, may very well be Braun's var. *asperum*, though there may be a form with smooth spines connecting *P. asperum* with *P. Boryanum*. This form of mine (FIG. 14) is plainly Lagerheim's *P. duplex* var. *reticulatum* ('82, *pl. 2. f. 1*).

P. clathratum A. Br.

In *Pediastrum clathratum* A. Br. we have a species of the Diactinia in which the four-lobed cell type has been carried to its extreme development. It is a fairly common and abundant species, apparently vigorous and well adapted to the conditions it finds. In the extreme length of its cell lobes as compared with other species of the Diactinia, *P. clathratum* is obviously a climax type. What we may call the body of the cell in *P. Boryanum* (FIG. 12) has gone over almost completely into the four spinous lobes. The cell is quite H-shaped, with cross-bars little or no thicker than the arms (FIGS. 15–18). As a result, the adaptation of the lobed form of the cells to the exigencies of colony formation, with cell numbers





FIGS. 15 and 16. *Pediastrum clathratum* A. Br. Sixteen-celled colony and type diagram. Fig. 15 × about 300.

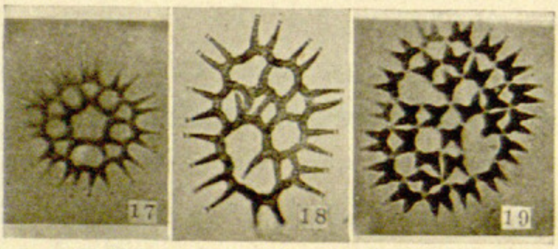
produced by bipartition, works out in quite a different way from that in *P. Boryanum* and *P. asperum* (FIG. 13). It is a type in which the four-lobed form in its extreme development has resulted in a reduction of stability and compactness in the organization of the colony as a whole. The result is a light and open structure which may be better suited to conditions of life in the plankton.

The intercellular angles are hard to measure because of the very limited areas of contact between the cells but there can be no question that the variations from 120° are so slight as not to be accurately determinable by the means I have used. The slenderness of the lobes makes possible in the highest degree compensatory curvings and bendings so as to give quite equal pressure and tension relations between the surfaces of contact of the cells. The extreme length of the lobes has brought with it a new type of cell grouping in the colony. I have had an abundance of material of this form and have not seen a single sixteen-celled individual with the common cell arrangement 1 + 5 + 10, found in *P. Boryanum* and *P. asperum*.

Nitardy (*pl. 8. f. 13*) refers to *P. clathratum*, a sixteen-celled colony with the ordinary arrangement found in *P. asperum* 1 + 5 + 10. The cell form also is plainly that of *P. asperum* rather than that of *P. clathratum*. Chodat's ('01) figures of what he identifies as *P. duplex* are both of the *clathratum* type. His figure 151 is of an irregular older colony nearer the stage of reproduction, but figure 152*b* shows the type configuration of the cells.

The type arrangement seems to be that shown in the diagram (FIG. 16), five cells surrounded by eleven cells and the center of the colony an open pentagonal or oblong area. Such a colony is bilaterally symmetrical about the axis *mn*, as shown in the diagram. The outer series of cell contacts is in threes except at the pole *m*, where there is a contact between two. The inner series of contacts is all in twos. The central intercellular space is, as noted, pentagonal and more or less elongated in the axis of the colony. With the variation in the shape of the central intercellular space the whole colony becomes either rounder or more oblong. Compare FIGURES 15 and 17. In correlation with the length and slenderness of its cell lobes *P. clathratum* is a climax form in its development of intercellular spaces. The outer series of intercellular spaces consists of five inequilateral lens-shaped and five shield-shaped openings bounded by two and three cells respectively, with the large oval and four-cornered intercellular space near the pole *m*, bounded by four cells and bisected by the axis of symmetry of the colony. No such configuration is found, so far as I have observed, in any other species of the Diactinia so far described, and yet the cell form shown in FIGURE 14 connects *P. clathratum* with *P. asperum* very closely. This figure is from material collected in Wisconsin and I have quite a series of photographs showing cells of this form in colonies with 16, 32 and 64 cells, but I have never seen one of these colonies with the 5 + 11 cell configuration of *P. clathratum*. My figures of *P. clathratum* are from material collected at Woods Hole, where the typical form is common as well as the less developed types of *P. asperum*, but I have not found with these forms colonies exactly like those from Wisconsin.

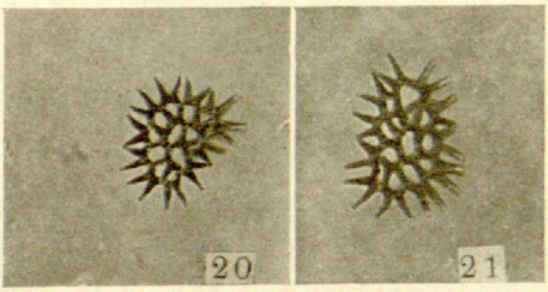
We have here two types, which, as the confusion in the literature shows, can be connected very closely by all possible intergradations in cell form and yet it seems clear that either when the modification of the cell form passes a certain point or as a result of modifications of the cell polarities a change in the type configuration of the colony results. There is no good evidence in the literature that colonies with the 5 + 11 configuration of *P. clathratum* and those with the 1 + 5 + 10 configuration of *P. asperum* can arise from the same parent colony and, as noted above, it must be left to further culture work to show whether this is possible.



FIGS. 17, 18, and 19. *Pediastrum clathratum* A. Br., irregular colonies. 17, circular colony, × about 175; figure 18 showing quite clearly the pear-shaped bodies at ends of spines, × about 200. The colony shown in figure 19 is about ready for reproduction, × 175.

The configuration of such colonies as those shown in FIGURES 15–17, involving the absence of a central cell, the increased variety of form in the intercellular spaces, and the increased number of paired cell contacts is certainly more complex and further removed from that of a simple 1 + 6 + 12 least surface group than is the type of sixteen-celled colony of *P. asperum* (FIG. 13). Greater delicacy in the contact and pressure responses of the swarming zoospores is certainly necessary to achieve it. It is the most highly specialized configuration I have yet observed in any of the species of the genus, though whether greater delicacy of response is necessary for its production than for that of the ring-shaped eight-celled colony of *P. simplex* is not easy to say.

The colonies are very commonly irregular and indicate very clearly that the normal contact relations are not necessary for the development of the typical cell form, as is illustrated by the interior cell with one free spine shown in FIGURE 18, and by De Wildeman's ('00, *f. 18*, p. 104). I have been able in several cases to observe the reproduction of the species. The cells become much swollen but still show a very deeply lobed form as compared with *P. asperum* at the corresponding stage. FIGURE 19 shows a thirty-two-celled colony which is about ready for reproduction and FIGURES 20 and 21 show two very irregular young colonies,



FIGS. 20 and 21. Young, irregular colonies of *Pediastrum clathratum* A. Br., × about 400.

whose birth I observed in a sealed preparation. They are only a few hours old but the cells show the contours characteristic of the species. It is of interest to compare these figures with FIGURE 14 as to the forms of the cells.

The whole colony is relatively fragile and is ordinarily bent and curved so as to make a good photograph impossible. The bristle-like projections from the ends of its cell lobes are extremely well developed and are brought out faintly in some of my photographs. The colonies are very sensitive to currents in the water and seem almost self-motile at times. It is very difficult to find one quiet enough for photographing and the varying position of the apical bristles, now all close together in a parallel pencil and now widely diverging as shown in my figure of *P. simplex* (FIG. 11), would seem perhaps to be a factor in the wabbling, tipping, and trembling movements of the colonies. I have, however, seen no movement of the bristles. The species illustrates the possibility that an orthogenetic tendency which is adaptive in a specific particular when moderately developed may in its extreme development become adaptive in quite a different connection.

P. angulosum (Ehrenb.) Menegh.

This form (FIG. 22) represents a type of the diactinial cell which seems quite remarkable for its constancy and the name and species have been less juggled with by descriptive writers than many others. The characteristically short oblique spines with the wide sinus between them show very clearly that the

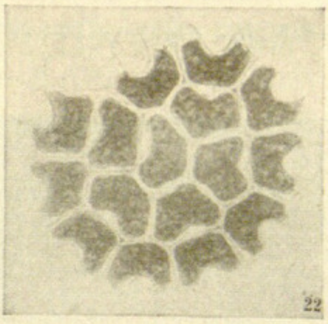


FIG. 22. *Pediastrum angulosum* (Ehrenb.) Menegh. Irregular sixteen-celled colony, × about 325.

morphogenetic tendency to the production of such projections involves other factors than merely those of length. It is a widely distributed and fairly common form and yet apparently has developed no such series of fluctuating variants as have *P. Boryanum* and *P. pertusum*. De-Toni ('89) recognizes no varieties of it. Nitardy ('14) has apparently never seen it and refers it without adequate evidence to *P. Boryanum*. The colonies tend to high cell numbers and in the 32- and 64-celled types have quite regularly a somewhat reniform outline which is suggested also in the sixteen-celled colony. That the cell form is in any way adapted to or determines this configuration of the colony is not obvious, and the form-determining factors are not so readily recognizable as in the other Diactinia.

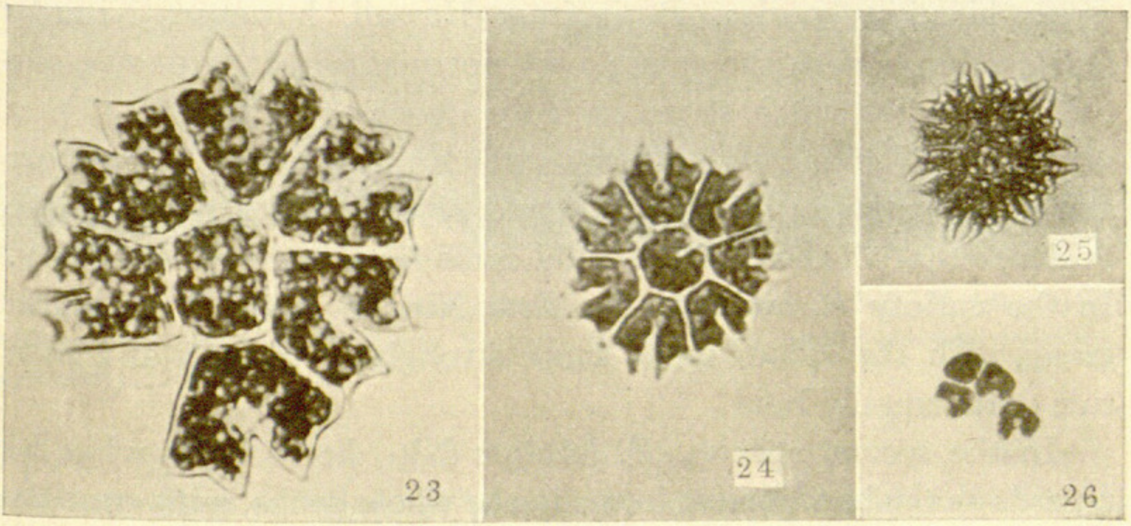
I shall discuss the species further in considering the general question of the relation of the larger cell numbers to the configuration of the colonies in another paper. The shortness and form of the spines suggest in some degree those of *P. Ehrenbergii*, but the species cannot be regarded as in any proper sense a transition form between the Diactinia and Tetractinia.

D. *Pediastrum tricornutum* Borge.

This species, representing perhaps a series of *Triactinium* (Nitardy makes it *Diactiniopsis*), I have not seen. It differs characteristically from other types in that the three spines do not lie in the same plane and hence have no part in determining the intercellular contacts in the colony. Only eight-celled colonies have been figured so far—one cell in the center surrounded by seven. Such a form could hardly be conceived as developing from the Diactinia by progressive variation. It may have originated from a form like *P. integrum* as a representative of quite a different line of development or it may have connections with *Coelastrum* in quite a different series.

E. **Tetractinium.**—*Pediastrum Ehrenbergii* A. Br.

The Tetractinia illustrated by the common *P. Ehrenbergii* (FIGS. 23, 24, 25, 26) are those types in which the two spines or



FIGS 23, 24, 25, and 26. *Pediastrum Ehrenbergii* A. Br., with varying degrees of lobing of the cells. Figure 26 shows a four-celled colony with one cell almost free but showing none the less the characteristic wedge-shaped form, × about 350. Fig. 23 × about 1000, Fig. 24 × about 700, Fig. 25 × about 550.

lobes of the Diactinia tend to become more or less deeply bifid. The species commonly occur in four-, eight-, and sixteen-celled colonies and consist in the latter of a group of four or five central cells surrounded by, respectively, twelve or eleven peripheral cells.

In this group again the splitting or doubling of the spinous projection of the cell in its incipient stages foreshadows the further development of this character through the whole series. The incised or bifid tips and the doubling of the spines appear in graded stages of development which suggest very strongly that the species have been produced as end members in series of continuous variants. Under *P. Ehrenbergii* and its synonyms we find included by most authors forms in which the degree of lobing varies widely. In some forms the cells are only bluntly bifid (FIG. 26). In others there is every degree of inequality between the two points of the bifid spine, suggesting that the forms may have arisen from the Diactinia by the budding off of an accessory tooth on the main spine, or at another point on the body of the cell rather than by splitting the tip of the spine itself (FIG. 25).

Nitardy's treatment of the group recognizes the depth of lobing and the degree of separation of the points as the principal basis for distinguishing the types and his two species, with a variety under the first, form what it seems to me is in part at least a natural series.

In his first species, *P. incisum* Hassall, however, Nitardy includes forms with the spines very unequally cleft (FIG. 24), one half frequently much more strongly developed ('14, *pl. 5. f. 7* and *pl. 7. f. 8*) along with others in which the spines are very short and even blunt ('14, *pl. 7. f. 6*, *7*, and *11*). There is no adequate evidence that all these forms could come from one mother colony. In the variety *P. incisum* var. *Rota* Nit. he includes a natural group with the spines much more strongly developed and as a rule quite equally bifid.

In the second species, *P. lobatum* Nit., he includes what he regards as the handsomest forms in the whole genus, with strongly developed lobes deeply bifid (*pl. 5. f. 4*). This is plainly Braun's and Cooke's *P. Rotula* Ehrenb. The five species and four varieties recognized by De-Toni also show characteristic differences in the cell form and lobing but reliable figures are not available for grouping them in an evolutionary series.

I have never seen in *P. Ehrenbergii* the 1 + 5 + 10 configuration which is so common in the Diactinia. In the eight-celled colonies the common arrangement is 1 + 7, with the central cell having the appearance of being rather crowded and suppressed in its development though quite regularly showing the narrow notch characteristic of the cell form of the species (FIG. 24). This apparent crowding of the central cell in a group of 1 + 7 is quite contrary to what one observes in *P. simplex* and other species. It is due to the pronouncedly wedge-shaped form of the cells. That the cell form is, as in other species, hereditary and not dependent on the pressure of adjacent cells for its development is shown in FIGURE 26, which represents an irregular four-celled colony, one of whose cells is almost free and has none the less developed the wedge-shaped form.

The quadrifid cell form apparently does not lend itself to the formation of symmetrical least surface configurations with regular intercellular spaces as does the duplex form. I have seen no colonies in which there was any indication of the utilization of the quadrifid character in the interior cells of a colony in developing symmetrical intercellular relations. Braun's figures of *P. Rotula* ('55, *pl. 6. f. 5–12*) suggest that such cases may exist. Braun's

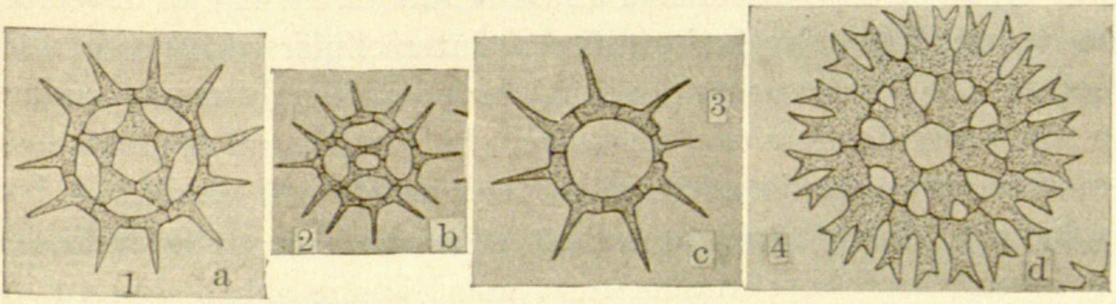


FIG. 27, *a, b, c, d*. Reproduced from Nitardy ('14). *a, b, c, P. triangulum* (Ehrenb.) A. Br.; *d, P. Rotula* Ehrenb., sixteen-celled colony showing bilateral symmetry.

figure ('55, *pl. 6. f. 5*) and Cooke's figure ('84, *pl. 18. f. 2d*) are fine examples of bilateral symmetry in eight-celled colonies of *P. Rotula* Ehrenb. In the sixteen-celled colonies the central group of four or five may make a ring with a four- or five-sided intercellular space in the center and the peripheral cells may also make a very perfect ring-formed series of eleven or twelve. There are, however, no relations of symmetry further than this general concentricity between the cells of the two series shown in any figures except one by Nitardy ('14, *pl.* 5. *f.* 4), which I have reproduced (FIG. 27*d*). It would seem that the tendency to lobing which fits so perfectly with the principles of least surfaces and binary fission in the simpler forms of the diactinial type has here gone too far and become distinctly non-adaptive as far as the symmetrical grouping of the cells is concerned. The tendency to the lower numbers of cells in the colonies of these species is, if real, a curious correlation, since the quadrifid form of the cells would not in any case seem capable of limiting the number of times they should divide in reproduction.

DISCUSSION

The general relations of the *integrum*, Monactinium, Diactinium, Triactinium and Tetractinium types suggest at once certain evolutionary possibilities and limitations in very clear form owing to the extreme simplicity of the characters involved. Evolution in the whole group has proceeded by modification of the cell form. It is quite obvious, as noted, that a species with one spine could not become gradually modified into a species with two spines in any other way than by returning to the spineless type and then advancing on quite a different line of development resulting in typically different intercellular relations in the colony. We have no evidence of the possibility of transforming a *simplex* type into a two-spined type by the gradual development of a second spine in addition to the one already present or by splitting the single spine. A form with one long, well-developed spine and one short, rudimentary spine is not only unknown in nature but is quite inconsistent with the colonial organization of the cells in the plate-shaped groups which are characteristic of the whole genus. The only obvious evolutionary routes from a one-spined to a two-spined type are either as noted by a change back to the primitive *integrum* type and a new start in a characteristically different direction or by sudden mutational transformation, perhaps to be considered a reduplication, by which a form with one spine becomes at once a form with two equally well-developed spines. There is an analogy here with the reduplications in the lobing of fern fronds and pinnae by which the common sports of the Boston fern have been produced (see Benedict, '16).

That it is mere analogy is, of course, obvious from the fact that the phenomenon is intracellular in the one case while in the other it involves the morphogenetic behavior of many-celled tissues and organs. Given this change of cell form and the diactinial type of colony would result directly, the same polarity and cell interrelations being involved in both cases.

We have, further, manifestly orthogenetic groups in most of the subgenera. Given the tendency to the development of two spines and the species of the two-spined group are at once foreshadowed as are the species of the Monactinia, Triactinia, and Tetractinia by the presence of the possibility of developing one-spined, three-spined and four-spined or bifid-spined cells, respectively. Given cells which adhere in groups, at the same time having a tendency to develop thick spinous projections with catenoidal deformation of the entire cell body, and the whole genus is foreshadowed. Such series certainly illustrate one form at least of the many types of change which have been characterized as orthogenetic, though the use of such a term is not specially illuminating in the absence of evidence as to the structural features of the cells which have determined their characteristic forms. A fuller cytological study of the cells of *Pediastrum* may serve to throw light both on the nature of cell polarities and the means by which such orthogenetic transformations are brought about.

The transition from the *simplex* to the two-spined type, as noted, could only come about either by a change giving the new character in functional development at once or by a return to the primitive *integrum* type and a new start. The same is true as to the possibility of change from the two-spined to the three-spined type. On the other hand, the change from the *simplex* to the trispinous form might quite well come about by the gradual development of two additional spines with or without the degradation of the single existing spine. To be sure, the three spines do not lie in the plane of the colony as does the single spine, but the readjustments which this difference between the two types involves are by no means inconceivable.

It is notable that in *Pediastrum clathratum* the interior cells show almost as fully developed lobes as those on the periphery and in this respect again I am inclined to regard it as a more specialized type even than *P. asperum*, though it is obvious that there is less differentiation between its cells than is found in *P. Boryanum*, in which the interior and the peripheral cells differ notably in their form. In *P. clathratum* and *P. asperum*, however, the hereditary cell form has become apparently so fixed that it comes to expression even under the difficult conditions of the interior cells. If, as I have suggested ('18), the adaptive oblong four-lobed cell form originated and developed in direct response to the environmental limitations and stimuli imposed on sixteen cells adhering in a plate-formed colony and with a tendency owing to their partially fluid consistency to assume a surface tension form, *P. clathratum* certainly represents the most extreme expression of this evolutionary trend. The advance has been from such unspecialized and uniform cells as those of *P. integrum* through *P. Boryanum* with its cell differentiations to *P. asperum* and *P. clathratum* where all the cells are much alike again but vastly more specialized in form.

The relations of *P. simplex* and *P. triangulum*, as I am recognizing them, illustrate the same point. In the sixteen-celled colonies of *P. simplex* the interior cells differ regularly from the peripheral cells by the absence of the spine, though as shown in figure 4 an interior cell will develop a spine whenever it is so placed with reference to an intercellular space that this is possible. In *P. triangulum* both interior and peripheral cells develop spines and the configuration of the colony is altered accordingly by the achievement of symmetry relations which permit each cell to express much more fully its inherited form tendencies. That these form tendencies are really present equally in all the cells of *P. simplex* also is shown in the eight-celled ring-shaped colonies where every cell has an equal chance to achieve its full morphogenetic possibilities and the result is a remarkable uniformity in the size and shape of all the cells.

The development of spines and the four-lobed cell form in *P. asperum* seems to have to do with the compactness and surface tension relations of the cells in the colony as a group, while in *P. clathratum* the length of the spines results in a light, open structure of the colony perhaps adapted to life in the plankton.

Schroeter ('97) and many others have noted that various species of *Pediastrum* may be plankton organisms.

The gradual appearance of the bifid spine in the Tetractinia is certainly a further development of the tendency to lobing of the cells and the group forms an obviously orthogenetic series, but here the bifid spine is quite unadapted to the development of cell groups with the bipartition cell numbers. In cases where symmetry, either bilateral or merely concentric, in the arrangement of the interior cells of the eight- or sixteen-celled groups is achieved it is at the expense of the bifid tips which appear, if at all, only as a broadening of the ends of the spine which hinders rather than helps the achievement of equal contact and pressure relations among the cells.

The whole *Pediastrum* group seems well calculated to show that fixed trends in development do not necessarily imply adaptation, though frequently resulting in highly specialized structural differentiations which are plainly adaptive from the standpoint of the life habits of the organism. Further, openness and lightness with increased surface in the colony as a whole is the same thing as deep lobing of its body for the single cell. But the development of a rounded least surface contour for a group of cells made up of the bipartition numbers 4, 8, 16, 32, etc., requiring an oblong form and perhaps favoring the lobing of the cells, is thus quite a different thing for them from the same tendency to round up expressed in their individual masses. In order to make a surface tension group under the given conditions the cells must lose in some degree their own tendency to assume the surface tension form and yet, as I have pointed out elsewhere ('18), this anomogenous condition imposed upon the cells in achieving their interrelations in the colony becomes then fixed in heredity so that the cell develops the characteristically lobed form even when as a result of accident it develops in almost complete freedom from contact and pressure relations with its sister cells.

I have referred to the interactions by which the type pattern of the colony is achieved as based on the polarities of the swarmspores and their sensitiveness to contact and pressure stimuli. That there can be no mosaic inheritance in the case of these colonies formed by groups of free-swimming zoöspores is, as I have pointed out before, sufficiently obvious. It is also clear that no spatially differentiated representation of the organization of the colony in the organization of the mother cell could have any bearing on the method of transmission of the type configuration of the colony. In *P. clathratum* both the colonies and the cells are bilaterally symmetrical, both show polar differentiation, the colony in one axis and the cell in at least two axes, and yet the polarity and bilateral symmetry of the cell are in no sense representative of the polarity and bilateral symmetry of the colony. Neither predetermines the other directly though there can be no question here that the cells as independent units build the colony and their properties determine its properties. Surface tension is a common factor in determining the form of the cells and through the adhesion of the cells to each other in determining the rounded outline of the colony as a whole, but as I have already pointed out it is the inherited anomogenous consistency of the cells which is of most significance in determining their form and it is their motility, polar differentiations, and sensitiveness to pressure and contact stimuli which make it possible for them to achieve the highly symmetrical and characteristic interrelations shown in the pattern of the adult colony. I am discussing elsewhere ('18) the possible relation of these contact and pressure interactions in the primitive ancestral cell group to the development of the form of the cells on the principle of functional hypertrophy. However it may be with this question, which involves the difficult problem of the inheritance of acquired characters, there can be no doubt that, as noted, in the species as one finds them the cell form in its major outlines is fixed by heredity and can be achieved by the cell when free and quite independent of pressure relations with other cells in the colony. That the typical cell form is developed to the extent that opportunity offers regardless of how the cell is placed in the colony is indicated by the perfection of the free lobe in one of the interior cells of the colony shown in FIGURE 18 and by the development of a fairly good spine on one of the interior cells of the colony shown in FIGURE 4. More extended evidence on this point is presented in connection with my study of *P. asperum* ('18).

It seems to me, further, clear that the functional polarity and the capacity of the cells to respond to pressure and contact stimuli are not fundamental properties present in full degree in the ancestral types of the group but that these characters have increased and become specialized with the gradual development of the highly modified and lobed form of the cells. Simple adhesion of the cells in a palmelloid mass may have been the initial stage in colony formation. Light reactions may have favored the development of the plate-like expanded form though this is achieved now by the polar differentiation and reactions of the swarm-spores quite independently of the direction of the light.

These reactions to pressure and contact and the resulting form determinations are typical examples of biogenetic processes in Hertwig's sense. It is quite possible that such reactions may be the determining factors in the root behavior which led Noll ('00) to assume morphaesthesia as a fundamental phase of morphogenetic behavior. Morphaesthesia is for Noll the expression of the capacity of lateral roots to regain a radial direction of growth after they have been forced out of it by an interposed obstacle—radial not to the point of origin of the root from the main axis but radial to the axis from the point at which the root becomes free from the obstacle. The capacity to regain such a generalized relation as that of the radius from any point of the axis opposite to which the root happens to be certainly implies a response to form-determining stimuli of the most delicate sort. Noll was inclined to regard it as a sort of direct reaction to the form of the whole organism by each of its parts. The only physical stimuli which seem to be involved are the pressure and contact interrelations involving weight relations, tensions due to bending, etc., between the cells themselves.

Whether or not such reactions are adequate to account for the radial growth of lateral roots with their much greater complexity of structure, there can be no question, it seems to me, that the assumption of a fundamental capacity to achieve symmetry is the natural suggestion from a study of the delicately balanced interrelations of the cells in such types as the sixteen-celled colonies of *P. clathratum* and the eight-celled ring-shaped colonies of *P. simplex*. Direct action of surface tension on the plastic though anomogenous cell bodies may account, as noted, for the final niceties of adjustment, but the grouping as first achieved by the free-swimming swarm-spores must be admitted to be a matter of cellular interactions and the major stimuli in such a series of adjustments must be contact and pressure. That chemotropism could play a rôle is hardly conceivable in view of the violent movements of the swarm-spores in the narrow confines of the mother vesicle. That in the last stages of swarming equilibrium should be reached in a situation of as nearly equal pressure and contact from all sides as is possible may seem to some to be merely a matter of physical necessity operating on what, from the conditions in the adult colony, might seem to be inert gelatinous four-lobed or one-spined masses, but in the fact that this equilibrium position is achieved by a group of freely swimming organisms, each with inherited cell-form tendencies which are certain to come to expression in greater or less degree, no matter how the cell is finally placed in the group, we find the proof that nothing less than the assumption of a capacity to respond to and maintain conditions of equilibrium when once achieved can adequately account for the symmetry of the typical colonies as we find them.

That the symmetrical spatial interrelations of the cells is no mere expression of the direct action of the physical principles of surface tension, adhesion, mutual pressure, etc., is further shown by the endless number of variations from the type configuration. There is good evidence here of trial and error by complex organisms with every type of error as well as degree of approximation to the typical fixed in the endless variations in detail which can be found in the configuration of the adult colonies. It is difficult to give an adequate picture of what one sees in watching the free-swimming swarm-spores darting here and there around and through the mass and the gradual appearance of order out of confusion with the coming to rest first of a peripheral series and then of the interior cells, but that cellular interactions of sensitive tropic units determine the symmetrical final configuration rather than the direct operations of surface tension, adhesion, etc., on the one hand or any mysterious controlling and adaptive principle of behavior seems to me the obvious suggestion from the facts. The evidence seems to me adequate for assuming a high degree of potency for such simple stimuli as contact and pressure between polarized cell units like those of *Pediastrum* in initiating and controlling morphogenetic processes.

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