Botany. — *The shape of cells in homogeneous plant tissues.* II. G. VAN ITERSON Jr and A. D. J. MEEUSE.

(Communicated at the meeting of September 27, 1941.)

4. *Suppositions, concerning physical causes of the formation of the cubo-octahedral cellform.*

We have communicated that as early as 1807 MIRBEL suggested that the cells assume their polygonal shape, owing to the fact that originally they are round bodies, flattening each other during their growth.

The idea to connect the form of the cells with the shape which plastic spheres assume, when assemblages of them are compressed through pressure on all sides, or when assemblages of inflatable spherical bodies are freed from their interstices by inflation in an enclosed space, has also been discussed by later investigators.

We shall first discuss the theoretical side of the problem.

When the faces with which the spheres on compression from all sides of the assemblages, or on inflation in an enclosed space, touch and flatten each other, cannot slide over each other, the form of the resulting bodies will be entirely determined by the method of stacking. An assemblage of equal spheres wherein the spheres are placed in the corners of a cubic partitioning of space will produce cubes, and an arrangement according to the closest packing of equal spheres produces rhombic dodecahedrons or extended rhombic dodecahedrons (depending on the position of the spheres in the successive plane layers of the stack) [1]. The way how to pack equal spheres in order to produce on compression orthic tetrakaidecahedrons was calculated for LEWIS by Prof. WILLIAM C. GRAUSTEIN (11); the spheres in the separate plane layers must be placed in squares, but with interstices between the neighouring spheres equal to 0.31 × the radius, the spheres of a superior layer must rest on four spheres of a lower layer.

Experimentally the proof of the correctness of these considerations cannot easily be furnished. It is difficult to cause uniform pressure on all sides of an assemblage of spheres and it is not easy to find bodies inflating

[1]) As early as 1897 W. BARLOW (A mechanical cause of homogenuity of structure and symmetry geometrically investigated, etc., Scient. Proc. Roy. Dublin Soc. **8**, 527—540 (1893—1898)) pointed out the circumstance that an assemblage of equal spheres in closest packing may be constructed in different ways, the centres of the spheres forming point systems with different symmetries. B. G. ESCHER (Over de regulaire en hexagonale dichtste bolstapelingen en de deformatie hunner bollen tot dodecaëders tengevolge van compactie, these Proceedings **43**, 1302—1310 (1940)) lately discussed the bodies which are formed on allsided compression of such arrangements until there is no space left between the spheres. Such bodies are rhombic dodecahedrons and extended rhombic dodecahedrons (for the latter see Fig. 1d in the first part of this communication).

equally in all spatial directions. Some investigators have caused peas to swell in an enclosed space, in imitation of a famous experiment by G. L. L. DE BUFFON (2). One of those who tried this was R. GANE (6) but he was not successful, neither with globes of dough, which he caused to expand by fermentation. F. T. LEWIS (20) informs us that after an experiment with peas, which were made to swell in a brass cylinder, he found an average number of 12.13 faces on 200 peas, and in another experiment with 400 peas the average was 12.14 faces. When he considered that some faces were bounded by intercellular spaces he came to the occurrence of averagely 12 contact faces for one pea with other peas. This result was to be expected if the peas were indeed placed after a closest-packing-arrangement. Yet — for reasons which will be given later — LEWIS calls this experiment "unfortunate".

Some investigators have compressed stacks of equal spheres of plastic material unilaterally. GANE (6) used for this purpose spheres of plasticin, which he rubbed with talc powder and compressed in a cylindrical tumbler, in which he first shook them gently. Here bodies were obtained with lateral faces the number of which varied between 12 and 14. Yet we cannot attach great value to GANE's experiments, seeing that he also compressed equal plastic globes packed as closely as possible in a rectangular space in which experiment he did not get rhombic dodecahedrons, but bodies approaching the orthic tetrakaidecahedron. We have repeatedly made the same experiments and we did get rhombic dodecahedrons or extended rhombic dodecahedrons. On unilateral compressure of equal spheres these bodies naturally did not possess edges of uniform length, but on compression of ellipsoid bodies the resulting bodies had this property. The main fact is that from different stacks of equal spheres bodies with perfectly flat lateral faces and with straight edges are obtained and further it is of importance that on the resulting bodies right and acute angles may be observed and that each body may show more than 3 edges meeting in the same vertex. In the compressed plastic matter these figurations are perfectly stable.

These details exclude the explanation of the tetrakaidecahedral cell form *with curved edges and curved faces* as a result of compressure of originally spherical cells in closest packing and even in a packing after GRAUSTEIN.

A short time ago J. W. MARVIN made some very careful experiments concerning the compression of lead shot in cylinders. A provisional communication (22) appeared in 1937 and this is the treatise which confused LEWIS, making him attribute his own observations of swollen peas to an unfortunate experiment. MARVIN found an average number of lateral faces of 14.17 in shot which had been placed arbitrarily in a cylinder and had been compressed in it in such a way that all intervening space had disappeared, the shot located peripherally in the cylinder being omitted on counting the faces. This figure strikingly approaches the average value which LEWIS found for the number of lateral faces of the cells of elder pith, and led him to doubt whether shot in the closest packing produces rhombic dodecahedrons on compression.

Since then, in 1939, MARVIN (24) made detailed communications about his experiments. Among others he gives pictures of the result of shot compressed when packed in the closest way, rightly mentioning that in that case rhombic dodecahedrons are obtained. Further he investigated statistically the frequency distribution of the various lateral faces of compressed shot which had been poured into the cylinder without any precautionary measures. There is no doubt that the deviations from the rhombic dodecahedron in the latter case are to be ascribed to the fortuitous arrangement of the shot in this case. It should be borne in mind that even if the bottom layer was placed in such a way that each sphere touched 6 neighbours the arrangement of the shot in the next layers generally would not be the closest possible, as for that purpose the shot of the second layer should fall in *fixed* hollows of the first layer (these hollows are determined as soon as one of the shot of the secund layer has found a place in one of the hollows of the bottom layer). The compressure of spheres in a fortuitous arrangement never can lead to a *homogeneous* assemblage. So in our opinion the agreement of the average number of the lateral faces of compressed shot in these experiments with the average number of the lateral faces of cells in *homogeneous* plant tissues is of no account.

Therefore I shall not discuss the certainly interesting experiments of E. B. MATZKE (25) who compressed mixtures of large and small shot in different proportions until the air in between had disappeared. It will be clear that averagely there were produced more lateral faces on the large shot than on the small.

After what has been said above about the occurrence of tetragonal faces in cells in uniform tissues with sides curved outwards, and about the occurrence of corresponding faces in bodies of membranes of a solution of soap in a homogeneous soap-froth, one might be inclined to consider the shape of the cell as the result of the action of surface tension.

It would be superfluous to recall the fact that there has been a time when surface tension was indeed connected with the position of cell walls with respect to each other. L. ERRERA (4) and afterwards his collaborator E. DE WILDEMAN *compared* the perpendicular position of newly formed cell walls on those present before, and the cell structure of mature tissues with respectively the position of membranes of a soap solution against a moist solid wall and the position of membranes in soap-froth. Meanwhile the conception that in juvenile as well as in mature tissues the surface tension is the *causal force* of the arrangement of the cell walls, has been wrongly ascribed to ERRERA. As a matter of fact the investigator referred the botanist NOLL to an experiment of MACH, when at a congress at Wiesbaden — where ERRERA read a paper on this subject — NOLL remarked that from their origin cell walls should be considered as a solid and not as a liquid matter. From MACH's experiment, which will be discussed later, it appears that stretched rubber membranes — which are solid — may behave to a certain extent like membranes of a liquid. Yet ERRERA is himself guilty that people had a wrong impression of his conceptions, for in some of his publications he did not avoid the suggestion that the surface tension plays a part at least in determining the position of juvenile cell walls. This can be made clear from the following quotation, which will be of interest in our subsequent considerations. "In mature plant tissues the passive tension of the cell wall through turgor replaces active surface tension. Grouping according to angles of 120° is therefore maintained, or is even reached owing to later shiftings in cases where originally angles of 90° occurred!"

G. BERTHOLD (1) formulated the difference between the arrangement of juvenile cell walls and that of walls in older cell tissues thus that during the development each cell wall tries to become "a plane of *minimal area*" and that in mature tissues the "assemblage of cell walls in its entirety" tries to fulfil the requirements of the principle of the minimal area. For that latter purpose, he thinks, "the cells will later slide over each other and be deformed". BERTHOLD is very certain in his opinion that even the juvenile cell wall should not be considered as a liquid lamella and he tries to account for the perpendicular location of the young wall on the older ones by a tendency to equal division of space of the mother cell over the daughter cells.

It is well-known that in his book mentioned before D'ARCY W. THOMPSON enumerated instances in which the location of the cell walls according to BERTHOLD's principles may be observed. From the recent studies of R. SOUÈGES (30) on the development of vegetable embryos other instances may be taken.

Later investigations about the development of young cell walls and their deformations after the embryonic stages entirely exclude activety of surface tension in the formation of the cubo-octahedral shape. This does not take away from the fact that ERRERA's reference to the experiment of MACH and his observations on the activity of turgor as a deforming action on cell walls have not lost their significance. Therefore I wish to call the attention to that experiment. It was described by MACH (28) at a congress in Prague in 1868. Over the edges of a regular tetrahedron rubber membranes were stretched, after which the space enclosed by those membranes, into which a metal tube entered, was exhausted. The membranes then contracted to the same figure as the membranes of a solution of soap assume when a wire tetrahedron is immersed in a such a solution.

K. GIESENHAGEN (7) enclosed rubber balloons in glass vessels and then exhausted the space round the spheres; the rubber spheres then expended and flattened each other; the partition walls showed positions agreeing with those of cell walls in certain tissues. It was necessary, however, to moisten the balloons with paraffin oil, so that they could slide over each other.

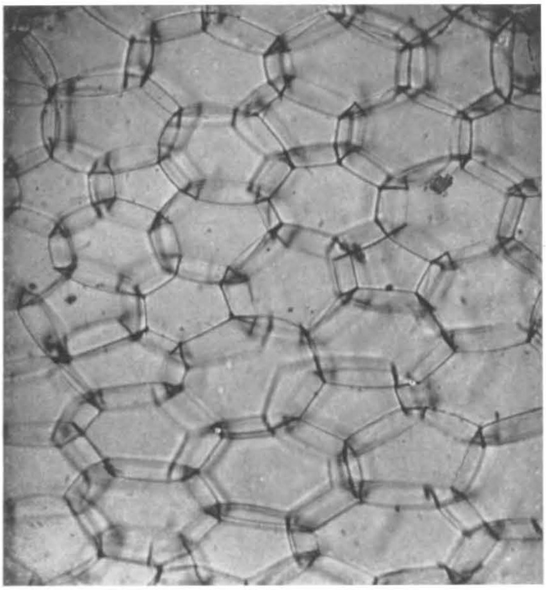


Fig. 1.
Transverse section of the cortical parenchyma of a root tuber of *Asparagus Sprengeri*. Magnif. 50.

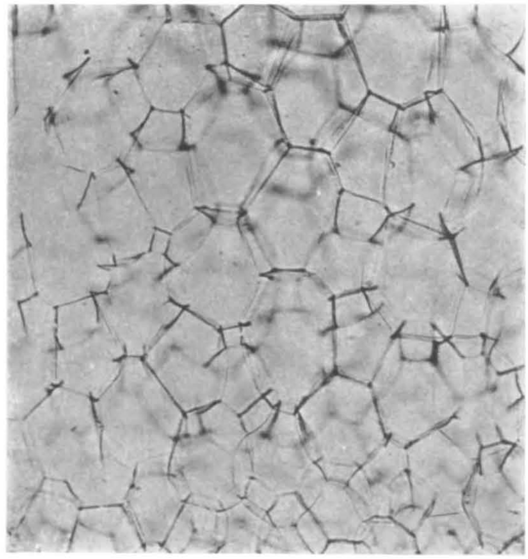


Fig. 2.
Oblique section of the same tissue with many tetragonal faces. Magnif. 50.

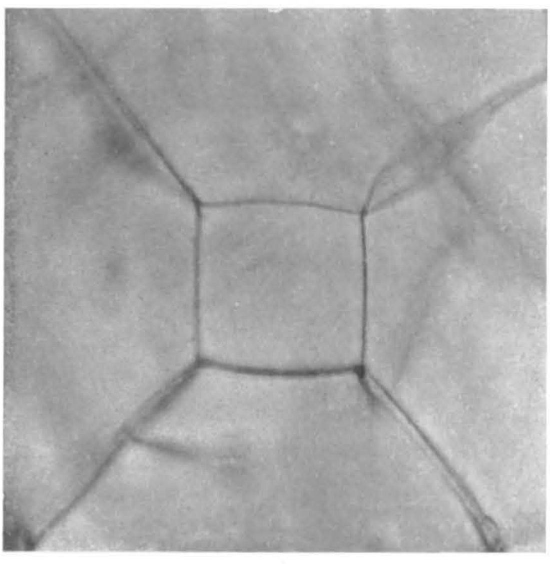


Fig. 3.
A tetragonal face with curved sides and parts of four adjacent hexagonal faces of a cubo-octrahedral cell of the cortical parenchyma of a root tuber of *Asparagus Sprengeri*. Magnif. 200.

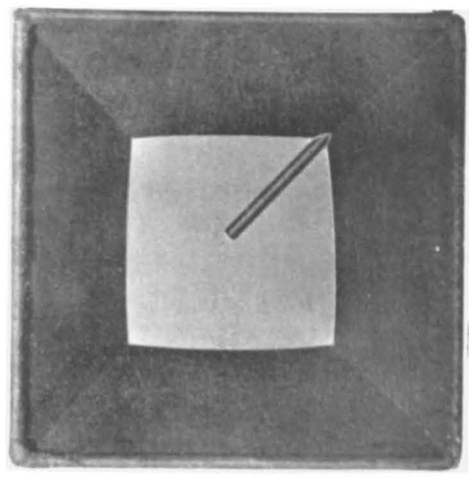


Fig. 4.
The tetragonal plane face with curved sides and the adjacent faces formed in the centre of a rectangular prismatic wire model (the sides of which were 10.2 cm, 8 cm and 10.2 cm). The faces of the model were entirely covered with plane rubber sheet, then it was exhausted by an air pump for which purpose a small tube entered the enclosed room to the centre (this tube is to be seen in the photograph). All the faces in the exhausted model are formed by two membranes. The model was illuminated from the back side, which causes the contrast between the tetragonal face and the other faces.

MACH's experiment may be repeated with other wire figures, for instance with the rectangular prism that Sir WILLIAM THOMSON used to demonstrate the tetragonal plane faces with curved sides of the cubo-octahedron with minimal area (see figure 2 in Part I of this communication); the rubber membranes in the centre of the prism assume a tetragonal shape with curved sides (see fig. 4 on the plate), which entirely corresponds with the shape observed in the experiment of Sir WILLIAM THOMSON with membranes of a solution of soap.

Now it may be assumed with ERRERA that in plant tissues the tension in the cell walls is caused by the turgor pressure of the cells. Further, a hypothetical explanation might be given of what happens in the development of a homogeneous cell tissue with cubo-octahedral cells with curved edges. It may namely be imagined that the cell walls under the influence of their tension take up such a position on growth that in total they assume a minimal area and that if they do not attain that position without changing their mutual arrangement, they will slide over each other in such a way (remember the paraffin oil in GIESENHAGEN's experiments) that they attain that position subsequently.

5. *The significance of the original location and of the growth of the cell walls for the arrangement of the walls of the mature tissues.*

Originally the senior author of this treatise actually thought that the explanation of the occurrence of the "body of Thomson" as the ideal cell form in homogeneous tissues was indeed that juvenile cubic cells, or juvenile cells of a rectangular or a hexagonal prismatic shape, when expending by their growth to maturity, slide over each other, changing their position, until the walls of each cell have obtained the minimal area, possible with the contents of the cells.

Meanwhile it is true that the possibility of the cell walls sliding over each other has often been assumed, but it has also repeatedly been doubted. A dissertation has appeared by A. D. J. MEEUSE (26) in which "the problem of the sliding growth in plant tissues" has once more been thoroughly studied, and from this it can be seen that in plant tissues such growth is out of the question. All the cases in which such growth was assumed may be interpreted differently. The exceptional cases in which cells get into contact with cells with which originally they had no contact must — as is proved by this investigation — be interpreted otherwise than by sliding of a cell wall over other cell walls.

In consequence one may expect the 14 faces of contact of the mature cell with neighbouring cells in homogeneous tissues to be present from the very beginning, that is to say from the moment the cells had been formed through division of other cells. This is actually seen to be the case in the investigation of meristems from which homogeneous plant tissues develop. In those meristems the juvenile cells are hexagonally prismatic, rectangularly prismatic or cubic in shape and in that form they are already bounded by 14 other cells. The cubo-octahedron develops when 12 out of those 14 faces take up another position when the cells increase in size, namely a position oblique to that of the original one. Two of the faces, those namely which may be considered as upper and lower, or as anterior and posterior faces, only move parallel to themselves. During this development all the edges and eight of the lateral faces of the cell body are curved. The change in the shape of the cells takes place in such a way that the ratio of the contents to the area increases; this may also be formulated by saying that the cell approaches the spherical shape more than would be the case if all the walls had remained plane and the edges straight.

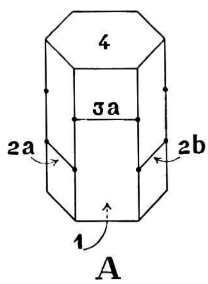
The opposite of the process decribed may be easily pictured, by placing a cubo-octahedron (with straight or with curved edges) of plastic material with a hexagonal face on a horizontal plane, imagining the body stretched vertically in such a way that the six double broken edges connecting the corners of the top and bottom faces of the cubo-octahedron are changed into straight edges, the body thus becoming a hexagonal prism. By horizontal stretching this prism may be changed into a rectangular prism and from that by stretching or compression in two perpendicular directions a cube may be obtained. If the same is imagined to happen to all the cells of a homogeneous tissue of cubo-octahedral cells the walls will not slide over each other; the hexagonal prisms, the rectangular prisms and the cubes that are the result of the deformation will then have 14 contacts with neighbouring prisms or with neighbouring cubes.

On studying juvenile tissues from which homogeneous tissues develop it is seen that they must be counted among the column- or platemeristems in the sense of O. SCHÜEPP (29). As an example we refer to the pictures of longitudinal and transverse sections of the meristem of the pith of *Juncus effusus*, occurring in a publication by R. A. MAAS GEESTERANUS (21), in these Proceedings. Its cells are hexagonal prisms and in the not too juvenile part of the meristem they form vertical columns of cells, owing to the fact that almost exclusively transversely placed partition walls are formed; each cell therefore touches one cell above and one under itself. Besides, these cells have contact sideways with twelve other cells. The same arrangement is found in the columnmeristem from which the cortical parenchyma of the tuber of *Asparagus Sprengeri* develops.

When these cells are inflated by turgor pressure, which will cause tension in the cell walls, then on growth of the cells the result will be the development of "bodies of Thomson", or of bodies which may be derived from them.

It is not necessary to assume that the bounding faces from the very beginning possess surfaces which bear the same ratios to each other as the faces of the "body of Thomson" do. When for instance one of the partitional faces is proportionally too small, there will on inflation be greater tension in it than in the other faces[1]). As a result the face in question will be more stetched and by growth will more increase its surface than the other faces do. When the inflation is continued long enough, and when the increase of the contents of the cell is equally possible to all sides, the influences discussed here will cause the curving of all the edges and of eight of the faces characteristic of the "body of Thomson", and the ratios of the surfaces of the bounding faces occurring in this body will also be attained.

From what has been said it follows that the shape of the cells in homogeneous cell tissues is determined for the greater part, though not entirely, in the meristem. In order to account for the occurrence of the "body of Thomson", the arrangement of the new cell walls in the meristem has therefore to be considered. I shall restrict myself here to a columnmeristem constructed from hexagonal columns. If the cubo-octahedral cell form is indeed preformed in this meristem, the arrangement of the cell walls in one of the cells forming such a column, and that of some of the walls of adjacent cells, must be approximately as pictured in fig. 5 (in this picture is found a perspective view of the cell and moreover it is folded out in the plane of drawing).



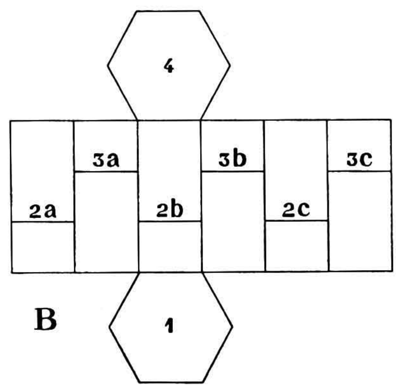


Fig. 5.

A. Hexagonal prismatic meristimatic cell in contact with 14 others. B. The same cell, all faces folded out in the plane of drawing.

The horizontal walls are numbered in the order in which they are supposed to be deposited; the walls 2a, 2b, 2c and 3a, 3b, 3c are horizontal walls of neighbouring cells; the walls indicated by 2a, 2b, 2c are supposed to be formed simultaneously or nearly simultaneously and the same holds good for the walls 3a, 3b, 3c.

If it is assumed that the youngest part of the meristem is found at the top of our picture, it is plausible that the horizontal cell walls have developed in the order indicated by the figures by the side of the walls. In order to explain why the arrangement of the horizontal walls comes about as is shown in our picture, the theory may be brought forward —

1) This becomes clear when one imagines a regular, hexagonal network of equally thick and equally tautly stretched rubber threads, and one of the sides of a hexagon shortened.

very plausible in the light of newer investigations — that for the formation of cell walls a certain substance is necessary which is supplied from the older part of the meristem, but which is consumed in the formation of the wall [1]. If at first only wall 1 is imagined to be present and new cell wall forming substance is imagined rising *regularly*, it is more likely that the next cell wall will not be formed within the cell pictured, but in an adjacent cell. If for instance the formation of cell wall 2a follows that of wall 1 it will be most probable, owing to the consumption of the substance in consequence of the formation of the new wall, that other new cell walls are formed in cells not located in the immediate neighbourhood of wall 2a. Thus it may be understood that walls 2b and 2c are formed about simultaneously with wall 2a.

If following the deposition of the walls 2a, 2b and 2c wall-forming substance is imagined to rise with the same regularity, then, owing to the consumption of the substance by the walls which are in course of construction, it will be the turns of walls 3a, 3b and 3c to be formed. It stands to reason that on further supply a new wall in the completely pictured cell, so wall 4, will next be formed.

In a "platemeristem" similar circumstances may account for the preformation of the cubo-octahedral cells, here all-sided supply in the plane of the substance introducing the formation of the cell wall must be assumed. In a "columnmeristem", constructed from columns of cubic cells, we are probably confronted with a case intermediate between a columnmeristem of hexagonal columns and a platemeristem.

Although these considerations are of a purely hypothetical nature, they may serve to make it clear that simple circumstances in the meristems may cause the arrangement of the cell walls according to the scheme discussed.

We will bring forward that these considerations likewise explain the occurrence of cell shapes deviating from the cubo-octahedron, which exceptional shapes occur in great numbers even in highly uniform tissue. Slight disturbances in the supply of the substance, which determines the deposition of the new cell walls, may cause such modifications that they cannot be eliminated by the subsequent regulating activity during the further development of the cell, described in the foregoing pages.

For several of the subjects discussed we finally refer to A. D. J. MEEUSE's dissertation, published lately [2].

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[1]) Naturally nucleus division preceeds the formation of a new wall; properly speaking we should therefore say: the supply of a substance causing nucleus division, but in order to simplify the trend of thought we indicate it as a substance necessary for the formation of a new wall.

[2]) In some respects the considerations exposed here differ from those of MEEUSE; this applies especially to those at the end of this communication. It is to be regretted that MEEUSE has not distinguished between the "body of Thomson" and the "orthic tetrakaidecahedron" (see his dissertation page 61), which makes misunderstandings possible. The above communication may help to remove those.

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