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ON THE
OCCURRENCE AND ATTRIBUTES
OF
PENTAGONAL SYMMETRY

C. M. BREDER, JR.

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INTRODUCTION

IT IS A STRIKING FACT that in the various papers and books on the nature of organic symmetry, both recent and ancient, there is surprisingly little comment on pentagonal or pentamerous forms. This is not because of a rarity of occurrence of objects displaying such characteristics, for, although not ubiquitous, five-part units are certainly common in both animal and plant design.

Considering only fairly recent contributions, one may take, as an example, the 1116-page volume of Thompson (1942) and fail to find any full discussion of the nature of this type of organic partitioning. Essentially the same situation is to be found in other recent but more specialized considerations of the properties of space, such as Breder (1947), Steinhaus (1950), Bonner (1952), and Weyl (1952). This is also true of the earlier discussions of Hilbert and Cohn-Vossen (1932), of which there is a recent English translation by Nemenyi (1952), and of Lartigue (1930). The last-named, however, in his somewhat mystical approach, does consider a few interesting aspects of five-part designs. Writers on the broad aspects of morphology in reference to animal evolution, such as Swinnerton (1949) and Gregory (1951), likewise do not take up a consideration of the causes or consequences of pentagonal organization.

In the study of developmental mechanics, echinoderm larvae have been used extensively. Although the work has been directed to these forms before the assumption of the pentagonal design by the adults, there is a notable absence of any consideration of the cause for the transformation of the early stages into a five-part adult. Child (1941), in summarizing a large part of this field of study, writes, "Echinoderm development presents perhaps the most remarkable sequence of symmetries and asymmetries of any animal group," but does not develop the discussion into any possible reasons why this fact might be associated with a pentamerous adult.

Evidently at least one of the reasons for such a situation is that the pentagon does not lend itself to readily understood physical and mathematical notions of utility and function as do the hexagon and equilateral triangle, which are treated extensively in most of the above-mentioned discussions. None the less, several groups, including both animals and plants, have developed a five-part symmetry as a whole or special structures with a five-part symmetry. The present contribution is to be considered as a first specific approach to the problem.

The number five and pentagonal designs have figured prominently in ancient mythology, magic, and theology and still exist in numerous present-day symbolic designs. Not the least interesting aspect of such considerations can be found in some of the dynamic consequences of five-part symmetry. These consequences extend into the behavior patterns both of those organisms possessing it in some form and of those reacting in some way to designs of this order. Organisms as different as honeybees and men clearly show striking attitudes and responses with respect to this form of symmetry.

Because it is impossible to understand the purposes of this paper without a solid grasp of the simple geometric peculiarities of both pentagonal and dodecahedral constructions, all necessary elementary geometrical and trigonometrical details are included, and because most of its readers will not be mathematicians, all the geometrical details necessary to follow the discussion have been diagramed in such a way as to make the meaning clear.

Most of the material on which these studies were made was obtained at the Lerner Marine Laboratory at Bimini in the Bahamas, where an abundance of five-part organisms is especially conspicuous. There is, of course, the prominent and varied echinoderm fauna as well as a striking number of obviously five-petaled flowers, such as *Hibiscus*. It is probable that this notable display of five-part symmetry was instrumental in initiating the present study.

Invaluable advice and criticism of the manuscript was given by Mr. James A. Fowler on the mathematical aspects of the subject. Dr. Bobb Schaeffer read and criticized the manuscript as a whole, Dr. Mont A. Cazier and Dr. Theodore Schneirla examined the entomological allusions, and Mr. W. Clarke checked the identity of the echinoderms mentioned.

GEOMETRICAL CONSIDERATIONS

BEFORE THE IMPLICATIONS inherent in the appearance of pentagonal structures in nature are considered, the geometrical characteristics of five-part forms are reviewed, with emphasis on the features that are found to be primarily concerned with the structural possibilities of organisms and the nature of the spatial limitations that a pentamerous design imposes.

A regular pentagon is shown in figure 1, with the incommensurate relationships between its radius (and that of a circumscribed circle), its apothem (and the radius of an inscribed circle), and its face. This figure is the regular polygon with the least number of sides that cannot be fitted as a mosaic to cover a surface completely. Polygons of four sides and of three sides can do this and, because a hexagon is made up of six equilateral triangles, it, too, can cover a surface completely, as is indicated by the diagrams of figure 2. All regular polygons of a larger number of sides agree with the pentagon in leaving some surface area uncovered by any possible arrangement.

If the sides of a regular pentagon are extended, they each meet the extensions of alternate sides to form a five-rayed star as shown in figure 3. Here is indicated the relationship between various parts of the design additional to the relationships indicated in figure 1, together with an inscribed and circumscribed circle about the star. The relationship of inscribed and circumscribed stars to each other is shown in figure 4. This obviously provides a different and more rapidly expanding series than does a nest of simple circumscribed pentagons. The further details of these numerical relationships are given in the Appendix. Considered another way, the five-pointed star is formed of all diagonals that can possibly be drawn in a pentagon. That is, each apex is connected with every other apex; together they form the star inscribed in a pentagon. The two inner stars of figure 4 illustrate this. The number of diagonals is equal to the number of sides. In polygons other than the pentagon, the number of diagonals may be either greater or less than the number of sides, less than the number of sides in polygons of fewer than five sides, and greater than the number of sides in polygons with more than five sides. The number of diagonals in a polygon may be expressed by

$$d=\frac{n(n-3)}{2}$$

where d = the total number of diagonals and n = the number of sides. The pentagon is seen to be at a point of change of relationships, that is, where the number of diagonals switches from less than the number of sides to more than the number of sides.

A regular polyhedron with each face a pentagon, the dodecahedron, which has 12 such faces, is shown in three aspects in figure 5. This is the regular polyhedron made up of faces having the largest number of sides possible, but not the largest number of faces. The icosahedron, with 20 faces, that is made up of equilateral triangles is the one with the largest number of faces possible. Thus the pentagon represents the figure that breaks with the possibility of an all-over surface coverage and is the polygon with the maximum number of sides possible in the construction of regular polyhedra. The development of the surface of the dodecahedron is shown

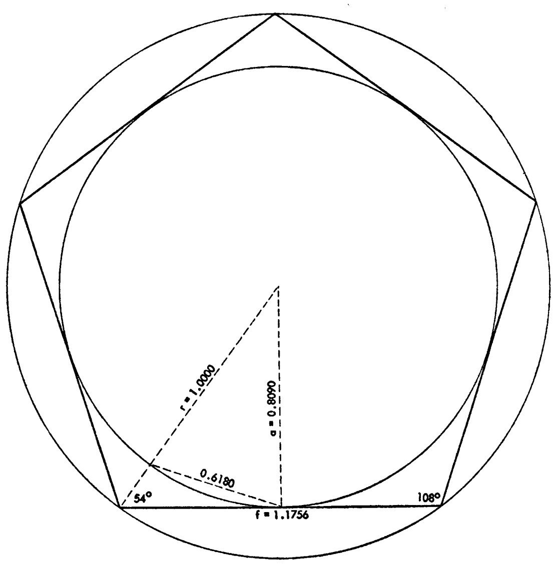


FIG. 1. Basic pentagon showing relationships of parts to the radius and to inscribed and circumscribed circles.

in figure 6; the relationship to the third illustration in figure 2 is clear. A cross section of the dodecahedron is indicated in figure 7, together with the relationships of the various dimensions. It is to be especially noted that the section is an irregular but symmetrical hexagon, in which one pair of opposite sides is shorter than the other two pairs. Fifteen such sections are present in a dodecahedron.

If the surfaces of the 12 pentagons be extended in a manner comparable to the extension of the edges of the two-dimensional pentagon, a stellate figure results, three aspects of which are shown in figure 8. For convenience, it can be thought of as 12 mutually intersecting stellate pentagons or as a dodecahedron, on each face of which is constructed a five-sided pyramid. The development of the surface of this figure is shown in figure 9; this development is comparable to that of the dodecahedron of figure 6. A cross section of the stellate dodecahedron is shown in figure 10 to be that of the inscribed dodecahedron, with the addition of four equilateral triangles on the four long sides of the basic hexagon. This is strictly comparable to figure 7. The numerical relationships of the parts are

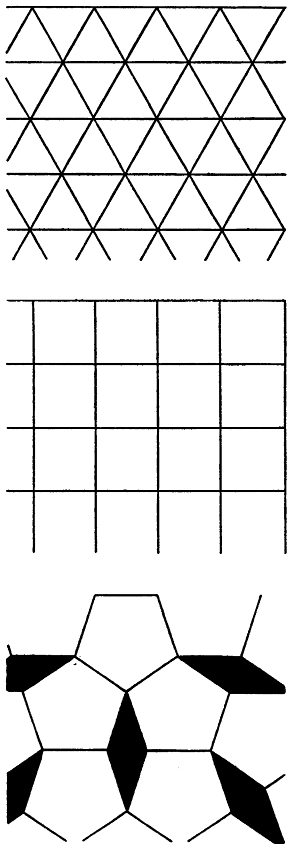


FIG. 2. Mosaic coverage of a surface of the first five regular polygons. See text for explanation. After Breder (1947).

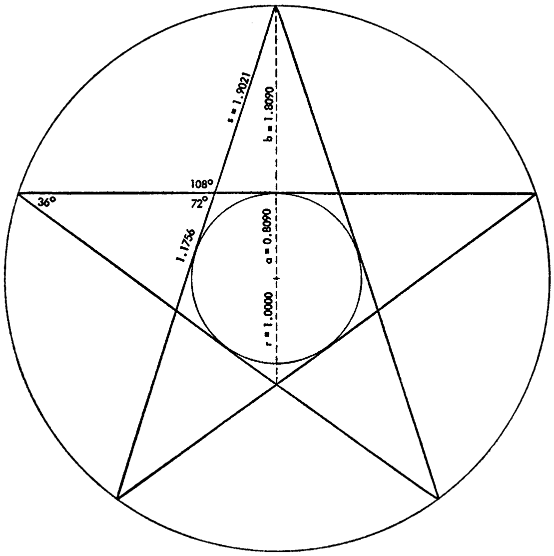


FIG. 3. Basic stellate pentagon showing relationships of parts to the radius and to inscribed and circumscribed circles.

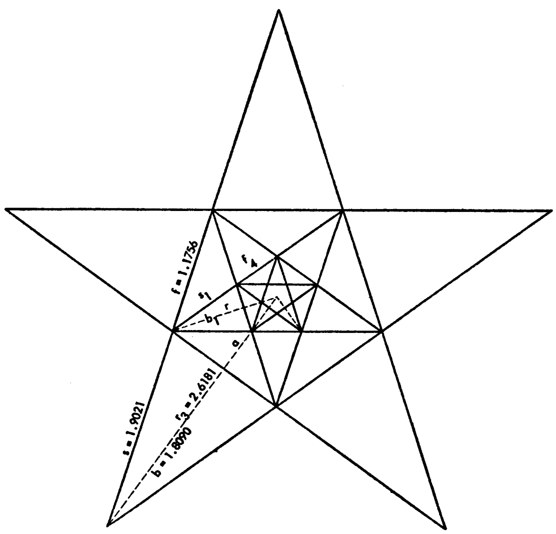


FIG. 4. A series of three inscribed stellate pentagons showing their mutual relationships and radii.

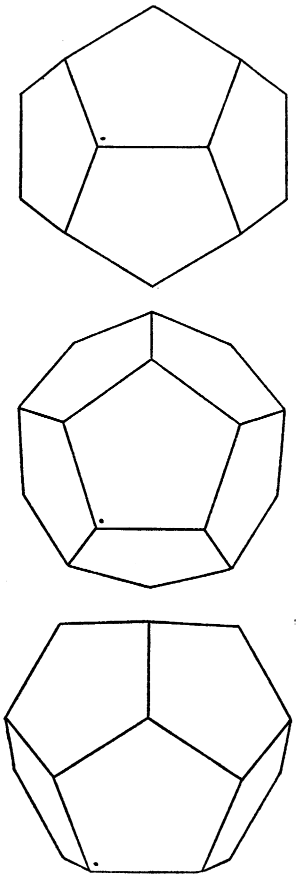


FIG. 5. Three perspective views of a regular dodecahedron: edge, face, and corner, respectively, facing the viewer. The three views from the top down may be considered as successive appearances as the figure rotates on a horizontal axis in the plane of the paper passing through the centers of the two vertical edges of the top picture. Rotation of near side is downward. The mark on one face is the same in each view and serves to orientate the viewer.

indicated. Further details of this sort are given in the Appendix.

In such considerations, it should be recalled that the regular polyhedra bear polar relationships to one another in the following specific ways. That is, a polygon inscribed in a dodecahedron so that its corners are at the centers of each of 12 pentagonal faces is an icosahedron. Conversely a dodecahedron can be inscribed in an icosahedron in an identical fashion. The cube and octahedron bear similar mutual relationships. An inscribed or circumscribed tetrahedron is another tetrahedron. These features are very explicitly illustrated by Steinhaus (1950), who also illustrated the relationship of the cube to the rhombic dodecahedron. The latter can be constructed by the addition of a pyramid to each face of a cube and is not to be confused with the regular or pentagon-dodecahedra discussed here. In a similar manner a rhombic triacontahedron can be built with a regular dodecahedron as a basis. In all such constructions the face of the new figure is a plane at right angles to the plane of symmetry of edge included. The new figure differs from that produced by the extension of the faces of a dodecahedron, which is the stellate dodecahedron discussed above. Such a stellate dodecahedron can be inscribed in a regular icosahedron where every point of the star is at the corner of the icosahedron.

The isosceles triangle which forms each point of the stellate pentagon has an apical angle of 36 degrees and two basal angles of 72 degrees each, that is, each is twice the size of the apical angle. Bisecting one of the basal angles and producing the line to the other

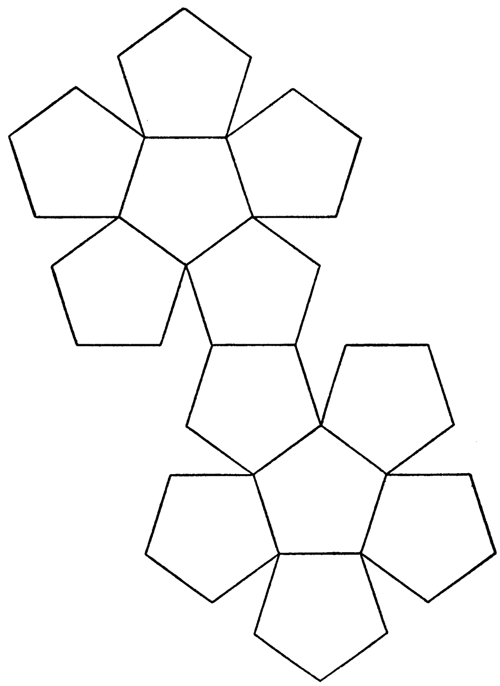


FIG. 6. Development of a dodecahedron. Note the relationship to the arrangement of pentagons in figure 2.

side divides the triangle into two other triangles, one of which is a gnomon of the first and the other is similar to the large triangle. This bisecting line, common to the two triangles, is parallel to the face on the other side of the pentagon and lies in the face of a pentagon circumscribing the first.

The chord of the angle between the radius and the apothem equals the continuing fraction 0.6180. . . . This same value is shown in the relationship between the angle at the tip of the stars in the stellate forms with the face of the pentagon forming its base, i.e., f/s as in figures 1, 3, and 4 yields this same decimal. This value, the final term in the famed Fibionacci series, must appear in any discussion even touching on considerations related to the study of phyllotaxis.

Repeated bisections of the basal angles of the successive triangles of the stellate point, with angles of 36, 72, and 72 degrees as shown in figure 11, produce a geometrical series with some interesting features. As noted above, such a bisection produces two triangles, one similar to the original and the other its gnomon. Obviously, two such series can be obtained which are mirror images of each other depending on which of the two basal angles is bisected successively. Equivalent points on these successive figures lie on a logarithmic spiral, which necessarily is the case in any geometrical construction of this sort, a matter that has been extensively discussed by Thompson (1942). In this triangle the side is 1.6180 . . . times the base, which is the face of the generating pentagon. Successive sides and successive bases in this series of triangles bear the following relationship to one another:

$$\text{Next higher } f \text{ and } s = 1.6180f \text{ or } s;$$
$$\text{next lower } = f \text{ or } s/1.6180.$$

These relationships for three successively larger and three successively smaller triangles are given below.

f	s
4.2357	6.8534
2.6179	4.2357
1.6180	2.6179
1.0000	1.6180
0.6180	1.0000
0.3813	0.6180
0.2295	0.3813

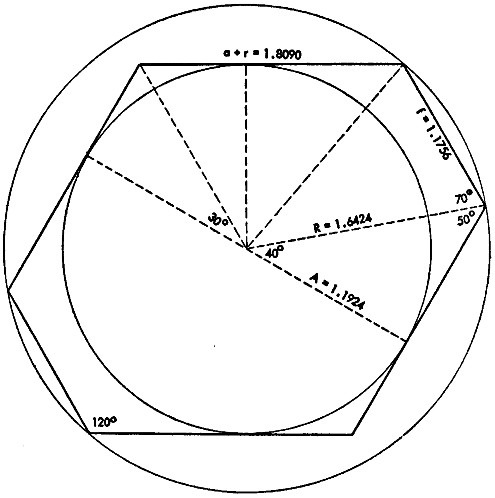


FIG. 7. Cross section of a dodecahedron through any two opposite edges showing relationships of the parts and to an inscribed and a circumscribed sphere. Note the relationship to the top view of figure 5.

The values of f and s on one line represent those of one triangle. Note that the two columns of figures are identical, displaced by one line. This is because the side of one triangle becomes the base of the next larger.

Each of the sides and bases of the nested triangles represents the face of the pentagon with which the stellate form is associated. The pentagons, which are shown separately in figure 12 for the sake of clarity, have their centers, or for that matter any other homologous points, lying on another logarithmic spiral, as is indicated. Each successive pentagon, numbered in the figure for easy reference, touches its next larger and its next smaller member at an apex, the angles between them being 72 degrees. If the series of pentagons is counted along one of the five axes of symmetry which pass through the centers of these pentagons, it is found that, when counted from the low numbers to the higher, as indicated, there are series of three figures along each axis differing by three and one. Series separated by three have their faces in one line and those separated by one have an apex in common. That is to say, the series in figure 12 run as follows: 1-4-3, 2-5-4, 3-6-5, 4-7-6, 5-8-7.

In a continuation of this series of pentagons, no further centers lie on these lines.

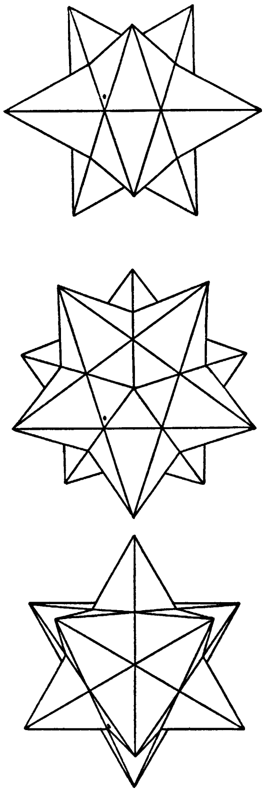


FIG. 8. Three perspective views of a stellate dodecahedron comparable with those of the dodecahedron of figure 5. The rotation and the marked face is the same as in that figure.

Other centers in sets of three with the above numerical relationships lie on lines parallel to those drawn in figure 12. For example, a line drawn through centers 2 and 3 and produced to the right would intersect the next larger pentagon (not drawn), which in this notation should be 0. The same relationship would exist, namely, 0-3-2, and so on indefinitely. These pentagon centers are also spaced at the apices of isosceles triangles similar to the ones that form their faces, as, for example, triangles 3-4-5, 5-6-7; also the triangle 1-2-3, not drawn; and the smaller one, 7-8-9. Note that these are all in normal numerical order. Obviously a mirror-image series with a reversed spiral could be constructed but has been omitted for the sake of simplicity; its nature can be readily understood by reference to the simpler figure 11. Pentagons in figure 12 numbered 1, 4, and 3 would be common to both spirals. That is, the spirals would intersect symmetrically at the centers of these pentagons and any other pentagons on the vertical axis of the figure.

If the generating triangle, instead of being "rotated" in one direction, is alternated to right and left, a series of nesting pentagons is produced which pinch out to one of the basal angles of the star-pointed triangle shown in figure 13. The dotted series of pentagons result from counterclockwise movement, while the solid pentagons, with which they alternate, result from clockwise movement. Note that the centers of the pentagons are respectively on a line above and on a line below the bisection of the basal angle by an equal amount. By elementary trigonometry this can be shown to bear the following relations:

Centers of upper pentagons (solid lines)	40°23′+
Bisection of basal angle	36°
Centers of lower pentagons (dotted lines)	31°37′−

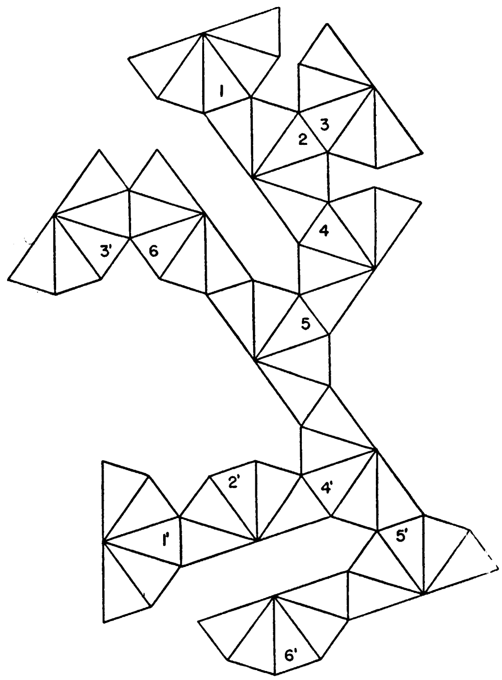


FIG. 9. Development of a stellate dodecahedron. As with the simple dodecahedron of figure 6, this divides into two halves but cannot be so drawn as a unit because of overlapping. Each element in the two halves is numbered, with its opposite number primed. If 3′ is attached to 2′ as 3 is attached to 2 and 4′ cut away from 5, it will be seen that there are two congruent figures.

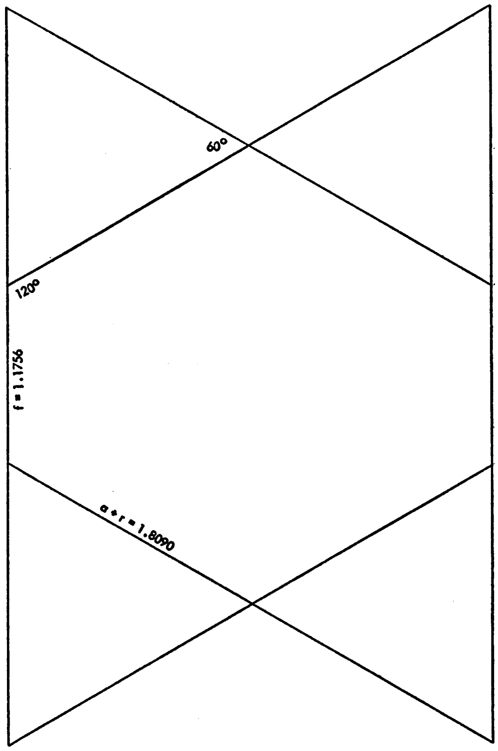


FIG. 10. Cross section of a stellate dodecahedron comparable to that of the dodecahedron of figure 7.

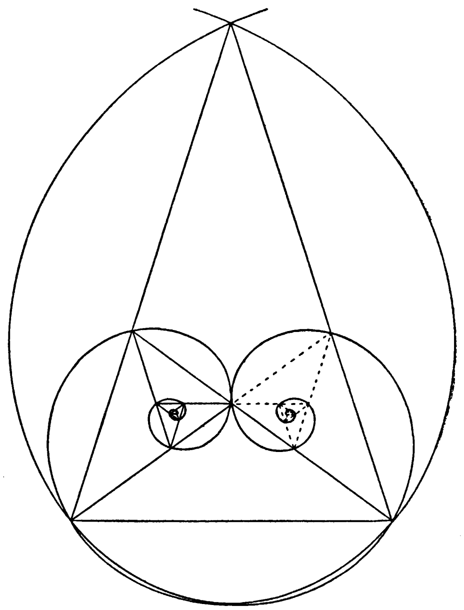


FIG. 11. Diagram of the successive bisection of a basal angle of the triangle forming the point of the star in a stellate pentagon. The left-hand spiral results from a clockwise "rotation" of the triangle; the right-hand spiral from a counterclockwise "rotation" of the triangle, shown by dotted line.

Obviously another like series could be constructed from the other basal angle, and it would bear a mirror-image relationship to the first. It would differ from the previous construction in that there would be no pentagons in common with both series. This can readily be seen from the disposition of the one set shown in figure 13. As this series has been produced by what might be thought of as an oscillating movement, it is not surprising that no logarithmic or other spiral is discernible and that the centers and other points of reference lie on straight lines radiating as a pencil of rays from the angle of derivation.

With this much elementary geometry for convenient reference, a consideration of the physical manifestations of pentagonal designs in organisms may be undertaken. An attempt is made to recognize, first, the general pattern of pentagonal design and, second, what restrictions this kind of organization implies.

THE FAMILY OF CURVES generally known as Grandus' curves, considered by him in 1728 in reference to the arrangements of the parts of flowers and most recently discussed by Thompson (1942), forms a convenient point of departure for a preliminary examination of five-fold symmetry. The equation of this curve is

$$r = a + b \cos n\theta.$$

Figure 14 illustrates the general nature of the curves it produces, all scaled so that r does not exceed unity. The upper figure represents various values of a greater than or equal to 1, with b equal to 1 and n equal to 5. The lower figure represents various values with a less than 1 and the other values as before. It is evident that as a approaches ∞ or b approaches 0, a circle becomes the limiting value of this family of curves. As a approaches 0 the equation approaches $\cos \theta$ as a limiting value. The value of n determines the number of parts the figure shows, here held at 5. When a equals 500 the lowest value of r equals 0.999 (when scaled so r is equal to or less than 1.0), while other values show changes only in the fourth place.

One feature to be noted in the "growth" of such curves is that where a is equal to or greater than 1, each leaf is in regular sequence as the curve is drawn, as it must necessarily be in order that curves such as are shown in the upper part of figure 14 will result. When a is less than 1, as in the lower part of figure 14 where there are 10 leaves, five large and five small, the curve, as it normally would be drawn through a series of successive points, crosses the center of the figure and traces alternately a large and a small leaf. When a equals 0, what were the large and small leaves

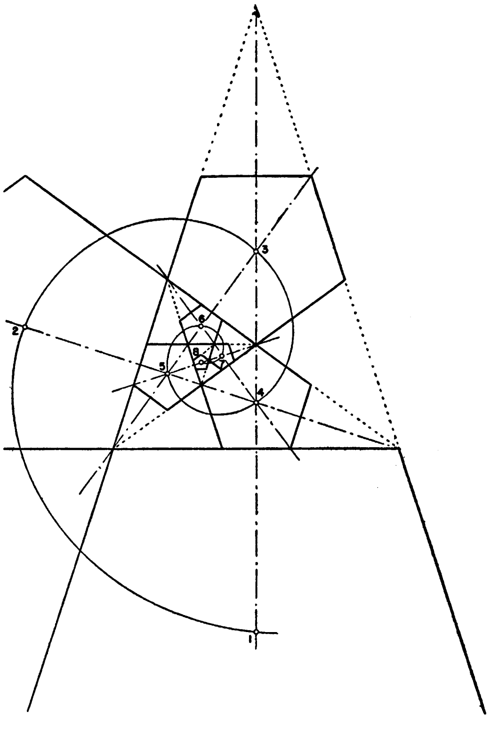


FIG. 12. Diagram of the deployment of the pentagons of which one stellate point is shown in figure 11. The centers of these pentagons necessarily lie on another logarithmic spiral. How these line up on the five pentagonal axes is indicated by the dot-and-dash lines.

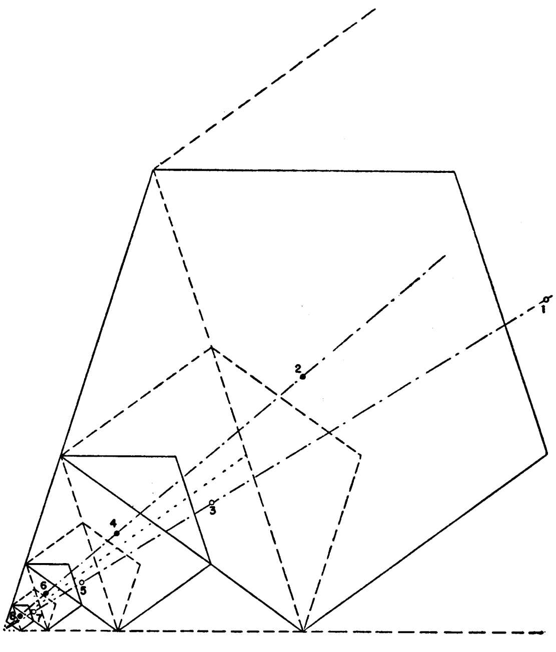


FIG. 13. Diagram of the nesting of pentagons that results from an alternating right and left turning of the "rotating" triangle. The dotted series are derived from a counterclockwise movement and the solid series, with which they alternate, from a clockwise movement. The centers of both series lie on axes that are an equal angular distance above and below the bisection of a basal angle of the stellate triangle.

are identical in size, and again a five-petaled figure is obtained. This differs from the figures in which a is equal to or greater than 1, in that it resembles those in which a is less than 1, for, in following the line, one alternately traces the leaves first to one side and then to the other, and it may be thought of as having double values or tracing twice around to trace to completion. This is actually, of course, merely the limiting case for values of a that are less than 1 but greater than 0.

An example of how some of these curves approximate organisms is given by Thompson (1942). He shows the graph of

$$r = \sin 5/3\theta$$

as an illustration of one of Grandus' curves representing a five-petaled flower. Without modification this is already a close approximation to the basic outline of the petals of a blossom of *Hibiscus rosa-sinensis* Linnaeus. This curve is redrawn as figure 15, with the measured values of a comparable *Hibiscus* flower indicated as dots. The means of these values compared with the values given by the equation are shown below; the radii of the petals of both flower and equation are reduced to unity for purposes of easy comparison.

	EQUATION	MEASUREMENT	$e-m$
Radius of petals	1.0000	1.0000	0.0000
Greatest width of petals	0.6103	0.6809	−0.0706
Radius of greatest width	0.6444	0.6729	−0.0285
Radius of crossing curves	0.5000	0.5319	—0.0319

It is to be noted that, although the means of the flower values are all greater than those expressed by the equation, the difference in no case exceeds a figure in the second decimal place. Figure 15, which shows the measured values on each petal, indicates the extent of variation both plus and minus. When the inherent variability of flowers such as this and the natural difficulties in taking measurements of them are considered, it would seem that this flower is in close agreement with the above expression.

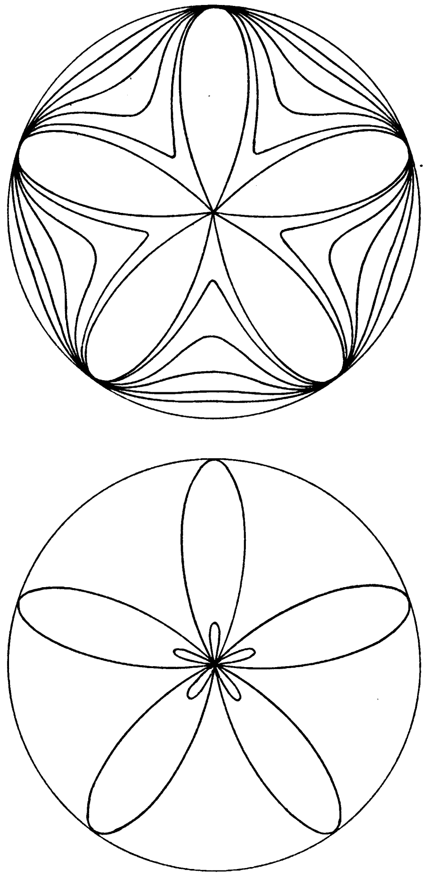


FIG. 14. Graphs of the equation $r=a+b\cos n\theta$. In all, $b=1$ and $n=5$, all reduced to the same scale, i.e., with the maximum value of $r=1$. Upper: $a=1, 2, 4, 8, 16, 32$. Lower: $a=0.64$. With values of a less than 1, the figures cross the center to form a smaller "leaf," as shown. Because of the complications this introduces, only one curve is shown here, but it is obvious that where $a=1$, as above, the small leaves have an $r=0$, while as a grows smaller and smaller the smaller leaves enlarge until, where $a=0$, there are again five equal leaves.

Greater refinement could, of course, be achieved by measuring a statistically significant number of flowers such as this and thus obtaining a measure of the departure from the equation that the group of blossoms showed. For the present purposes this would be of no value for, as is shown below, such differences would require only the introduction of small modifications of the primary formula in order to bring the equation in as close agreement with the growth as might be desired. The emphasis here is rather on how close these natural objects approximate sim-

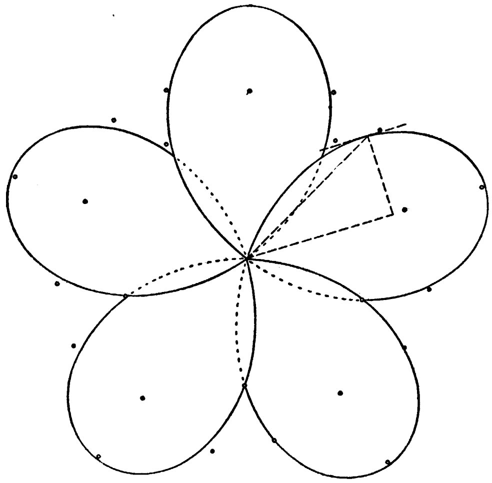


FIG. 15. Curve of the equation $r = \sin 5/3\theta$. Points indicate measured length of petal, greatest width of petal, and the distance of the latter from the center. A triangle on one of the leaves (dashes) indicates the greatest width of the figure based on the equation and its relationships. With the radius of the leaf = 1.0000, the following values obtain: radius of greatest width down center of leaf = 0.6103; one-half of greatest width of leaf = 0.3222; radius to edge of leaf = 0.6901. See text for full explanation.

ple equations. The points of reference taken (the greatest petal width, its distance from the center, the length of the petal, and where its outline crosses its fellows on either side), it should be noted, suffice to determine the basic nature of the curve.

In connection with the modification of this equation and others similar to it, any new algebraic or trigonometric quantities that are introduced need be restricted only by the consideration that the resulting figure must cleave to the five-part division of a circle. If the value 5 is not integral with reference to the circle some other symmetry appears, and if incommensurate values appear special difficulties arise. If the values are commensurate but involve a much higher order, rosettes are formed. A very slight fractional departure from any commensurate relationship may immediately lead to a very complex formation, a matter discussed at some length by Breder (1947).

Figure 16 shows a first approximation to the outline of the sea urchin, *Lytechinus variegatus* (Lamarck). The small circles along the curve indicate the position of the edge of the shell at its high and low points of fluting and their departure from a separation of 36 degrees. Where there is a difference in the latter, a short line indicates the true position of such a figure of five parts. The solid curved line is the graph of the equation

$$r = 65.45 - \cos 5\theta.$$

The closeness of fit is obvious, and it is doubtful if any method of measuring and the variation of one animal from another would permit a much closer approximation, by the very nature of the material. The value for a was derived from the measurements in the following manner. The mean of all 10 radial measurements was equated to a from which the value of r in the equation could be calculated. The mean of the measurements differed from the calculated values by 0.05+, where the maximum value of the equation is reduced to 1, while the mean of the measured angles differed from true pentagonal values by a mean of 0.4 degree. The small spread of the extremes is well indicated in figure 16. Only three are sufficiently removed from the theoretical values of r not to be on or in contact

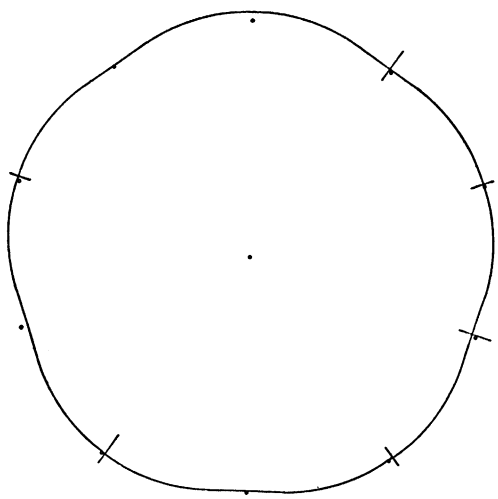


FIG. 16. Outline of a *Lytechinus variegatus* shell. Solid line is polar graph of the equation $r = 65.45 + \cos 5\theta$. Small circles represent actual measurements of an individual. Angular displacements of the measured high and low points, where present, are indicated by short radial lines marking the true symmetrical division.

with the line of the equation, while five for θ are evident. In the actual calculations the mean of five larger values of r was equated to unity. This is a mere convenience for proportionality, as appears below, and the equation is transformed to

$$r=\frac{64.45-\cos 5\theta}{65.45}.$$

If another, and rather similarly shaped, echinoid be taken, such as *Tripneustes ventricosus* (Lamarck), the equation for its outline is closely defined by

$$r=\frac{84.66-\cos 5\theta}{85.66}.$$

The outline of this equation, together with the measured points of the example with respect to both the radii and their angular distances, is shown in figure 17. A photograph of this specimen is shown in plate 1, figure 1. The genital pores, arranged in a group of five about the proctal plates, are seen to have the apices of the pentagon they form along the radii of the least diameters, while the apothems are measured along the larger radii. This is, of course, the arrangement to be found in a stellate pentagon, as in figure 3, where the inscribed pentagon has its greatest radii along the least radii of the star and vice versa.

The nearly circular proctal opening is 0.086 that of the mean of the larger radii. These relationships are shown both in the plate referred to and in figure 17. Evidently (without further emphasis on the subject) echinoids of this general type differ only in slightly changed numerical values for a and b in the equation under consideration. The outlines of these urchins, although clearly on a pentagonal basis, do not depart widely from the limiting circle.

In this particular case, it is notable that angles of the set of shorter radii vary more from the theoretical than do those of the set of larger radii. As measured from a starting point, the top position of figure 17, where there is a difference between the ideal and actual, the latter all fall short of the former, as can be noted from the relative positions of the small circles and the short lines cutting the curve. Also, the lengths of the set of shorter radii vary more from their mean

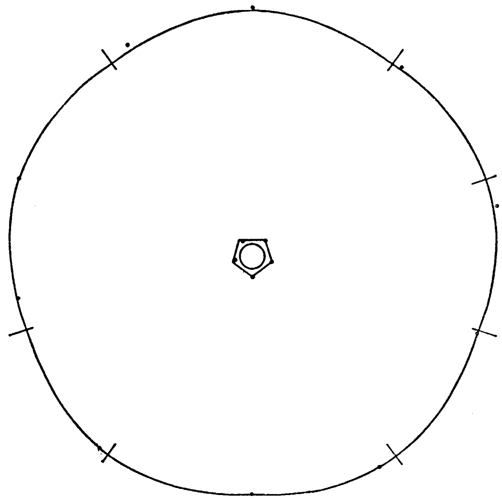


FIG. 17. Outline and some details of a *Tripneustes ventricosus* shell. The solid line is the polar equation of the equation $r=65.45+\cos 5\theta$. The pentagon has a radius of 0.086 of the greater radii. As in figure 12, the small circles and short lines indicate the true positions of these elements as measured on a test.

than do those of the set of larger. Sign considered, the sum of the differences from the mean of the set of smaller radii is 1.5, while that of the larger set is 0.0, their plus and minus differences being equal. Also, in absolute terms, the maximum deviation of the smaller is 1.5 and that of the larger 0.9.

The departure from a pentagon of the spacing of the genital openings is obviously involved with the introduction of some asymmetry by the nature of the madreporite. The small size of these central structural features cannot be handled in satisfactorily fine detail by measurement with simple instruments.

The form of *Clypeaster rosaceus* (Linnaeus), shown in plate 1, figure 2, for example, evidently does not fit into the above scheme. It is, furthermore, clearly and unequivocally bilateral. If, for purposes of analysis, it is assumed that this form is an elliptical modification of practically circular forms, the following calculations can be shown to yield some rather striking results. The polar equation of such an ellipse with, from column 1 of table 1, M (the semi-major diameter) equal to 2.00 and m (the semi-minor diameter) equal to 1.56 reduces to

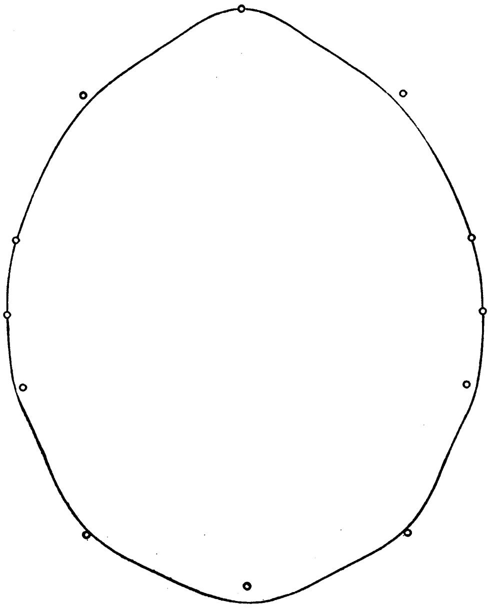


FIG. 18. Curve of the equation

$$p=\frac{65.45+\cos 5\theta+\dfrac{0.6084}{1-0.6258\cos\theta}}{68.0759}-0.2\sin\theta.$$

Means of the measurements of two *Clypeaster rosaceus* are indicated at intervals of 36° from *M* and at *m*. Curve of the equation is drawn from values calculated for every 18°.

$$p=\frac{0.6084}{1-0.6258\cos\theta}.$$

If this is added to the equation that has already been shown to hold for *Lytechinus*, quite arbitrarily as a point of departure, the values that result approach those of *Clypeaster*, but not quite close enough to be considered an excellent approximation. Inspection shows, moreover, that the differences between the values measured and those obtained by the equation

$$p=65.45+\cos 5\theta+\frac{0.6084}{1-0.6258\cos\theta}$$

bear a fractional sine relationship to each other. The greatest difference between the values calculated and those measured is 0.19, where θ equals 90 degrees. If this fractional sine value is subtracted from the above equation and divided by 68.0759 to reduce the value where θ equals 0 degree, the following full expression is obtained:

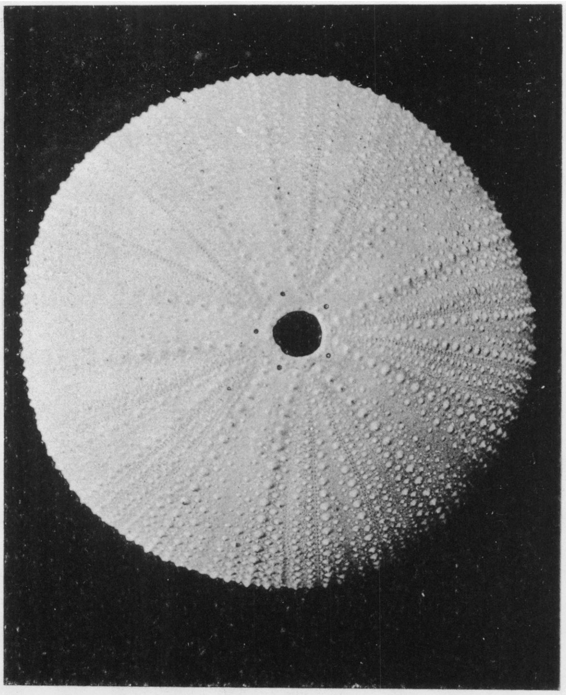
$$p=\frac{65.45+\cos 5\theta+\dfrac{0.6084}{1-0.6258\cos\theta}}{68.0758}-0.19\sin\theta.$$

As is indicated in table 1 and illustrated in figure 18, this equation, based on the test of *Lytechinus*, modified by the equation for the appropriate ellipse, and with the introduction of a minor sine modification, approximates the outline of *Clypeaster rosaceus* very closely. It will be noted that there are departures only in the second decimal place for only four of the values, and the mean divergence from the measured values is only -0.004. These indicate clearly that the variation in these creatures is greater than the difference of the equation from their mean, which suggests that the proximation is as close as the material involved could possibly permit.

A single individual of *Clypeaster* (*Stolonoclypus*) *subdepressus* (Gray) (pl. 1, fig. 3) referred to this same system does not show so close a fit. It happens that the major and minor elliptical axes in all three individuals used were identical, so that it was not necessary or possible to modify the basic ellipse. Two values differed by more than 0.1, and the rest by less than that, with a mean divergence of -0.013. If anything, it would be surprising if this highly modified form retained so close a resemblance in outline to the comparatively little-modified *Clypeaster rosaceus*.

The use of the Grandus equation and its modification by the introduction of the equation of an ellipse of the eccentricity of the *Clypeaster* shell would appear to be easily understood and justified. The justification for the further introduction of fractional sine values may not be so evident, which bears on the fact that, as a starting point in these considerations, the specific equation developed around one form of Regularia was used to develop the equation of one form of Clypeastridea, namely, *Lytechinus*. The fractional sine values that it was necessary to introduce evidently bear on the nature of this basic equation. It is conceivable that these modifications of the basic equation indicate more than incidental transformation constants. They may reflect some presently obscure biological or physical influences.

Likewise it is obvious that the equation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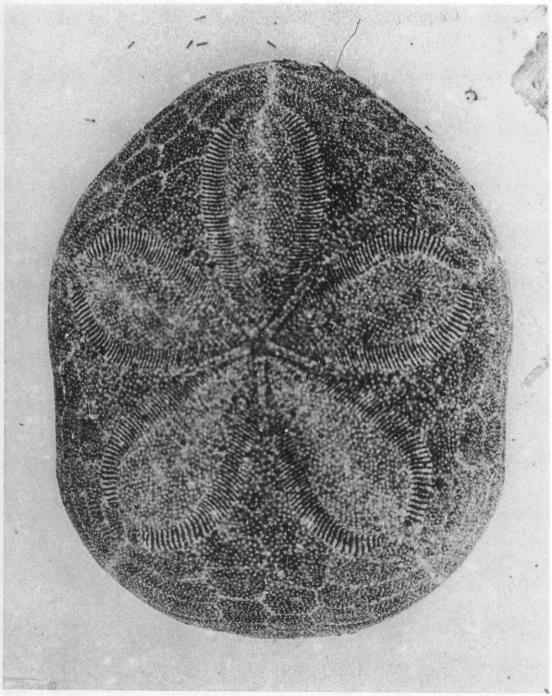
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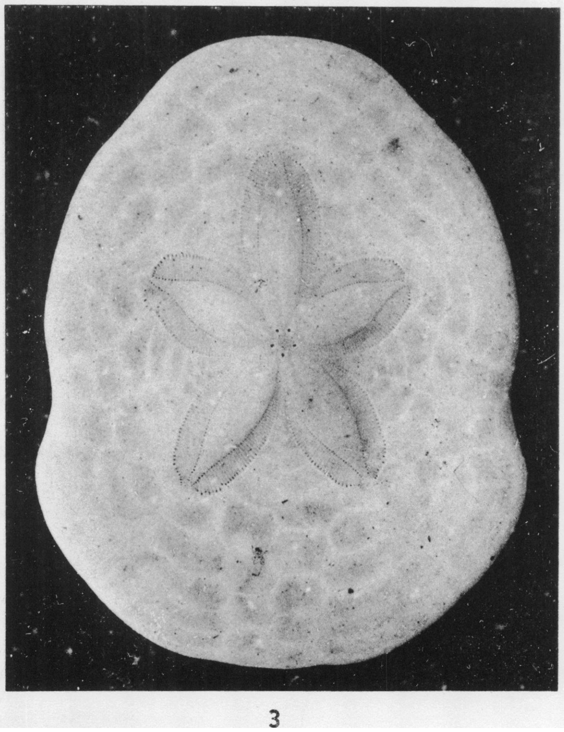
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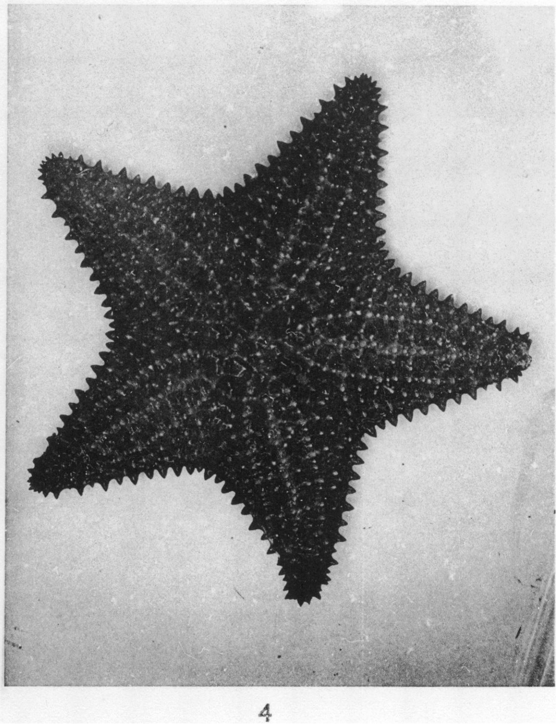
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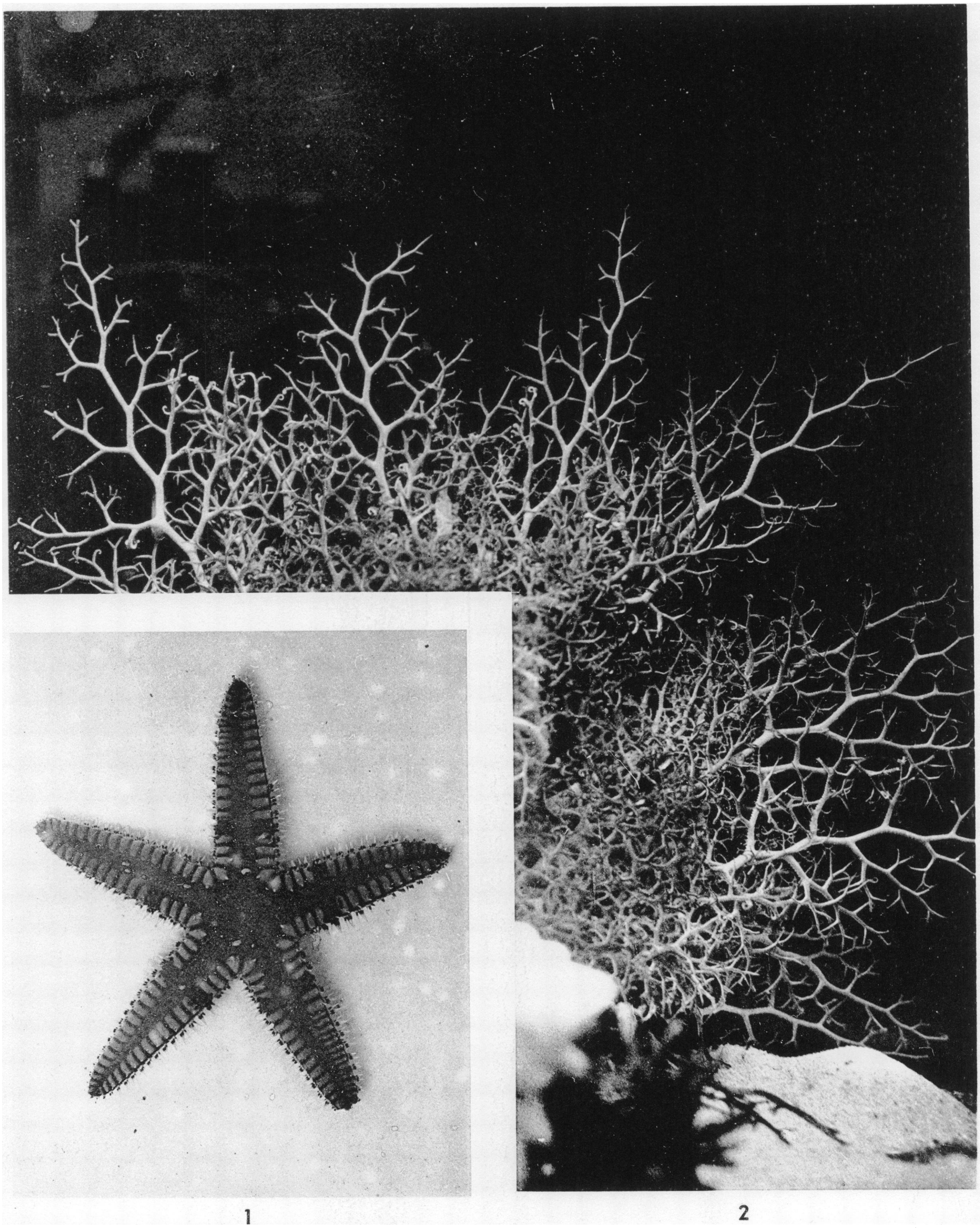
Specimens used for the calculations in the present paper. 1. Shell of *Tripneustes ventricosus*. 2. Shell of *Clypeaster rosaceus*. 3. Shell of *Clypeaster subdepressus*. 4. Medium-sized individual of living *Oreaster reticulatus*



1. Living individual of *Astropectin duplicatus* similar to the one used in the calculations for the present paper
2. Living *Astrophyton muricatum* from which the measurements in this paper were taken

TABLE 1

COMPARISON OF MEASUREMENTS AND CALCULATIONS FROM SIMPLE EQUATIONS OF *Clypeaster*

θ	Measured[a]	Calculated	Difference	Individuals[b] No. 1	No. 2	No. 3
0	1.00	1.00	0.00	1.00	1.00	1.00
36	0.89	0.85	+0.04	0.89	0.89	0.89
72	0.81	0.81	0.00	0.83	0.79	0.80
90	0.78	0.78	0.00	0.81	0.75	0.78
108	0.77	0.80	−0.03	0.81	0.77	0.82
133	0.89	0.87	+0.02	0.94	0.85	1.03
180	0.89	0.95	−0.06	0.95	0.83	0.83

[a] This column is the mean of individuals No. 1 and No. 2, both *Clypeaster rosaceus*. The mean difference between this column and the calculated values is −0.004.

[b] Individual No. 3 is *Clypeaster subdepressus*. The mean difference between this column and the calculated values is +0.013.

here given for *Clypeaster* could be reduced to still simpler terms. For present purposes, further analysis would be merely diversionary, as the equations are developed here only for purposes of illustration. Their further extension would only lead into the general province of equation transformations which have no specific bearing on the particular nature of five-part symmetry.

If the petaloid ambulacrum which forms a design on the dorsal surface of these creatures is treated in a similar manner,

$$p=\frac{2.69}{4.13-\cos\theta}$$

because the largest "petal" is the anterior one and it is 0.86 of the radius of the test on which it lies which has been equated to 1.00. The extreme values of each "petal" compared with the mean of the measurements of the two examples are compared below:

PETAL NUMBER	VALUE OF p Calculated	Measured	DIFFERENCE C−M
1	0.86	0.86	0.00
2	0.70	0.70	0.00
3	0.82	0.73	0.09
4	0.82	0.73	0.09
5	0.70	0.70	0.00

Likewise, if similar values are calculated for the considerably different petaloid ambulacrum of *Clypeaster subdepressus*, based also only on the extent by which it is shorter than the radius of the test on which it lies, the following similar tabulation may be displayed, based on the equation

$$p=\frac{2.03}{4.13-\cos\theta}.$$

PETAL NUMBER	VALUE OF p Calculated	Measured	DIFFERENCE C−M
1	0.65	0.65	0.00
2	0.39	0.47	−0.08
3	0.61	0.55	0.06
4	0.61	0.55	0.06
5	0.45	0.47	−0.02

Here, again, the departures are greater than in the case of *C. rosaceus*, as would be expected. That form showed a mean departure of 0.036, evidently because of the slight influence of some fractional cosine variant not readily measured. *Clypeaster subdepressus*, although with greater variation, hovered closely about the measured values, so that the mean departure was only 0.005.

It is clear that an introduction of the proper Grandus equation could be made here with appropriate modifications to illustrate the petalation of the ambulacral pattern. It is, however, not the present intention to discuss the various and multitudinous ramifications of mathematics more than is necessary for the proper development of the discussion on the nature of pentagonal symmetry as displayed by organisms.

The curves, in view of the manner in which they were produced, are remarkable fits. For

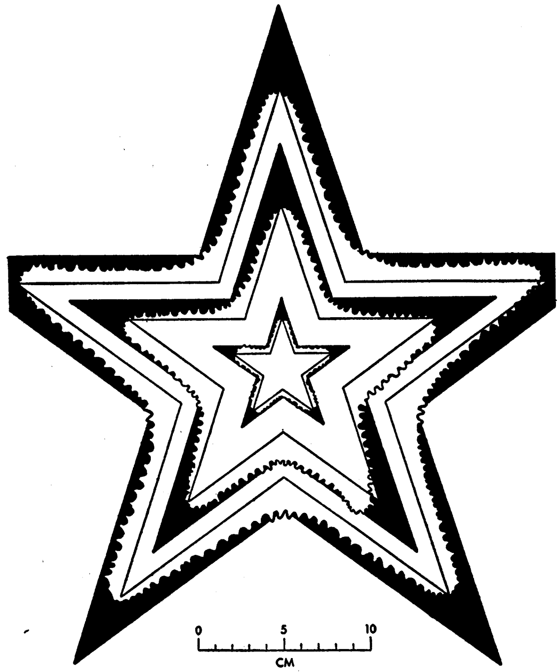


FIG. 19. Outlines of three living *Oreaster reticulatus* of different sizes concentrically arranged for comparison with appropriately proportioned stellate pentagons. Each *Oreaster* has two attendant stellate figures, one based on the radius of each star point and the other on the radius of the low point midway between two successive star points.

the outline of the shell itself an equation based on the mean of a very distantly related form was modified only to the extent of including the changes brought on by reference of it to the values of an ellipse as long and as broad as the sea-bisquit. The central design was produced by similar means by invoking a Grandus curve limited only by the greatest and least values of r derived from the object itself. Considered this way it is surprising that the divergencies are not greater than were found and can be taken as good evidence that these forms are controlled to a considerable extent by transformations in the elemental geometry of the system.

The following paragraph explains in detail the mathematical procedures employed.

All calculations have been carried out to the fourth decimal place but have been reduced to two for this paper. The form of the equation for the curves of Grandus as here used makes b a divisor of the rest of the terms rather than a factor of the cos, i.e.,

$$r = \frac{a + \cos 5\theta}{b}.$$

The limitation of extent of the Grandus curves was done in the following manner, where r_M and r_m are the maximum and minimum values of r as measured on the object:

$$a + \cos 5\theta = r_M b$$
$$a - \cos 5\theta = r_m b$$

or

$$a + 1 = r_M b$$
$$a - 1 = r_m b.$$

When these two simultaneous equations are subtracted, a is eliminated and, with the values for r_M and r_m inserted, b is found. The equation of the ellipse is derived as follows:

$$r = \frac{a}{b - \cos \theta}$$

where a and b are derived from $M/2$ and $m/2$, the major and minor semi-diameters measured on the ellipse, as below

$$b = \frac{\cos 0°}{\cos 0° - m/2} = \frac{1}{1 - m/2}$$

$$a = b - \cos 0° = b - 1.$$

It is interesting to note that Thompson (1942) devoted four pages in his great work on the form of sea urchins without once mentioning the ubiquity of pentagonal design in the group. He confined himself entirely to a consideration of the form of sea urchins in reference to the influence of gravity on a deformable test of varying absolute size and contents. The treatment would be equally applicable to any similar object without reference to its degree of symmetry.

The large starfish, *Oreaster reticulatus* (Linnaeus), shown in plate 1, figure 4, somewhat approximates a stellate pentagon. The extent of this approach is indicated in figure 19, which shows three different-sized individuals with comparable stellate figures. For each starfish there are two figures, one star based on the radii of the arms and the other based on the radius of the included pentagons, that is, they are based on the radii midway between the arms. The outlines of the three *Oreaster* have been traced from photographs of living individuals as found on the sea floor. Part of the irregularity of position is due to the fact that the starfish were not relaxed, so that the arms were not necessarily in their precise median position. Measurements as used here are given in table 2, together with various calculations based on them.

If the radius of the pentagon forming the central portion of such a star-shaped figure is made equal to 1.0000, then the radius of a circle circumscribed about the points of the the stars equals 2.6181, i.e., the sum of the altitude of the star, 1.8090+, and the apothem of the pentagon, 0.8090+. This ratio may be expressed as

$$Y=0.3820X$$

where X = the radius of the star tips and Y = the radius of the figure at points halfway between successive tips. This is shown graphically in figure 20, together with the three ratios of the three *Oreaster*. From table 2, it can be calculated that the preceding equation must be multiplied by 1.3686 to fit the proportions of this starfish. The equation then becomes

$$Y=0.5228X.$$

It is evident from this and figure 19 that as this organism grows, through the size range considered here at least (a 5.22+-times increase from the smallest to the largest), there is little evidence of any heterogony. It is also evident that the bulk of the departure from the stellate figure is in the failure of the arms to grow to a relatively attenuated tip and of the reëntrant angle to fill in. In figure 19, it would appear that the filling-in of the reentrant angle increases with age. The smallest figure shows the arms to be very nearly straight lines closely paralleling the attending stellate figures, a feature obviously not so in the two larger figures. This apparent filling-in, however, is spurious, as is clear from a consideration of table 2 and figure 20. The change that takes place, which causes the appearance, is that the tips of the arms become more pointed; the result is that the arms taper not so nearly parallel to the sides of the stellate figures. The arm tips of the smallest size are definitely truncated as compared with those of the larger sizes. Actually, the two dimensions under consideration hold

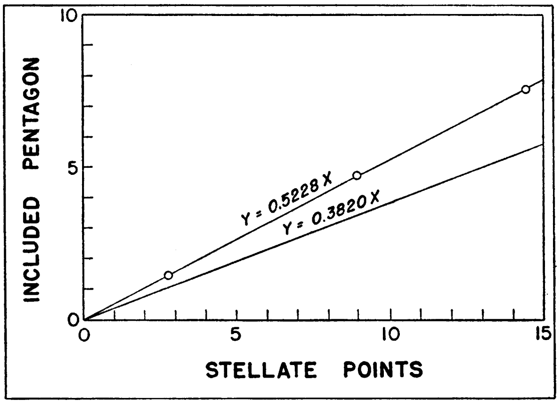


FIG. 20. Comparison of the ratio between the radius of a star point and the radius of the included pentagon with the equivalent measurements on *Oreaster*. The three open circles represent these values for the three oreasters shown in figure 19.

to a most pronounced constant relationship, as indeed they must for the straight line of figure 20 to be valid.

It might be considered that the outline of *Oreaster* actually approaches a hypocycloid. However, as the generating circle must be one-fifth of the radius of the base circle to produce a hypocycloid of five cusps, it follows that *Oreaster* is not approaching such a figure, for the following reasons. With the radius of the fixed circle = 1.0000, the radius of the generating circle becomes 0.2000, and the depth of the intercusp curves becomes 0.4000. Actually the intercusp curves of *Oreaster* are much deeper—0.4774 (1.000−0.5228). These values would seem to require a prolate hypocycloid, a construction that is impossible because the tips of the cusps would then form exterior loops, whereas (if anything) *Oreaster*, with its rounded tips, seems to suggest a curtate hypocycloid, but such curves all have an intercusp depth of less than 0.4000 and are quite unlike the observed form.

It can also be easily shown that the curve between arm tips does not approach a parabola, because the squares of any two chords perpendicular to the axis of a parabola must be to each other as their respective distances from the vertex. When the mean of five *Oreaster* interarm curves with the abscissa as axis is plotted, the following values for X

and Y can be measured:

X	Y	$(2Y)^2$
4.0	2.4	23.04
5.0	4.0	64.00
6.0	5.3	112.36
7.0	6.5	169.00
8.0	7.9	249.64

The curve does not approach a parabola because

$$\frac{4.0}{8.0} \neq \frac{23.04}{249.64}$$

nor does any of the other combinations for the above list of values. The other conics are similarly eliminated.

With the elimination of these common curves, as having no bearing on the question of the outline of *Oreaster*, a reference back to the stellate form first mentioned naturally leads to a consideration of the applicability of some form of exponential expression.

It can be demonstrated that the introduction of cos 5θ as an exponent in an equation of the form

$$p = a^{(c-b \cos 5\theta)}$$

or

$$p = a^{(b \cos 5\theta)} + c$$

yields outlines more in accordance with those of various starfish, including such forms as *Oreaster* and *Asterias*.

For illustration and comparison with figure 19 a curve drawn according to the following equation is shown in figure 21 (upper)

$$p = \frac{4.14^{\cos 5\theta} + 4}{8.14}.$$

In this form, $a = 4.14$, $b = 1$, and $c = 4$. The denominator, 8.14, is merely a proportionality factor, useful in the drafting of such curves to a convenient scale. These values were obtained by taking the mean length of the arms and the mean of the low places between them, which, if the length of arms is taken as 1, becomes 0.5210. With these two quantities corresponding alternately to every rotation of 36 degrees, the equation was worked backward to determine the absolute terms of the equation. Its agreement with the whole form of the *Oreaster* outline is notable. It is clear that suitable alterations of the values of a, b, and c could be used to describe a large variety of starfishes. Measured and computed values are shown comparatively in table 2.

It is not necessary to labor the point or to indicate that appropriate values lead to curves closely resembling those developed on another basis for the echinoids, which is to say that the exponential equation is a more general one than equations developed earlier. The first sufficed for the Echinoidea but does not suffice for the Asteroidea.

An interesting aspect of this formula is that if the exponent be made negative then forms are developed which are not represented at all in echinoderms. They do appear with some frequency in flowers, however, in both basically five-part and three-part forms. In them are found many of the simple flowers with pointed or scalloped petals. These variations have nothing in particular to do with pentagonal symmetry, however, as they appear in flowers of other degrees of symmetry about as frequently as they do in the five-part flowers. It would seem as though the echinoderms were able to construct only figures with positive exponents, while the flowering plants could with equal facility arrive at designs that could be expressed by means of negative exponents. This difference is similar to the differences illustrated by Breder (1947) obtained by reversing the direction and consequently the sign of one of the components of his curve-drawing device.

Most of the starfish outlines typified by *Asterias* or other more or less similarly formed genera may be very closely approximated by this equation

$$p = a^b \cos 5\theta + c$$

with values of a between 7 and 8 and corresponding values of $b = 1$ and values of c between 3 and 2. Some, however, do not fit nearly so prettily as does *Oreaster*, for example. If we examine the case of *Astropectin duplicatus* Gray, shown in plate 2, figure 1, and treat it in a similar manner, about the closest approximation that could be obtained by the equation

$$p = \frac{7.43^{\cos 5\theta} - 2.54}{9.97}$$

yields differences from the measured values shown in table 2. These in some instances exceed 10 per cent. The disposition of the differences between the calculated values minus measured values is indicated below:

θ	d
0	0.000
9	−0.002
18	−0.113
27	−0.064
36	0.000

It is clear from this tabulation that the influence that is responsible for this difference is related to the corresponding values of the sin of 5θ. A much closer fit is obtained by introducing such values into the equation as are shown in table 2 and figure 21 (lower). This procedure is related to that used in the consideration of the elliptical influence displayed by *Clypeaster*, where sine values found a minor expression.

Although this agreement is probably as good as can be readily expected in organisms with such considerable individual variation, it seems to be not quite so close as in *Oreaster*. The point of this part of the discourse is that exceedingly simple equations or slight modifications of them suffice in most cases to define closely the outlines of these organisms. Obviously any form such as one of these organisms could be approximated with increasingly complex equations up to an expression for the regular stellate pentagon, where the number of new members necessary for such an equation becomes infinite. Although many of these forms apparently approach such a figure or other geometrical constructions, they have not reached a point where a plethora of trigonometric functions makes calculations difficult or impossible. Figure 19 should be referred to in this connection, as it was prepared principally to emphasize the similarities and differences between such an organism as *Oreaster* and the straight-line geometrical figure that could be considered as the limiting form in the direction of stellate structural development.

It is also to be noted that both starfishes under discussion are amply provided with tubercles, which have not been treated but undoubtedly could be by an extension of the equations into sufficient complexity. It may be noted in passing that in both species the outlines of the tubercles bear a marked resemblance to the outlines of the respective arms.

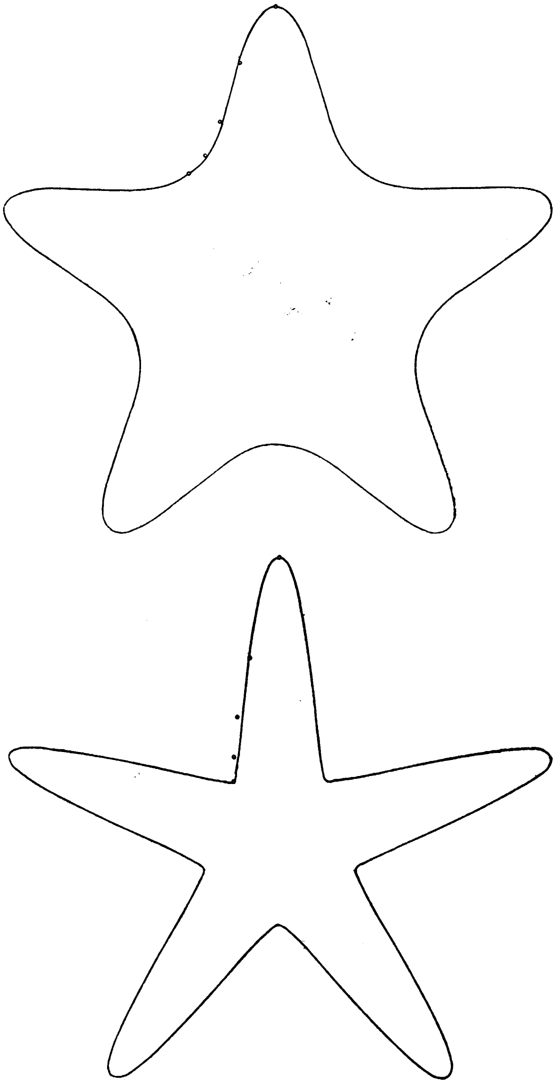


FIG. 21. Curves of exponential cos 5θ. Upper: Curve of the equation

$$p=\frac{4.14^{\cos 5\theta}+4}{8.14}.$$

Small circles show measured values on *Oreaster reticulatus*. Lower: Curve of the equation

$$p=\frac{7.43^{\cos 5\theta}+0.56 \sin 5\theta+2.54}{9.97}.$$

Small circles show measured values on *Astropectin duplicatus*.

While it is perfectly reasonable to consider an organism as a tangible graph of the forces

TABLE 2

MEASUREMENTS OF *Oreaster* AND *Asteropectin*

Object	X^a	Y^b	R^c	S. E. X	S. E. Y
Comparison of *Oreaster* with stellate pentagon					
Stellate pentagon	2.618	1.000	2.618	—	—
Oreaster No. 1	2.765	1.445	1.9135	0.01	0.00+
Oreaster No. 2	8.990	4.700	1.9128	0.03	0.00+
Oreaster No. 3	14.421	7.539	1.9129	0.07	0.04

θ	Measured p^d	Calculated p^e	Difference, M−C
Comparison of *Oreaster* No. 3 with exponential equation			
0	1.000	1.000	0.000
9	0.807	0.827	−0.020
18	0.635	0.614	+0.021
27	0.547	0.536	+0.009
36	0.521	0.521	0.000
		Σ	0.028
		Mean	0.006

θ	Measured p^d	Calculated p^f	Difference, M−C
Comparison of *Astropectin* with exponential equation			
0	1.000	1.000	0.000
9	0.671	0.709	−0.038
18	0.468	0.410	+0.057
27	0.343	0.319	+0.024
36	0.268	0.268	0.000
		Σ	0.043
		Mean	0.009

[a] X, the mean of the measured lengths of each arm from the center, in centimeters.
[b] Y, the mean of the measured lengths of the low points between successive arms from the center, in centimeters.
[c] The ratio between the equivalent high and low points in a stellate pentagon when $Y=1.000$.
[d] Mean of p for each corresponding value of θ, reduced to maximum $p=1$.
[e] Calculated from the equation

$$p=\frac{414^{\cos 5\theta}+4}{8.14}.$$

[f] Calculated from the equation

$$p=\frac{7.43^{\cos 5\theta}+0.56\ \sin\ 5\theta+2.54}{9.97}.$$

that molded it into the form it displays, that in itself does not necessarily tell us much about how they operated to produce the observed result. A mathematical equation descriptive of the outline, for example, of a sea urchin tells no more about the nature of the organism than does a graph of population trends about the food habits of the population other than to give a possible suggestion of its adequacy. This is not a criticism of either approach to the two subjects but merely a delimiting of what certain approaches can and cannot be expected to accomplish. Thus far only the final forms in which organisms are found have been considered and not by which of a multitude of different methods they reached the form displayed.

If we take, for example, *Oreaster* and consider not so much its resemblance to stellate pentagonal figures but rather the possible methods which produced the result, we are led into some rather interesting speculations. Starting at the time when the bilaterally symmetrical pluteus transforms to some pentagonal form, whether it be in the form of the initial pentagonal plate or just an organization of five radiating axial gradients, there is immediately established a primary geometrical problem. Will the gradients be axial to the corners of the pentagonal structure or nexus of forces, or will they be at right angles to the faces of the pentagonal influence? Everything about the arrangement of plates of both sea urchins and starfishes seen by us indicates that the greatest growth is normal to the pentagonal faces and not from the corners of the primary pentagon. That is to say, such pentagons have their faces bisected by lines through the arms or greatest widths and points in line with the lesser growths between them. This would seem to be not unlike the condition described by Haas (1948) for Bryozoa in which the successive individuals grew outward primarily in five "arms" from the originating pentagonal individual, until this growth was interfered with by outside influences. (See fig. 22.)

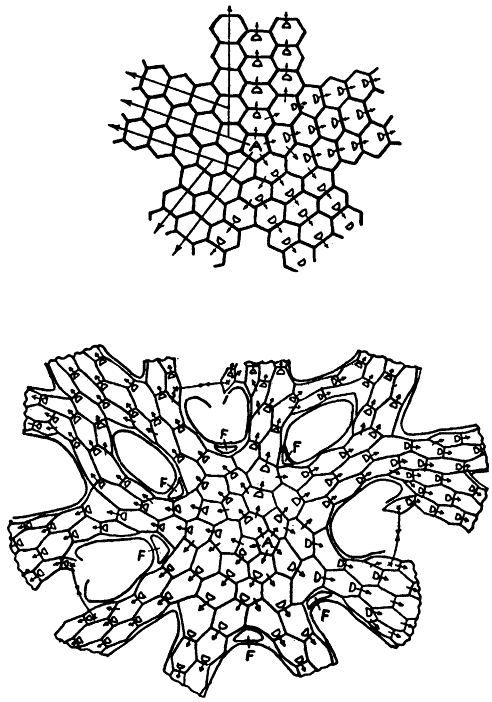


FIG. 22. Growth of the bryozoan *Sertella septentrionalis* Harm. After Haas (1948). Upper: Schematic diagram of an ideal colony. Lower: An actual colony as found in the open sea. *Abbreviations*: A, the originating pentagonal organism, the "ancestrula"; F, fenestrations in the colony.

This may in fact be related to certain features common to the process of regeneration in animals. It has been shown that in both plants and animals growth from a cut surface strongly tends to be normal to the face of that surface. In fact, it was demonstrated long ago by Barfurth (1891) that regrowth could often be directed merely by placing the cut at right angles to the direction it was desired to have the new growth take. Of this, Needham (1952) wrote as follows: "Thus the main axis of a regenerate is often determined by the surface of amputation and is normal to it (Barfurth's rule), even when this is oblique or even at right angles to the main axis of the parent. The blastema is symmetrical about its new axis. Sometimes, however, as in *Bipalium*, . . . and in other animals . . . the rate of regeneration at each point along an oblique surface is determined by its level in the parent axis and the regenerate continues this axis." The possible relationship of the tendency of blastema to become organized at right angles to the cut surface and the conflict that sometimes appears because of the axis of organization of the parent material with the growth of such radiate forms as starfish is evident. In these forms the lineal axis, X axis of a Cartesian graph, becomes angular displacement, θ of a polar graph. In *Oreaster*, as shown in figure 19 of the three sizes, it almost seems as if the smallest were growing arms straight out, normal to each face of the primary pentagon, which, as time goes on, will become modified by mutual interference, so that growth is greatest along a line bisecting each face where it is most remote from its neighbors and least at the corners where evidently the influence of the adjacent member is greatest.

Evidently related to, or rather interacting with, the above growth behavior is a tendency to grow in a circular form. In fact, much of the difference in form between the echinoids and the asteroids seems to be rooted in the relative strength of the two tendencies. Thompson (1942) surprisingly dismissed the

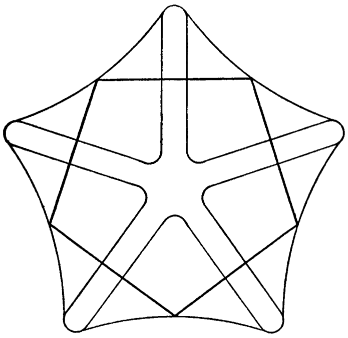


FIG. 23. Diagram of the inversion of a stream under pressure emerging through a specified orifice. Orifice, in this case pentagonal, is indicated by heavy line. Outline of emerging stream at point of full inversion is indicated by lighter line. The view is with stream issuing perpendicular to plane of paper.

whole matter of the shapes of sea urchins with the statement, "We need not concern ourselves in detail with the shapes of their shells, which may be very simply interpreted, by the help of radial coordinates as deformations of the circular or 'regular' type." He then went on to discuss the amount of flattening in terms of the relationship between gravity and the rigidity of the echinoid test.

An interesting model of the plastic relationship between a pentagon and a five-armed radiate figure can be found in certain studies of hydraulics. A fluid such as water emerging through a thin plate under considerable pressure shows a short distance from the plate the "vena contracta," where the stream is smaller in cross section than the orifice, with the water moving at proportionately greater velocity. A little beyond this point occurs the striking phenomena of "inversion." If, for example, the hole through which the water is emerging is in the form of a pentagon (as in fig. 23), after the "vena contracta" is passed the cross section of the stream is a series of five ribs which are in the form of a five-pointed star inverted in reference to the deriving pentagon. That is, the star points correspond to the apothems of the orifice. Farther from the orifice other conditions are demonstrated, but they do not concern the present problems. It is to be noted, of course, that this inversion of high's and low's between a pentagon and a five-pointed figure, based on the reaction of a fluid to purely physical forces, is very suggestive of the conditions found in a starfish in reference to its central plate and final outline, as indicated in figure 24.

In further consideration of the starfish, another feature demonstrated in figure 24 is that the developing ossicles are not all pentagonal, but certain of them are hexagonal. That is, the secondary radials, five in number, are elongate hexagons, one opposite each angle of the central plate. The radials, all pentagons, are deployed to point alternately to an arm tip and the low point between arms. Other plates running out to the terminal are all hexagonal. This scheme, whatever utility it may have or what structural bases it may reflect, demonstrates that it is perfectly possible for the developing echinoderm to produce both pentagons and hexagons. This is noted here lest it be incorrectly inferred that there is some stricture on the developmental methods of these animals that forbids their tissues to produce a six-sided structure.

The basic tendency towards a pentagonal construction is evidenced in an interesting fashion in the so-called basket star, *Astrophyton muricatum* (Lamarck), usually seen as a tangled ball of interminably repeated bifurcations of the primary five arms of a starfish. If such an animal is permitted to move about

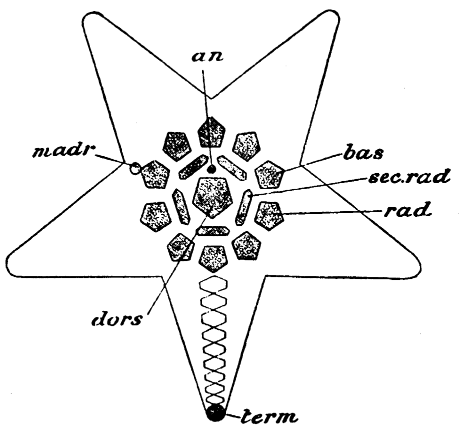


FIG. 24. Diagram of the relationship of the central plate in a young starfish to its outline. After Parker and Haswell (1910). *Abbreviations*: an, anus; bas, basals; dors, central; madr, madreporite; rad, radials; sec. rad, secondary radials (infra-basals).

at will in an aquarium, sooner or later it spreads out one or more of the arms against the vertical glass sides of the aquarium, as shown in plate 2, figure 2. Although this is an active living animal, bending, coiling, and reaching with its dendritic appendages, it quickly becomes evident that the angles between the successive forkings, if a few are measured, are very regular and similar and in fact are not far from the central angle of a pentagon—72 degrees.

Measurement of 50 angles at random showed an arithmetic mean of 76 degrees, an excess of 4 degrees in an actively exploring group of arms.

It might, with considerable reason, be thought that the angles from base to apex in the continued branching of an arm of the basket star are governed by the same principles as those governing the branching of blood vessels and not by some seemingly arbitrary considerations of theoretical symmetry. The principles of arterial branching, so clearly summarized by Thompson (1942), could not be expected to lead to this kind of uniform branching, with angles between large basal branches so similar to the finer terminal branches. A statistical comparison of the basal halves with the distal halves of the angles measured shows that there is no significant difference between the two,

$$d/f_d = 0.34.$$

A similar comparison between each half with 72 degrees shows 1.9 and 1.5, respectively. The lengths of the central segments in any arm from base to tip clearly follow a regular decrement. Fifty segments measured successively along the length of five arms, when plotted against the number of the segment, evidently fall along a straight line which fits closely to the equation

$$Y = 0.2130X$$

where X is the number of the segment starting at any place and Y is the length of that segment; that is, each segment is 0.2130 units less than its predecessor as one moves from base to tip.

As in the animal kingdom, where one entire phylum is basically designed around the salient features of pentagonal symmetry, so in the plant kingdom one great group is also dominated by that kind of design—the exogens, or dicotyledons. The endogens, or monocotyledons, on the other hand, are dominated by a tripartite order of symmetry. Even where there have been great modifications of the basic patterns in the exogens such as reduction, reduplication, and the development of great asymmetry, in most cases it is possible to trace the basic five primitive divisions. Furthermore, any garden or roadside will yield an abundance of forms which show in their inflorescence an expression of simple pentagonal symmetry similar to that found in the echinoderms.

Related to the above is the arrangement of the leaves of a plant. The vast study of this subject, phyllotaxis, is summarized by Thompson (1942) and by Richards (1948) who give a very lucid discussion of the difficulties students are prone to when clear distinction is not understood between biological activities and the geometrical characteristics of space and the nature of number in the purely mathematical sense. The following comments are brought into the present study by the fact that botanists have shown that there is a marked tendency for leaf arrangements in the dicotyledons to have reference to the figure five and that this has evidently an organic connection with pentamerous flowers.

On a stem, for present purposes considered as a cylinder, leaves may obviously be arranged around the diameter in lengthwise series or spiraling about it, so that the distance between successive leaves has both a transverse and a longitudinal component. Perhaps it is simplest to express it as follows, with the surface of the stem conceived of as a developed cylinder, as in figure 25,

$$d = \frac{\sqrt{c^2 - p^2}}{a} \text{ and } \tan\theta = p/c$$

where d = distance between adjacent leaves, c = circumference of the stem, p = pitch of the spiral, i.e., the distance from the first leaf of reference to the next directly above it measured longitudinally, and a = number of spaces between the leaves.

In these formulas the limiting forms are found as a simple circle about the stem in which $p = 0$, and as longitudinal arrays along

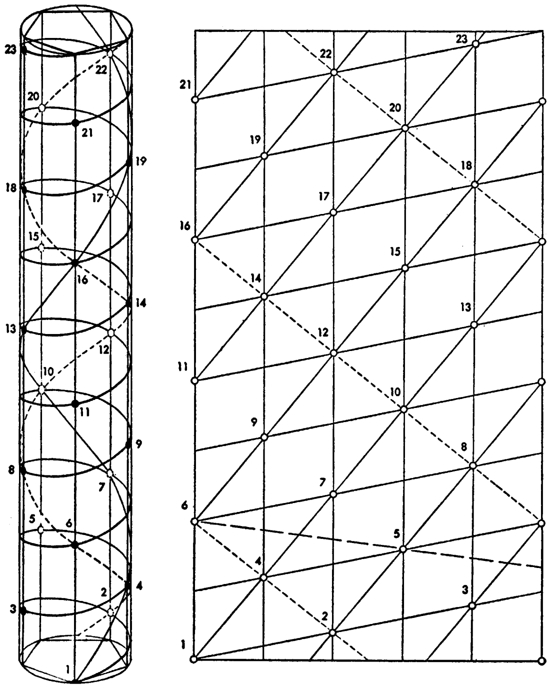


FIG. 25. Diagram of the relationships of parts of a phyllotactic system related to pentagonal organization. At left is a phantom view in which the near points are shown in black and points on the other side of the cylinder are in outline. At right is the same construction developed. Numbers serve to identify points and relationships. Unnumbered points at extreme right of the developed cylinder are identical to points numbered at the extreme left. The dashed line is not shown on the phantom view, nor the solid line beginning 2, 5, 8, 11. Otherwise the lines shown are the same in both diagrams.

it in which $p=\infty$. This does not involve the number of leaves, which is determined by a, but only their lineal arrangement on the stem.

It is, of course, recognized that stems are properly considered as cones, but in many cases the sides are more nearly parallel than can be measured accurately. This formula represents, then, the limiting form, in which the slope approaches 90 degrees. The other limiting form, an extremely flattened cone, in which the slope approaches 0 degree, becomes similar to the flat-faced flower discussed above. Other forms, such as a pine cone, of which the outline is an ellipse, need not be discussed here; they are well covered by Thompson (1942).

In typical pentagonal phyllotaxis the angular distance between successive leaves, lengthwise on the stem, is not 72 degrees but 144 degrees. This is expressed by the earlier students of such matters by a fraction, in this case $\frac{2}{5}$, in which the denominator measures the number of divisions of symmetry, and the numerator the number of revolutions that occur before another leaf appears directly above the first, or the number of spaces or spiral intersections from one leaf to the next leaf along the length of the stem. It is the equivalent of saying that there is a leaf every 72 degrees, but the next one along the stem is twice that or 144 degrees around it.

If, however, the leaves are counted in another way, that is, to the next nearest leaf, not along the axis but around the stem, a rather pretty difference becomes apparent. This is perhaps most easily demonstrated by figure 25; in this development of a stem, small circles marking leaf scars have been numbered serially according to the $\frac{2}{5}$ phyllotaxis noted above. The value assigned to p has been made equal to w, the arc subtending θ, for convenience in drawing but could be assigned any ratio. This then makes the nearest leaf $p/2$ farther along the stem and $\frac{2}{5}$ around the stem. A spiral connecting them is shown as a solid line, and the numbers along it run sequentially, 1, 2, 3, etc. If counted the other way, i.e., to the nearest leaf around the stem, the numbers run, as indicated by the solid line, 1, 4, 7, etc., and the pitch of the spiral is much steeper. Here $p=6w$ and the phyllotactic fraction $=\frac{1}{5}$. Instead of a single spiral there are three spirals which wind around like multiple screw threads. The other two series have the sequences 2, 5, 8, etc., and 3, 6, 9, etc. It is obvious that whichever method of measuring is chosen is perfectly arbitrary. Nor is this all. A similar series winds about the cylinder in the opposite direction. This series of "left-handed" threads is indicated by the dotted lines bearing to the left and passing through numbers 2, 4, 6, etc., and 1, 3, 5, etc. If measured to the next nearest, along the axis the series appears in regular numerical order, as in the first series mentioned but separated by $\frac{3}{5}$, as is indicated by the dashed line. This indicates the complication inherent in phyllotaxis and is as far as we need penetrate for present purposes. The above is a mere suggestion of what is carried out to its logical conclusion involving the Fibionacci series by Thompson (1942) and Richards (1948). Similar matters in reference to the placement of the scales of fishes are discussed by Breder (1947). The elongate holothurians, especially Synapta, show no spiraling of structures; all subscribe to the formula given in which p equals ∞.

As pointed out above, it is not the present purpose to go into a statistical or phylogenetic analysis of pentagonal organic forms. The foregoing analysis is sufficient for the demonstration of principles and for reconnoitering the field to determine if a rational explanation could be developed for the widespread occurrence of five-part organic constructions. It is possible to develop index numbers, such as the values of a, b, and c in the equations, that would be expressive of form. Such index numbers might make possible more precise phyllogenetic analysis than verbally described differences permit. It is moreover, interesting to note that the ancestral and all extinct Cystoidea showed as perfectly developed a pentagonal symmetry as do recent forms. While for purposes of studies of the evolvement of this geometrical system such a situation would be useful, it gives no clue to the origin of this tendency. Apparently the Class Cystoidea developed, in its ontogeny, from a dipleurula-like larva from which it was evidently derived phylogenetically. This would seem to refer the efficient cause of the five-part pattern to some mechanism brought into play at the time of metamorphosis throughout the group during its whole existence, suggesting a rather remarkable stability for this type of symmetry.

STRUCTURAL CONSEQUENCES

IN GENERAL TERMS the geometry of pentagonal symmetry has been reviewed, and a few examples of its manifestation in both animals and plants have been given in the preceding pages. Some attempt to discern the underlying reasons for its presence at all, for its restriction to certain groups, and for its almost complete dominance within those groups can now be made. First, some reference must be made to the theory of polyhedra and the absence of regular polygonal or regular polyhedral symmetry in crystal structure. Of this Weyl (1952) wrote: "While pentagonal symmetry is frequent in the organic world, one does not find it among the most perfectly symmetrical creations of inorganic nature, among crystals. There no other rotational symmetries are possible than those of order 2, 3, 4 and 6." In writing of architecture, the same author considered pentagons very rare and said that formerly he " . . . knew of only one example and that a very inconspicuous one, forming the passageway from San Michele di Murano in Venice to the hexagonal Capella Emiliana. Now, of course, we have the Pentagon building in Washington." There is little doubt that such structures are uncommon, but a variety of others could no doubt be found on a thorough search, probably most of which would be more or less irregular pentagonal outlines, such as old Fort Pitt on the site of present Pittsburgh. (See, for example, Anon., 1954.)

That crystals cannot form regular pentagonal structures is evidently related to the constraints on the crystal-forming molecules which force them into the well-known crystal lattice structures. That it is impossible to fill space completely or to cover a surface completely with regular dodecahedra or regular pentagons, respectively, is apparently basic to the impossibility of inorganic materials to develop this type of symmetry. How organisms, both plant and animal, have avoided this restriction is one of the more intriguing questions which arise in deliberations of this kind.

Related to this is the limit placed on the design of the so-called regular and semiregular polyhedra which are discussed at some length in terms of their biological implications by Thompson (1942). For the moment we need only recall their general nature by means of the following tabulation:

NAME OF BODIES	ANGLES	SIDES	NUMBER POSSIBLE
Platonic	Isogonal	Isohedral	5
Archimedean	Isogonal	Not isohedral	13
Catalonian	Not isogonal	Isohedral	13

The Archimedean bodies can be considered primarily as Platonic bodies with their corners truncated in various ways so that new but not equal sides appear. The Catalonian bodies on the other hand may be considered as Platonic bodies with appropriate additions reciprocal to the Archimedean bodies. Still another family of bodies can be produced by extension of the surfaces of the above bodies to their intersection with other faces. These bodies have reëntrant angles, of which the stellate dodecahedron is an example. In the case of the cube, such a construction is impossible, because it would result in a three-way cross with each arm extending to infinity.

The failure of these restraints at various levels to obtain in organic structures is evidently rooted in two primary facts—the nature of the materials involved and the nature of the forces involved—and the further fact that neither confines the construction to the use of strictly straight lines.

Thompson (1942) shows a photograph, after Leduc (1911), of an "artificial cellular tissue" formed of a potassium ferrocyanide diffusion in gelatin in connection with his discussion of hexagonal symmetry in such structures. When all the complete polygons in the figure in reference to the number of sides are counted, the tabulation that is shown at the top of the next page is possible:

Number of Sides	Frequency	Per Cent of Total	Remarks
5	7	12.5	33.9% have other than six sides by actual count
6	37	66.1	
7	12	21.4	

Writing about this illustration, Thompson noted merely, rather picturesquely, the following: "The regularity leaves something to be desired; there are even places where a pentagon is smuggled in instead of a hexagon."

It would appear that such surface coverage is related not so much to some uniform geometrical configuration as to the deployment of units on a flat surface according to the Fibionacci angle which is so elegantly shown by Richards (1948). He shows that in such a system the maximum number of contacts is seven and the minimum is five, with transitionals of six sides. This is in close agreement with the counts made of the gelatin structure. Thus even in an artificial physicochemical situation, which was used for illustrating the hexagonal principle, it is seen that the hexagon does not have an overwhelming majority.

From part of a dragonfly's wing, again from Thompson (1942), which presents a much more complicated situation involving marginal members which are often four-sided figures, the following tabulation can be made:

Number of Sides	Frequency	Per Cent of Total	Remarks
4	27	7.1	52.2% have other than six sides, with a considerable bias towards 5
5	136	35.9	
6	182	47.8	
7	36	9.2	

Because the marginal cells tend to be four-sided and the internal ones to be six-sided, it is natural that in the transition the number five is relatively large, a feature not present in the gelatin model. The pentagonal cells were found to be principally located close to four-sided ones.

Harper (1908), quoted by Bonner (1952), gave comparative figures for the number of sides to the polygons formed by the alga *Hydrodictyon*, the so-called water net, as follow:

Number of sides to polygon	3	4	5	6	7	8	>8
Per cent of total polygons	1+	8+	29−	43−	12−	4+	2−

It is to be especially noted that, while the hexagons are most numerous (almost one-half), pentagons are next (over one-quarter); also, that the polygon with seven sides is less than one-eighth of the whole, and all the remaining forms are much fewer in number. Because of the manner in which these nets are formed, which is discussed at length by Bonner, the above figures may be taken as fairly representative of the ratios of the variously sided polygons to be expected in more or less generalized organic packings. The number of pentagons present is 67+ per cent of the number of hexagons, while the seven-sided figure is only 28+ per cent, and all the others taken together constitute only 35− per cent.

Comments by other students of these problems indicate the general attitude towards pentagonal structures. For example, Weyl (1952) states simply, "The symmetry of 5 is most frequent among flowers," or, "A page like the following (fig. 36) from Ernst Haeckel's *Kunstformen der Natur* seems to indicate that it also occurs not infrequently among the lower animals. But biologists warn me that the outward appearance of these echinoderms of the class Ophiodea is to a certain degree deceptive; their larvae are organized according to the principle of bilateral symmetry." This is, of course, true but actually beside the point. The developmental history of any organic or inorganic symmetrical structure could be similarly included, but it is of interest only from the standpoint of developmental mechanics. Also, the fact that probably no organic symmetry is absolute only underlines the evidently compulsive nature of the influences driving any form to its given kind of general symmetry. It is easy to infer a functional necessity for such polarized motile bilateral structures as ships, airplanes, spermatozoa, or beetles. In five-sided organisms, or those of any degree of symmetry above two, it is not easy to develop a valid reason why any particular degree of symmetry was selected as against all others, for all seem equally well prepared "to march off in all directions at once." Nevertheless, many, if not all, starfish have a preferred orientation in reference to movements of translation.

A tendency to develop reduplicative parts is a strongly marked feature of both plants and animals. These repetitional units have been designated "polyisomeres" when they are similar and "anisomeres" when some of a series have undergone modification. A review of considerations such as these is in the 1951 book by Gregory, which is the most recent treatment of the matter by the creator of these two very useful terms. Their relationship to the present study is clear and their relationship to general concepts of symmetrical organization is discussed by Breder (1947). In one sense this investigation of pentagonal symmetry may be considered a study of how such units behave under the constraints imposed by the nature of space and specific geometrical limitations.

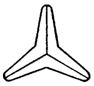
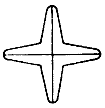
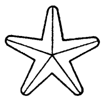
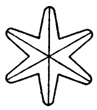
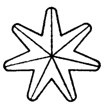
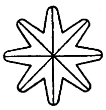
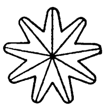
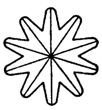
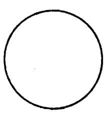
Pertinent to this problem also is the fact that usually the outside form of an animal shows its most nearly perfect display of symmetry. As noted above, this is certainly an important feature to active bilaterally symmetrical animals, a condition essential to the development of any considerable speed. Such animals are of course markedly asymmetrical in their various internal organ systems. The "plumbing" is fitted in where needed and where space permits without destruction of the outer contour. This is as true of a fish as it is of a submarine. The fact that each detail of an organ or bit of apparatus has its own symmetry, its components have their own symmetry, and so on can usually be related to some evident structural or, in the case of the vascular system and the digestive tract, various hydrostatic and hydrodynamic principles. The point of the above is that in the case of bilaterally symmetrical animals there are evident clear reasons for all the symmetry externally and the absence of it internally. A consideration of the echinoderms shows a similar situation where the external form in general terms is just as allegiant to its chosen degree of symmetry. It is the internal parts that show deviation from its basic geometry in a manner quite analogous to that shown by bilateral animals. Because this is so, as any reference to echinoderm anatomy will show, it would seem unlikely that the locomotor needs of bilateral animals are the only, or even the dominant, influences at work in molding the definite patterns the animals will take. At this stage, it seems to be impossible to ascribe a reason or a multitude of influences to explain the basis of biological and environmental forces demanding a pentagonal symmetry. However, as is developed below, from an unexpected source, a not unplausible basis is available for building a hypothesis.

That organisms, both plant and animal, cleave to certain types of symmetry according to their kind is shown in a highly abridged summary in table 3. Those that have departed from it to a greater or less extent still show the evidences of phyletic impressment, either in the detail and suppression of structures no longer of major importance or in the overriding emphasis of some part at the expense of others. The fact that there is this retention of the basic pattern, even when the animal has evolved into something quite different, is, of course, a measure of the strength of the controlling influence, probably often but not necessarily the same one that caused a particular symmetry to develop in the first place.

That so many echinoderms approach either a pentagon or its stellate form is of considerable theoretical interest. It would seem that among the starfish and sea urchins at least, the pentagon, the stellate pentagon, and the circle formed mathematical limiting outlines which many species approximated but never quite reached, with series of forms extending from one to the other by easy transforma-

TABLE 3

DISTRIBUTION OF ORGANISMS BY DEGREE OF SYMMETRY

Degree[a]	Form[b]	Angle[c]	Diagonals[d]	Illustrations and Notes
0			—	Amoeba, amorphous forms in general and where no axis or plane of symmetry is present
1		360	—	Bilateral forms in general, nearly all animals not specially mentioned elsewhere in this table, but which show polarization
2		180	—	Double-ended forms, as some diatoms, etc.
3		120	0	Basic pattern of flowers of monocotyledons
4		90	2	Basic pattern of certain coelenterates, or as multiples of this degree Sponge spicula in the Tetractinellida; also as multiples of degree 2
5		72	5	Basic pattern of flowers of dicotyledons, of echinoderms, of vertebrate body section of distal ends of tetrapod limbs and of oral armature of priapulids
6		60	9	Basic pattern of certain coelenterates, especially Hexactinia, and the details of many packed structures as honeycombs; also as multiples of degree 3
7		51 3/7	14	Structures of this order or higher, except those that can be considered as multiples of the above are rare or absent
8		45	20	Multiples of degree 4, or degree 2
9		40	27	Multiples of degree 3
10		36	35	Multiples of degree 5
∞		0	∞	Limiting form—a circle

[a] Degree of symmetry as defined by Breder (1947). Also number of sides of the corresponding polygon, from degreee 3 on. [b] Diagram of representative form of basic symmetry. [c] Angle between identities in degrees.

[d] Total number of diagonals of the corresponding polygon $d = \frac{n(n-3)}{2}$.

tions. The fact that the star represents all the diagonals of a pentagon, which in this polygon alone are equal in number to its sides, suggests various possibilities in the nature of their growth and the establishment of gradients varying in strength between a pentagonal and a stellate configuration. This feature alone suggests one possible physical reason for the tenacity to which these and other organisms cleave to their five-part condition. Obviously, if in the phylogeny or ontogeny of such animals the strains between adjacent points are overridden by the strains between diagonal points, the form continues to be of five parts, and the transformation is from pentagon to its stellate form, a situation that no other polygon provides. If such behavior occurred in forms of some other order of symmetry, such a change would include a numerically different order of symmetry readily calculable from the formula given in the remarks above on the basic geometry of a five-part object. Table 3 indicates the relationships between polygons and the sum of all their diagonals.

An interesting aside to the relationship of the number of sides of a polygon to the number of diagonals possible is that the expression

$$d=\frac{n(n-3)}{2}$$

can easily be shown to represent a parabola in which

$$n^2-3n=2pd$$

where p is the distance from the focus to the directrix. The focus of this parabola lies at $-\frac{5}{8}$, $1\frac{1}{2}$, and the directrix lies along $d=1\frac{5}{8}$. The parabolic vertex is $-1\frac{1}{8}$, $1\frac{1}{2}$, and the latus rectum extends from $\frac{1}{2}$ to $2\frac{1}{2}$ on $n=\frac{5}{8}$.

The corresponding values for d and n of polygons lie at integral points along the only part of the curve which has both ordinates positive. This is shown in figure 26 and indicates graphically the unique position of pentagonal figures in reference to the relationships between the number of their sides and diagonals.

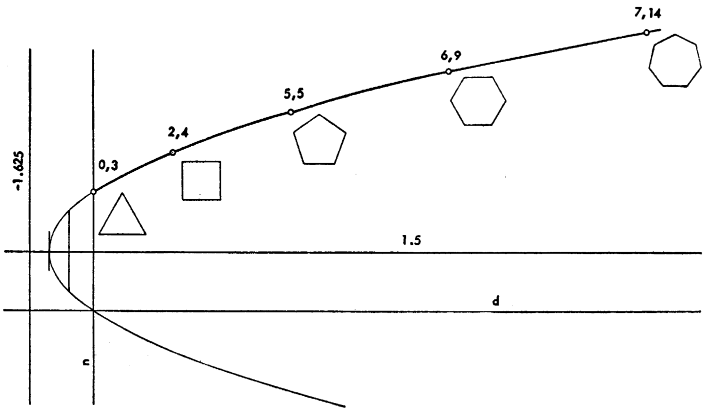


FIG. 26. Parabola of the equation

$$d=\frac{n(n-3)}{2}$$

indicating its relationship to ratio of sides to diagonals in polygons. See text for full explanation.

The part of the curve below the axis of the parabola passes through the origin, n and d both $=0$, opposite to the point expressive of the triangle, at 0.3.

The distances and mutual relationships between the five vertices of a pentagon and the significance for the purposes of this discussion may be most easily appreciated by reference to figure 27. Here the five vertices of a pentagon are represented by five small circles lettered from A to E. Vertex A has been connected with each of the other four by a heavy line. Thus the two sides and two diagonals that it is possible to draw from a single point are indicated. Three more of each are possible from the other points which, when drawn, complete the pentagon and its inscribed star. These have been omitted from the diagram for, at the moment, it is more convenient to consider the relationships of a single point to the four others. If this group of lines be treated as though they were vectors, three different parallelograms can be drawn. One of these (*ADGE*) appears twice; its mirror image, not constructed, would be drawn about angle *BAC*. The other two and different parallelograms are colinear and form parallelograms *ABHE* and *ACFD*. These parallelograms bear certain interesting and significant relationships to both pentagons and stellate pentagons as reference to figures 1, 3, and 4 will demonstrate. Triangle *DFC* is the stellate extension on side *DC* of pentagon *ABCDE*. Point *H* is at the juncture of two rays of a stellate pentagon inscribed in pentagon *ABCDE*. Point *G* is on a straight line passing through *BHD* where this intersects the side of a pentagon circumscribed about a stellate pentagon, of which *F* represents one ray and the central pentagon of which is *ABCDE*. Line *DG* is equal to a

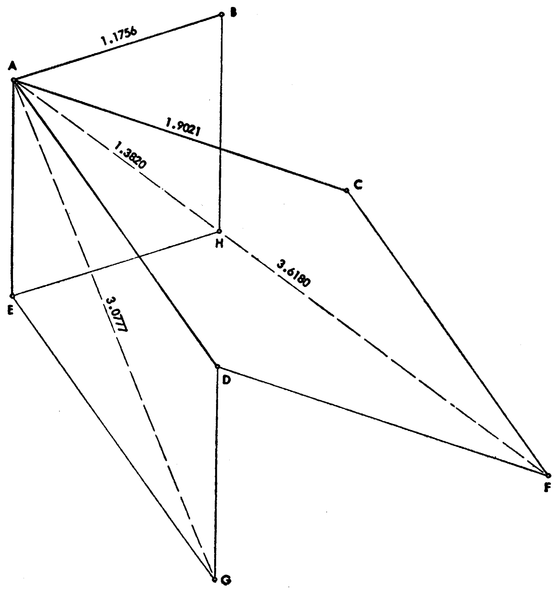


FIG. 27. Distances and relationships from one vertex (A) of a pentagon to the other four (B, C, D, E) and their resultants.

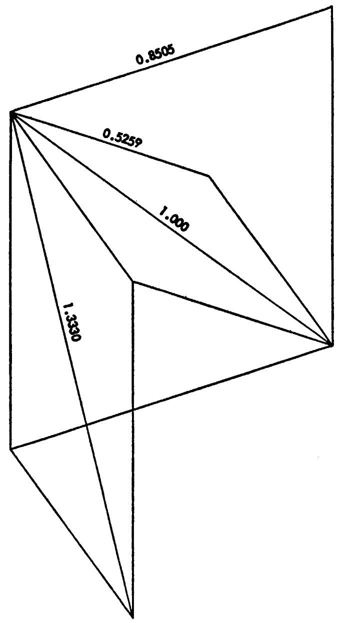


FIG. 28. Reciprocals of the distances used in figure 27 drawn as vectors. Primary angles as in that figure.

side of that pentagon by construction. With the radius of pentagon *ABCDE* equal to 1.000, the following values appear

$AH = 1.3820, AF = 3.6180 \text{ or } 2(a+r), AG = 3.0777.$

If instead of the distances between the five vertices, their reciprocal values be taken, an inverse parallelogram of forces can be constructed. If it is assumed that they are all equipotential, the relative influence on a vertex of the other four can be calculated. Interestingly, this comes out to be equal for the two colinear parallelograms and equal to *r* of the generating pentagon. The resultant between the adjacent vertex and the nearest diagonal is nearly a third more, as is indicated in figure 28, which represents the reciprocals of the distances shown in figure 27.

If the inverse of the squares of these distances be taken, instead of the simple reciprocal values, that one corresponding to *AH* of figure 27 becomes 0.5259, that of *AF* becomes 0.8505, and that of *AG* is 0.9168. The value of *AH* (0.5259) which was unity in the simple reciprocal treatment, there appeared as the reciprocal of the diagonals. A similar relationship is borne between the corresponding values of *AF* and *AB*, 0.8505 representing AB in the first and AF in the second. No such simple relationship appears between the corresponding values of AG and AD.

It is not necessary to labor the point at this time that these differing values, which measure the influence between these pentagonal points, must be considered in any study of the mechanics of development, a matter not examined in detail in this paper. It should be apparent from the preceding discussion, however, that the spatial relationships of the sides of a pentagon to its diagonals provide a very suggestive point of departure for a study of the reasons for the maintenance of a pentagonal organization when once established. Such a view would refer these reasons not so much to some peculiarity of the organisms involved, but rather to the properties of space and the unique features of the pentagon as compared with any other polygon. Here alone the sides show the same degree of symmetry as the diagonals. The "unexpected source" of the stability of pentagonal organization mentioned above would thus be the response of a dynamic physiological system to these geometrical features. This may be conceived of as "trapping" the structure or organism which has hit upon five as a divisional number.

If table 3 be referred to again, it becomes apparent that the vast majority of organisms show a very limited number of basic kinds of symmetry. These are degrees 1, 3, 5, and 6. All others are of much less frequent occurrence. The geometry of the stresses and strains in a dynamic structure of degree 5 has just been considered. Organisms of degree 1, the polarized bilateral organisms, are the only ones in which even a modicum of speed can be developed. Degrees 3 and 6, although geometrically very different from pentagonal construction, have their own unique qualities. In the case of degree 3, there can be no "competition" between points of influence as found in the pentagon. This circumstance produces another kind of stability and, unlike the pentagon, there is no possibility of switching between two designs of the same degree of symmetry. Degree 3, unlike degree 5, can cover a surface completely, as indicated in figure 2, and in so doing forms degree 6. This higher degree, the sides of which are twice those of degree 3 and the diagonals of which are the square of the sides of degree 3, merely makes a compound structure with the basic stability of lower number. The described geometrical characteristics of these degrees of symmetry and the absence of them from all other degrees suggest possible explanations as to why these few types of symmetry find expression over and over again in the most diverse kinds of structures to the virtual exclusion of the others.

It could be anticipated from general considerations that an exponential would appear, for the reason that much of organic growth is such that within very broad limits an individual of a given size is a gnomon of similar larger and smaller individuals or of itself at different ages. Some of the figures indicate the geometrical basis of gnomonic relationships which in fact represent a graphic basis of the exponential equations continually appearing in considerations of the growth of living forms.

It is of interest to note that the vertebrates, which are certainly as bilateral a group as any, have a very considerable disposition to divisions of five parts. The pentadactylate limb of the tetrapods is a striking example of division into five primary units which, once developed, has persisted through very diverse modifications while retaining or showing clear evolutionary evidences of its basic five-partness. This retention of five-partness has been traced back to the rhipidistian paddle by Gregory and Raven (1941). In one earlier classification the tetrapods were actually designated the Pentadactyla. A cross section of the primary vertebrate trunk shown diagrammatically in figure 29 again shows a basic division into five regions. The vertebrates show no other regular systematic tendency towards any of the other possible symmetries.

With such a condition and the recognized indications of affinities between the echinoderms and the chordates, and bearing in mind the fact that the bilateral pluteus echinoderm larva has in its being directives which in ontogeny cause it to become pentamerous, one is tempted to think that there must be some further evidence here of fundamental similarity. It is true that early fishes do not show this five-part condition of the basal bones of the fins and that modern teleosts are not notable for any conspicuous or general tendency to develop organs in groups of five, although five soft fin rays in the pelvics is characteristic of the acanthopterygians. From this some persons would no doubt wish to consider the pentadactylate limb as a development *de novo*. That it realized the figure five and not some other number in a group evidently akin to a group so five-dominated can equally well suggest that there may be some feature in the physicochemical structure of these two groups, at the molecular level, which tends to divide them into five-part structures when other influences do not suppress it, and to cause the number to reappear in some other mode when phylogeny has progressed to a point where such suppression no longer obtains.

Insects show a considerable tendency to have five-segmented legs and antennae, which is perhaps most marked in the Coleoptera, a group that may be used as an illustration. Six of the 12 superfamilies of beetles possess exactly five tarsal segments. The other six superfamilies contain at least some members which show reductions of various degree, according to the classification of Essig (1942). In his definition of the Coleoptera he wrote, " . . . tarsi one- to five-segmented, normally five. . . . " The five-segmented forms were once classified in the Pentamera, a group now considered purely artificial. Linnaeus similarly named a class of plants with five stamens, based on this pentandrous condition, the Pentandria, a name also now no longer used.

The beetle superfamilies in which all six tarsi have uniformly five segments are the Hydrophyloidea, Elateroidea, Dryopoidea, Dascilloidea, Ptinoidea, and Scarabaeoidea. Those in which various kinds of reduction have occurred are the Staphylinoidea, Canthoroidea, Cucujoidea, Mordelloidea, Tenibrionoidea, and Cerambycoidea. Evidently the original condition in beetles was one of five segments which has persisted strikingly, with reduction occurring as above described but with no evidence of any increase above five. There appears to have been no study given to possible reasons for this situation from the standpoint of locomotor advantage or any other functional utility.

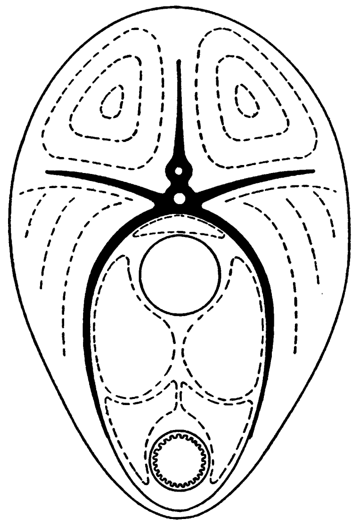


FIG. 29. Schematic transverse section of a fish indicating the basic five-partness of the structure despite its great restriction of areas for specific purposes.

The oral armature of the priapulids is arranged in a pentagonal design in which successive pentagons are nested, each smaller one rotated through 36 degrees from the position of the next larger. This was illustrated by Théel (1911). According to Hyman (1951), who puts these creatures in the Phylum Aschelminthes as a Class Priapulida next to the Nematoda, the genus *Priapulus* has five to seven of these pentagonal designs, while the only other genus (*Halicryptus*) in this small group has three or four. Figure 30, after Théel, shows the nature of this pentamerity. The following quotation from Hyman, on the history of our knowledge of the priapulids, bears on ideas in the present paper that are more fully stated below.

"The animal now called *Priapulus caudatum* is common in northern European waters and has been known to zoologists since the days of Linnaeus. It appears in Linnaeus's Systema Naturae first under the name *Priapus humanus*, later under the name *Holothuria priapus*, placed under the group Vermes Mollusca, a heterogeneous assemblage of soft-bodied invertebrates. The name *Holothuria priapus* was also employed by Fabricus (1870) who recorded the animal from Greenland waters, and by O. F. Müller (1806), who described and figured it from

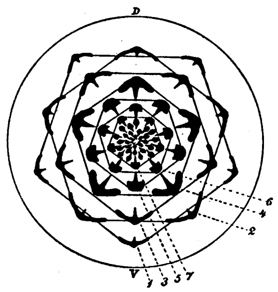


FIG. 30. The pentagonal oral armature of *Priapulus caudatus* Lamarck. After Thêel (1911). D, dorsal side; V, ventral side; 1–7, the seven interlaced pentagons of teeth.

Danish waters. The animal was generally believed to be related to echinoderms. Lamarck in 1816 realized that the animal was not a holothurian and gave it the name now in use, *Priapulus caudatus;* but it appears to the author, as also remarked by Theel, that *Priapus* is the valid generic name, not *Priapulus.* Cuvier continued calling the creature *Holothuria priapus* and to place it among the footless echinoderms, close to *Sipunculus.*"

The nested pentagons of denture at first glance may appear to be inscribed serially in such a manner that the radius of one is the apothem of the next larger, but actually this is only a very rough approximation of the condition found. Measuring the successive radii, beginning with the innermost, shows the nested pentagons of denture, except for the last three, to be larger than those of a geometrical construction of inscribed pentagons. The excess decreases regularly from the least to the largest as may be clearly seen in figure 30, in which the vertices of the innermost pentagons do not nearly reach the sides of the next, while the fifth pentagon just touches the sides of the sixth, and that one penetrates through the sides of the seventh, or outermost, pentagon.

Haas (1948) has demonstrated that the individual trochopore of the bryozoan *Sertella septentrionalis* Harm, which attaches itself to a solid to start a new colony, is pentagonal in outline. This original individual gives rise to five new individuals, one on each face of its pentagonal form. These new individuals and all subsequent ones are hexagonal. Haas's figures are reproduced here as figure 22, including his schematic diagram of the geometrical plan and an actual colony which departs rather far from the theoretical because of a wide variety of influences, which he discusses at some length. As in the case of echinoderm plutes, there are evidently no data or reasonable hypotheses as to why these animals develop into five parts. Good physical reasons exist, however, for the fact that in both groups the parts tend to become hexagonal as they spread out over a surface in close contact with one another.

At this point a further consideration of the coverage of a surface by pentagons may be usefully undertaken, in which are included mutual influences of adjacent structures such as those of pressure or other physical effects. Polyhedra are discussed above as stable structures not subject to deformation without rupture, which is not true of polygons in general but only of the first of the series, the triangle being an inherently stable structure. If these figures be constructed of rigid rods held together by pins at their vertices, this principle becomes mechanically obvious, as is commonly displayed at every turn, for example, in the trussing of a bridge or the behavior of a lazy gate. Casually, one would think that the upper limiting figure of this series, the circle, might also be stable. If, however, it is thought of in the above terms, as a polygon of infinitely short rods, it deforms readily into an ellipse, of which it is also a limiting form. In this sense a circular rod has no more stability than a rod made of a polygon of 20 sides or so, which is not to be confused with the resistance of a circular rod to bending, which is in another plane as compared with a flat strip across its least dimension. In other words, the more sides a polygonally sectioned rod possesses the less it is polarized towards differential transverse bending. Thus, a 20-side rod resists bending in every direction nearly as well as a circular one. A square rod, on the other hand, bends most easily in the two planes parallel to the faces of the section and resists most in the planes parallel to the diagonals, which is true, however, only of the polygons with an even number of sides. Those with an odd number of sides are so braced by the geometry of their design for all practical purposes as to resist bending in any plane equally well and in this respect resemble the circle. Because the resistance to bending is proportional to the square of the diameter of the section, it is clear that there is compensation in regular polygons such as an equilateral triangle and a pentagon.

When each of these forms is considered, not as the section of a rod but rather as a geometrical figure or of a rod of extremely short length so that it is in effect a disc, as for example, the Bryozoa above mentioned, it is possible to define certain physical necessities which must be observed by both mathematicians and growing organisms. Physical polygons of such a sort, excepting only the triangle, maintain their shape only if the internal pressure and external pressure are uniform throughout. From this fact it follows that a droplet of oil of the same specific gravity as the fluid in which it floats becomes spherical, or, when compressed between two flat and parallel surfaces, its outline becomes circular, which of course is true of any droplet as its support against the action of gravity is taken care of by the plates. A fully flexible bladder performs in the same way. A pentagon, for example, composed of jointed members, which is the geometrical equivalent of such a bladder, with five equal rigid edges, may serve conveniently as a model for this analysis. If, as shown in figure 31, an equal pressure is exerted on all five sides from the interior or exterior, the model will remain a regular pentagon. However, if, in the case of the pentagon held symmetrical by equal interior pressure, the pressure on one side is increased sufficiently the figure will snap into an isosceles triangle as shown in figure 31B. Each of the two sides of this triangle will equal twice its base. The altitude of the triangle will be 1.9364 times its base; its apical angle, 28 degrees 57 minutes, and the two basal ones each 75 degrees 31½ minutes. If, on the other hand, the internal pressure on one side is reduced sufficiently, the external pressure will snap the figure into the form shown in figure 31C, an equilateral triangle with the two "lost" pentagonal edges superimposed and depending from the triangle as a "tail."

Obviously the increase of internal, or decrease of external, pressure, in order to produce the figures shown, must equal or be greater than the algebraic sum of the pressures on the other sides. If it is less than that sum, the figures will take a position of equilibrium at some place between the pentagon and one or the other of the two distortions, which will be exactly proportional to the relative sizes of the two influences and may be used, in the event such figures are produced, to determine quite accurately the relative magnitudes of the forces involved.

The isosceles triangle with the altitude 1.22474 times the base we have not found represented in a natural object, which could be supposed to indicate that a bias of pressure in a cell or system of tissues of the sort described is unlikely, which, *a priori*, it would certainly seem to be.

The equilateral triangle is certainly abundant in organic forms both in its own right and as an element of hexagonal symmetry. Unlike the occurrence of the isosceles triangle noted above, the occurrence of the equilateral one is, *a priori*, one that would be expected. Uniform pressure within cells or systems of cells is of more common occurrence than variations in internal pressure, and the reverse is generally true of external pressure. The fate of the "tail" would presumably be that it would disappear or at least become indistinguishable from other separation membranes.

Two other transformations of the pentagon are shown in figure 31D and E. The first, a trapezoid with one base twice the size of the other, is produced by extra pressure between any two diagonal apices. This quadrilateral has angles of 60 degrees and 120 degrees and is immediately reminiscent of the equilateral triangle and its associated hexagon. The figure is obviously just half of a hexagon and consequently can be decomposed into three equilateral triangles. This figure appears in nature not as a trapezoid but either as a fragment of a hexagon or as three equilateral triangles.

The figure illustrated as figure 31E with a reëntrant angle is produced by extra pressure on the apex and results in two isosceles triangles similar to, but just half of the size of, B. These figures, with certain exceptions explained below, are the only regular ones into which a pentagon can be transformed, two from internal polarized pressure, or the equivalent external tension (B from an apex to the mid-point of the opposite face and D between two apices), and two from external pressure, or the equivalent internal tension (C from between any two alternate apices and E between an apex and the mid-point of the opposite face). These figures are thus inverse to each other, that is, B to E and C to D. The latter two develop angular features characteristic of hexagonal symmetry; and the faces involved. Oblique pressures would produce other figures, but each figure would be asymmetrical. All these potential figures are demonstrably intermediate between the figures actually used and can indeed be regarded as a limiting case of a whole series of transformations. For example, under oblique pressure E eventually is transformed into C, in which one triangle has a base small to vanishing point, and the other is an equilateral triangle. D eventually becomes like E if pressure on the long side is strong enough.

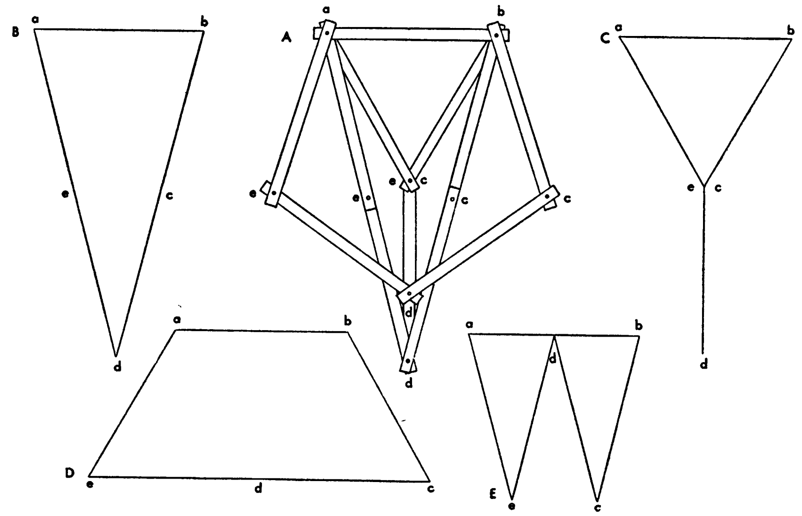


FIG. 31. Diagrams of distortions of rigid-sided pentagons. A. The primary pentagon overlain on two possible transformations. B. The resulting isosceles triangle. C. The resulting caudate equilateral triangle. D. The resulting trapezoid. E. The double triangle. Identical lower case letters have been placed at homologous apices of the figures for ease in visualizing the transformations.

former, features not recognizable as characteristic of any organic basic symmetry.

There are, of course, in a purely geometrical sense, other possible transformations, but they seem to have no possible biological significance, because they would involve the rupture of whatever organic constituents were involved. For example, it is possible to transform the pentagon into another figure of two triangles identical with those in E but with one triangle rotated to be opposite the base line, so that the two triangles touch the same corners, but oppositely. Obviously, as stated, all four figures in figure 31 are made with the pressure or tensions normal to the Likewise, this same figure reverts to a pentagon if the internal pressure is so feeble as to be balanced by the other forces, so that the two sides do not lie in a perfectly straight line but bend outward proportional to the balance between the forces involved. This is equally true of B.

A similar study of the other polygons shows that transformations of the even-sided ones are all collapsible to a line and all those of the odd-sided ones are not, for the simple reason that whatever metamorphoses are undertaken, an odd number insures that three sides will remain to form an equilateral triangle, as the pentagonal figures show. It is obvious that the more sides there are, the more transformations can be made. The triangle permits of no such transformations; the square, only of a collapse through a series of parallelograms to a straight line; the pentagon, to the condition discussed above; and the hexagon, to many more, all of which include figures of 60 degrees. The isosceles triangle with side and base in the ratio of 2 to 1 does not appear again until the next odd-sided figure, the heptagon, and from there on alternately, for reasons similar to those that prevent these odd-sided figures from collapsing to a line. They all can collapse from this isosceles triangle to some form of caudate equilateral triangle, as may be seen from the diagram of the pentagon transformations.

It would seem entirely possible that the form of the ossicles developing in young starfish, which is discussed above and illustrated in figure 24, has its roots in the geometry of transformed figures, with the added ability to develop on an angle in a side so as to increase the number of polygonal sides.

Still another set of systematic transformations can be made of such polygons, involving the length of the sides while the angles are held constant, which may be most easily visualized as the moving, parallel to the original position, of one or more sides inward. Several of these transformations are shown in figure 32. It is at once evident that they are quite different from those with the lengths of the sides held constant, but some of them appear from place to place in organic nature generally associated with regular ones, but near some boundary or limiting plane. These two types of transformations taken together can clearly give any polygon that it is possible to construct. It is sometimes useful, in studies of this kind, to think of a fully irregular polygon in these terms, from whence it is sometimes possible to interpret associations which otherwise could well remain meaningless.

In a change of polygons, as shown in figure 32, certain geometric regularities appear, which are useful in the present discussion. If, for example, one angle is cut off a pentagon, as in A, two polygons are formed of three and six sides, respectively. If two are cut off, as in B, polygons are formed of four and five sides, which, if three are cut off, simply become inverted as five and four, as shown in C. Also (not shown) there is the complement of A, with six and three sides. In general terms, this means the following:

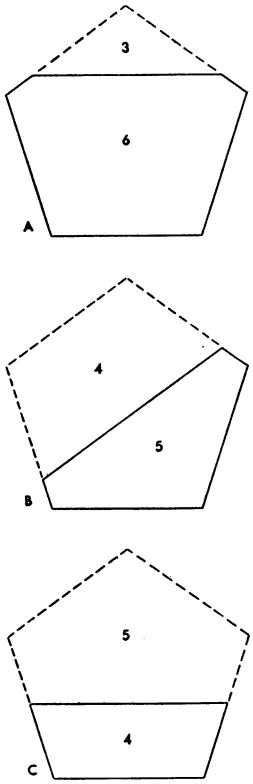


FIG. 32. Diagrams of distortions of changeable lengths in rigid-angled pentagons. See text for explanation.

Angles Spanned	Sides of Polygon Cut Off	Sides of Polygon Remaining ± Those of Deriving Polygon
1	3	1 more than number of sides
2	4	Same number as original polygon
3	5	1 less than original polygon
4	6	2 less than original polygon

If the dividing line reaches from a side to an apex or from an apex to another apex, the above numbers are modified in an obvious fashion.

It is clearly indicated in table 3 that by far the most usual designs are all in the lower orders of symmetry, those formed on a basis of the prime numbers 1, 2, 3, and 5 being

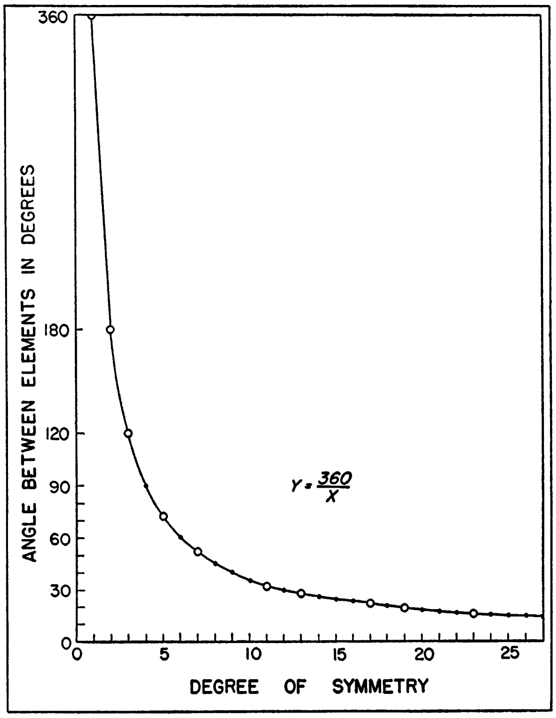


FIG. 33. Graph of the equation

$$y=\frac{360}{x}.$$

Circles indicate the integral values of x which are the "nodes" where symmetry occurs. Large circles mark the prime integral values.

in the vast majority, while those of a higher order are almost always multiples of them. If the relationship between the number of the degree of symmetry and the angle between identities be expressed as

$$y=\frac{360°}{x}$$

where x = the number of the degree of symmetry and y = the angle between identities, some interesting features of these relationships may be made a little clearer. This equation may be plotted as a graph, as is shown in figure 33. Integral values of x may be considered as nodes where a symmetrical construction is possible. At any values where x is not a factor of y, true symmetry does not occur, and it could be said that such a curve should not be drawn but represented only by the indicated nodes. However, the imperfection and distortions of symmetry seen in various organisms may well be developmental attempts to bridge or straddle between two adjacent degrees of symmetry as is indicated above for the partitioning of space in both a glycerine jell and a dragonfly's wing. The relationship of the prime numbers of divisions and their relationship to their multiples is clearly indicated. It is notable, too, that 5 is the largest prime number found in any abundance in organic structure, and

$$6=(\text{degree } 3\times 2)$$

is the largest degree of symmetry regularly found in any large quantity. The equation shows the curve to be an equilateral hyperbola, with $x=0$ and $y=0$ as asymptotes. If the equation is expressed in radians instead of degrees,

$$y=2\pi/x.$$

The values of y, the central angle in radians, all reduce to the reciprocal of $\frac{1}{2}x$.

One of the notable attributes that are indicative of the basic nature of pentagonal symmetry is that it occurs regularly only as the total form of independent units, or an attachment, if there is one, is always by means of a stalk or stem, which tends to be slender. Illustrations of the first are such five-part units as Eleutherozoa among the echinoderms and the body section of vertebrates. Illustrations of the second are such five-part terminal appendages as dicotyledonous flowers or the pentadactylate appendages of tetrapods as well as such attached echinoderms as are found in the Pelmatozoa.

The discussion of the relationships of the echinoderms in the 1949 edition of Parker and Haswell clearly indicates a recognition of the relationship of a stalked condition and a radiate organization. We cannot do better than to quote part of that passage:

"The presence of radial symmetry was once regarded as involving relationship [of the echinoderms] with the Coelenterata, which were grouped with the Echinodermata under the comprehensive class-designation *Radiata*. But on account of the presence of a bilateral symmetry underlying and partly concealed by the radial, we are led to the conclusion that whatever may have been the group of animals from which the Echinodermata were developed, there is every probability that it was a group with bilateral and not radial symmetry. The radial symmetry is evidently, as has already been pointed out, of secondary character; it is only assumed at a comparatively late period of development, and even in the adult condition it does not completely disguise an underlying bilateral arrangement of the parts. Accordingly, within the phylum itself, it is reasonable to regard those classes as the more ancient which have the radial symmetry less completely developed. Again, the free condition which characterizes all existing Echinoderms with the exception of a few Chrinoids is probably less primitive than the attached, since in other phyla the radial symmetry is co-ordinated with, and seems to be developed on account of, a fixed, usually stalked condition. Probably, then stalked Echinoderms were the progenitors of the existing free forms, and these were preceded by primitive free forms with pronounced bilateral symmetry. It appears to be most probable that this ancestral form possessed the most essential features of the *dipleurula* larva . . . ; i.e., that it was bilaterally symmetrical with a pre-oral lobe, simple alimentary canal with mouth on ventral surface and anus at posterior end; that it had a coelome, originally developed from the archenteron of the gastrula; and that it had a band of strong cilia running around the concave ventral surface. Such a dipleurula-like form became converted, it is supposed, into a fixed form, such as that represented by some of the extinct class of the Cystoidea. The fixation must be supposed to have become effected through the medium of the pre-oral lobe, and further changes must have involved the shifting of the mouth to about the middle of the free surface. From this primitive Cystoid, thus regarded as the most primitive of all known Echinoderms, the remaining classes, both fixed and free, have been derived." Gregory (1951) basically agrees with this statement and gives further comment on the interrelationships within the group as well as its relationships with other groups.

Contrariwise, this type of symmetry is not to be found in all-over patterns, which would seem clearly to be associated with its primary inability to cover a surface uniformly. On the other hand six-sided symmetry is to be abundantly found on the surfaces of such things as the test of cow-fish and the honeycomb. Architects found similar difficulty with the five-sided figure, as is indicated by Weyl (1952) who wrote, "The Arabs fumbled around much more with the number 5, but they were of course never able honestly to insert a central symmetry of 5 in their ornamental designs of double infinite rapport." The Pentagon Building in Washington stands as a separate complete unit for similar physical reasons.

A considerable effort was made to learn why the building was designed and erected in this unusual form. There was evidently no single powerful reason, either practical or sentimental, but rather the design apparently developed as a series of compromises, which is presented below as paraphrased architectural comment.

As is so often true in cases in which large undertakings of the magnitude of the Pentagon Building are concerned, it is difficult to state categorically that there was one specific reason for the pentagonal outline in preference to all others. Not the least, of course, was professional bent. There is considerable support for the view that any design that approaches a circle in outline has distinct advantages with respect to economy in distance and space. Obviously, the center of a circle is the nearest common point from which to reach any point on the circumference, and equally attractive is the proposition that a small ring within a larger ring provides the means of establishing at any point the shortest travel between the two rings. Thus, from an architect's view, a design approaching a circle is probably the most feasible means of achieving the maximum usable space, economy, and convenience, once it is decided to depart from the generally vertical layout so familiar in large cities.

The need for the Pentagon Building arose in time of national stress—a time when it would have been impractical to consider a vertical design requiring elevators and steel framing which a skyscraper design normally necessitates. Therefore, the fundamental decision was made that a low, sprawling type of structure would be the only feasible one. The site initially selected for the new building was bounded on two sides by streets that intersected at an obtuse angle, which, after a consideration of several alternative designs, seemed appropriate for a building that would have two prominent facades and main entrances, one on each of the intersecting streets. Problems of topography and layout, coupled with professional viewpoints and many other considerations that appear in deliberations leading to the design of major structures, finally resulted in a design for this particular site which was in effect an irregular pentagon. The site initially chosen adjoined Arlington National Cemetery. When objection was raised to the erection near this national shrine of a rather plain structure somewhat austere in exterior design, the appropriate authorities sought a new site. When the present site was selected, the design of the structure had progressed to the point where the authorities decided that the pentagonal plan should be adhered to. However, because the new site offered much more space than the site initially chosen, the initial design was modified from the irregular pentagon to the regular pentagon, which is the shape of the building as it now stands.

From the foregoing, it may be seen that it would be difficult to say that the eventual design of the Pentagon Building resulted from a single reason or decision pointed towards a specific end. Recollection maintains that the genesis of the design was primarily the obtuse angle caused by the intersection of two streets at the abandoned first-chosen site, and seems to be at least as much of a compromise as most organisms must make in their development.

Again, the coelenterates, although employing both four- and six-part symmetry, seemingly largely avoid that of five parts. It is to be noted that their design was no doubt fixed when they were sessile colonial organisms, the free-swimming medusa type doubtless coming as a later development. Actually, Parker and Haswell (1949) divide the Actinozoa into the Octocorallia in which the " . . . tentacles and mesenteries are always eight in number" and the Hexacorallia in which the " . . . tentacles and mesenteries are usually very numerous and are frequently arranged in multiples of five or six." Hyman (1940) writes as follows about the Actinaria (=Hexacorallia): "In typical hexamerous anemones, the number of pairs of septa in the various cycles is then: 6 (primaries), 12, 24, 48, etc. Other arrangements, however, often occur, especially octomerous and decamerous . . . types in which there are 8 (or 16) and 10 pairs of complete septa, respectively, and corresponding in the incomplete cycles. Thus the family Ilyanthidae, represented by *Haloclava* . . . is usually decamerous. Forms with five or seven pairs of complete septa also occur." While evidently pentamerous symmetry and its double are present in this group, it is far from dominant.

Naturally polyhedral forms are limited to forms that are polarized poorly, if at all. Such patterns are to be found most clearly displayed in certain Radiolaria. The oft-quoted Haeckelian figure, *Circorrhegma dodecahedra*, is a prime example shown by both Thompson (1942) and Weyl (1952). Of this figure Thompson writes, "If we may safely judge from Haeckel's figures the pentagonal dodecahedron of the radiolarian (*Circorhegma*) [*sic*] is perfectly regular, and we may rest assured, accordingly, that it is not brought about by the principles of space-partitioning similar to those which manifest themselves in the phenomenon of crystallization." Thompson goes on to treat at length the case of *Dorataspis* which appears to have a test built of hexagons and pentagons on impossible geometrical construction, unless curved boundaries are substituted for straight lines, a matter which in no way inhibits organic growth.

In discussing the meaning and significance of the use of mathematics in connection with regularities of plant form, Wardlaw (1952) wrote:

"The essential feature of a spiral phyllotactic system is that new leaf primordia, similarly placed in relation to the apical growing point and to primordia already present, are produced at similar successive intervals of time. A phyllotactic system or pattern of a more or less high degree of regularity results and this can be given mathematical expression.

"A point of general interest that emerges from a consideration of spiral structure in plants and animals is that these configurations, as in the shells of mollusks, bear little relation to the character of the organism by which they are produced. The mathematical analysis of the forms of shells, for example, gives no support to systematists who have used the different shapes of cephalopod shells for phylogenetic purposes. The same would be true of the use of phyllotactic systems in plants as a criterion of comparison in phylogenetic studies, unless there was also supporting evidence of a fundamental kind from other sources."

Thompson (1942), who is quoted by Wardlaw, has the following to say: "Again, we find the same forms, or forms which (save for external ornament) are mathematically identical, repeating themselves in all periods of the world's geological history: and we see them mixed up, one with another, irrespective of climate or local conditions, in the depths and on the shores of every sea. It is hard indeed (to my mind) to see in such a case as this where Natural Selection necessarily enters in, or to admit that it has any share whatsoever in the production of these varied conformations. Unless indeed we use the term Natural Selection in a sense so wide as to deprive it of any purely biological significance."

Wardlaw (1952), himself an experimental morphologist, very properly makes the following observation: "Investigators of phyllotaxis from a mathematical standpoint have paid insufficient attention to the relevant physical and physiological problems: those whose interest has centered on leaf formation have tended to neglect the positional, i.e. geometrical aspect. It seems desirable that the two aspects be examined together."

A brief but good history of the subject of phyllotaxis, together with a criticism of certain of Thompson's (1942) views, is given by Richards (1948). He favors a "field theory" rather than one based purely on the possibilities of geometrical packing.

An interesting approach to the reasons for the number of petals possessed by flowers can be made through the studies of Hertz (1931, 1933), Wolf (1933), and Autrum (1952). Leppik (1953), for instance, would refer the constancy of the number of petals of radiate flowers, which have few, to the ability of pollinating insects to discriminate between flowers on a basis of petal number. This ability and its limitations he considers as having been a factor in the evolution of flower design by selection. His experiments, in which insects were permitted the selection of a variety of flowers in regard to the number of petals, led him to state categorically, "The most favored number for bees is 5." He also wrote: "According to these experiments, bees are able to remember and distinguish the numbers 1, 2, 3, 4, 5, 6, 8, 10, and 12. It is remarkable that the numerical system of bees does not contain the 'magic' numbers 7, 9 and 13 but have double meanings for 3 and 5." This is most striking when considered in reference to table 1 above and the comments on it, which are based on purely structural data. It will be recalled that it was pointed out above that symmetry of an order higher than six is rare except for cases that are multiples of lower orders, e.g., 8, 10, 12, etc., not 7, 9, 11, 13, etc., a fact that is in exact agreement with what Leppik's bees were able to distinguish. Whether flowers evolved in accordance with the abilities and limitations of the insect nervous system, as Leppik suggests, or not, the present data cannot establish. That the same presences and absences of different degrees of symmetry appear in a review of organic objects as displayed in table 1 leads to the suspicion that something much more fundamental may be involved here than a floral evolutionary response to peculiarities of insect psychic life.

Finally it remains to consider the possible significance of this widespread distribution of five-partness, and to attempt to determine whether these varied and often unrelated organisms have "selected" five at random or whether there is an underlying biological or physical principle involved, which has guided such diverse things as dicotyledonous flowers, echinoderms, and tetrapod appendages to settle on that definite number of parts. Before this aspect of the problem is discussed, certain points and suggestions in the foregoing material should be consolidated. As is indicated in table 1, pentagonal order very definitely occurs in some groups and is as definitely absent from others. There is very little casual or incidental occurrence. That is, it appears as the basic pattern of flowers of dicotyledons, of echinoderms, of vertebrate body section, of the distal ends of tetrapod limbs, and of the oral armature of priapulids. Its occurrence elesewhere is not common but includes the following instances. The tarsi of half of the superfamilies of beetles have uniformly five segments, the other half showing various reductions in the number of segments. It is somewhat questionable whether such a linear series of five has any relationship to the present topic, which is primarily radial symmetry. The ancestrula of certain bryozoans is pentagonal, although all subsequent individuals are hexagonal. Except for a few coelenterates, discussed below, this list covers naturally occurring pentagonal symmetry and pentamerous clusters or series.

Coelenterates show great variation in the number of their radial divisions but most commonly have eight (Octocorallia) or six (Hexacorallia). The latter group shows much variation, including symmetry of 5, 7, and 8, and their multiples, 10, 12, 16, 24, 48, etc. It should not be surprising that a few reached five and 10 divisions, but they are actually a very small number in reference to the whole group, which is marked by a considerable symmetrical instability. Some forms change from one order of symmetry to another during ontogeny, as, for example, *Craspedicuspa* as it develops from the "*Microhydra*" stage. Finally, the flowers of monocotyledons are as devoted to a three-part design as are those of dicotyledons to five.

The point of the above oversimplified summary is simply that five-partness, where it appears, is held to with great rigidity, even when extensive evolutionary change has taken place. This does not seem to be the case to such a marked extent where other symmetries are concerned, as the coelenterates witness.

Although everyone recognizes, of course, that organisms are strictly limited by severe physical strictures at all times, little attempt has been made to understand how these strictures operate to produce the observed results. Obviously, they operate at all levels of organization, from the atomic to the gross. In the present paper the simple matter of why the pentagonal or five-part form has appeared so frequently is considered from its basic geometrical aspects. It seems that at this level of consideration the characteristics of the pentagon that make it unique among polygons have considerable bearing on the matter. At the molecular level of organization the basic asymmetry of the protean molecule may eventually be shown to influence greatly all manifestations of organic symmetry. It would seem that the next logical step would be to attempt to answer the perennial question as to whether or not the peculiarities of molecular organization are in fact reflected in the geometry of vastly larger aggregates of complex mixtures of various kinds of molecules. Until this question is satisfactorily resolved such studies as those discussed herein would seem to be blocked against substantial progress. It is essential to such investigations to understand whether geometrical patterns are determined by activity at the molecular level, in part at least, or are fully determined at higher levels.

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APPENDIX

NUMERICAL RELATIONSHIPS IN PENTAGONS AND DODECAHEDRA

In any pentagon with the radius taken as 1 the following numerical relationships hold:

Radius: $r = 1.0000$ = radius of circumscribed circle
Apothem: $a = 0.8090$ = radius of inscribed circle
Face: $f = 1.1756$
Diagonal: $d = 1.9021$
Central angle: $C = 72°$
Angle between adjacent faces: $F = 108°$
Values of circumscribed pentagon ($r = a_1$):

$$r_1 = 1.2361$$
$$a_1 = 1.0000 = r$$
$$f_1 = 1.4530$$

Values of inscribed pentagon ($r_2 = a$):

$$r_2 = 0.8090$$
$$a_2 = 0.6545$$
$$f_2 = 0.9511$$

To obtain corresponding values for any measurement of circumscribed pentagon, multiply by 1.2361, and for values of inscribed pentagon, divide by 1.2361.

Area of pentagons:

$$A = 5/4f^2 \cot 36° \times 1.721f^2$$
$$A = 4.7283$$

Relationships between parts:

$$r = 1.2361a = 0.8506f$$
$$a = 0.8090r = 0.6881f$$
$$f = 1.1756r = 1.4530a$$

Stellate values follow:

Star extended from a pentagon of radius: $r = 1.000$
Side of star: $s = 1.9021$ = diagonal of inscribed pentagon
Altitude of star: $b = 1.8090$
Face of star ($f + 2s$): $c = 4.9798$
Circumscribed circle ($a + b$): $r_3 = 2.6181$
Apothem of pentagon of r_3: $a_3 = 2.1180$
Face of pentagon of radius r_3: $f_3 = 3.0778$
Star inscribed in a pentagon of radius: $r = 1.000$
Side of star: $s_1 = 0.7265$
Altitude of star ($r - a_4$): $b_1 = 0.6899$
Radius of circle circumscribed about pentagon: $r_4 = 0.3833$
Apothem of pentagon of r_4: $a_4 = 0.3010$
Face of pentagon of r_4: $f_4 = 0.4506$
Side of star of r_4: $s_2 = 0.2775$

To obtain corresponding values for any measurement of circumscribed stellate pentagon, multiply by 2.6181, and for values of inscribed stellate pentagon, divide by 2.6181.

Area of stellate pentagon of radius: 1.0000
Point of star = 1.8094
Five points = 9.0469
Center pentagon = 4.7283
Total area = 13.7752

Relationships of triangle forming point of star, which is isosceles with angles of 36°, 72°, and 72°.

Bisection of either of the basal angles produces a similar triangle and its gnomon.

In such a series of triangles any side of the next larger is 1.6180 times greater. Also, the sides in all are 1.6180 times the base.

Relationship between parts where $r = 1.0000$

$$r = 1.2361a = 0.8500f = 1.4492b = 0.5253c$$
$$a = 0.8090r = 0.6882f = 1.1728b = 0.4250c$$
$$f = 1.1756r = 1.5433a = 1.7040b = 0.6176c$$
$$b = 0.6899r = 0.8528a = 0.5868f = 0.3624c$$
$$c = 1.9036r = 2.3530a = 1.6175f = 2.7592b$$

Polyhedral data:

Of the five platonic bodies, the first, third, and fifth have faces which are equilateral triangles; four, eight, and 20, respectively. The other two, the hexahedron (cube) with six squares for faces and the dodecahedron with 12 pentagons for faces, are the only regular polyhedrons possible.

The centers of the faces of a dodecahedron are the vertexes of an inscribed icosahedron, while conversely the centers of the faces of an icosahedron are the vertexes of an inscribed dodecahedron.

The sum of the face angles of any corner is $3 \times 108° = 324°$, that is, 41° less than a flat surface.

The distance between any two opposite and parallel faces = 2.3847 = diameter of an inscribed sphere. $A = 1.1924$.

The distance between any two opposite trihedral angles = diameter of a circumscribed sphere = 3.2848. $R = 1.6424$.

A cross section passing through the center of adjacent pentagons also passes through two opposite edges and bisecting the four intervening pentagons is an irregular hexagon. All interior angles = 120°, the two sides represented by edges $= 1.1756 = f$ of pentagon, the four sides each represented by $a + r = 1.8090 = 1.5388f$.

Area: $A = 6\frac{1}{4}f^2 \cot 36° = 8.605f^2 = 56.7396$

Volume: $V = 5f^3 \cot {}^2 36° \sqrt{2/4 \sin^2 36° - 1} = 7.631f^2 = 10.5463$

Four colors are necessary to paint the faces of a dodecahedron so that no two of the same color will be adjacent. This can be done in two ways, one the mirror image of the other.

Stellate dodecahedron:

Can be made up of 12 stellate polygons intersecting, or can be considered as 12 five-sided pyramids, one on each face of a dodecahedron with the face as its base.

The altitude of this pentagonal pyramid:

$$L = \sqrt{s^2 - r^2} = 3.1057$$

Altitude: $L = 3.1057r$
Area of sides of pyramid: $5 \times 1.8094 = 9.0469$
Area of stellate dodecahedron: $12 \times 9.0269 = 108.5628$
Volume of one pyramid: $V = 4.8508$
Volume of 12 pyramids: $V = 28.2092$
Volume of body: $V = 10.5463$
Volume of stellate dodecahedron: $V = 58.7555$

A cross section similar to that shown in figure 7 for the dodecahedron is similar to it but with three triangles equilateral "attached" thereto, the sections of four points of the star which are bisected.