AN ANALYSIS OF THE GEOMETRY OF SYMMETRY WITH ESPECIAL REFERENCE TO THE SQUAMATION OF FISHES

C. M. BREDER, JR.

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INTRODUCTION

SINCE ANY SCIENTIFIC DISCUSSION must be made with some reference to the morphology of the units under consideration, it is only natural that a wide variety of terms should have arisen in the various disciplines to express ideas concerning the systematic appearance of various regularities of form or their lack. These are apparently frequently satisfactory for the purpose for which designed and such have stood for long periods of usage. The terminology employed by crystallographers, for example, has long been relatively stable. Others are clearly not so satisfactory to their users, as evidenced by the frequent substitution of new systems of terminology. Morphological zoologists not infrequently devise new systems of usage, usually accompanied by a host of newly coined words to replace those of the older systems. This condition is perhaps unimportant in itself, except for matters of convenience in expression which may or may not be useful as it becomes necessary to discuss new concepts.

Since symmetry is basically concerned with the reduplication of parts arranged in definite geometrical relationship to each other, various systems of the current terminology might be supposed to show interchangeable relationships. However, without going into details at this point, a little consideration makes it clear that the terms in use, both in biology and in other fields, could be readily applied only to the special cases for which designed. All have been built up from the observed forms of the items under consideration and are very closely linked to the particular forms on which they are based. None possesses an abstract geometrical background, except that of the crystallographers, but because of the particular nature of crystal formation, even this is too specialized and limited for general application by extension. Since such may have utility, an attempt has been made to consider symmetry from a purely abstract, geometrical standpoint. In so doing it became necessary to devise an entirely new set of concepts. These concepts differ from others in that they are not in the least concerned with actual animals, plants, or minerals, or anything else of an objective sort; it might be considered a Euclidean approach to symmetry. As the series of propositions were developed, it became evident that they enabled one to think of various forms in a different light and to synthesize a formalized arrangement of parts into one unified concept. The present contribution is, then, an attempt to unify organizational concepts in diverse fields, offer a system of classification for so doing, indicate its utility, and point out the value of a theoretical approach to a field that has thus far been held by various purely pragmatic sets of terms. Illustrative examples have been purposely drawn from a variety of fields, many not biological, to emphasize the general application of the propositions. A development of geometrical aspects of the squamation of fishes has been used as an illustration of the nature of the fields into which such considerations may lead.

As discrete objects may take any conceivable form expressed in three dimensions, the following groupings have generally been employed with reference to symmetry. Such objects have been generally classified either as irregular (asymmetrical) or as symmetrical, that is, with their certain parts repeated and arranged so that they are similar about some plane, in the case of what is known as bilateral symmetry, or about a series of planes radiating from a common center with equal angles between them, in the case of what is known as radial symmetry. Patterns on a plane surface have been classified in a similar manner, but, as they are two dimensional, they are referred to axes instead of planes of symmetry.

Exactly what is meant by symmetry is not always precisely clear. Since our present concern is with the disposition of like parts of a whole, it quickly appears that the common dictionary definitions lead into a morass of logical difficulties, as is usual with definitions stemming from lay usage. We cannot, nor need we, attempt to give exact definitions at this point. The reasons for this will appear as the argument and development of the system progress.

In the effort to work out the many conceptual details essential to consider in con-

nection with the present study, it became necessary to call upon many persons with various specialized knowledge. Chief among these is Dr. Richard T. Cox, whose extensive knowledge of physics I found invaluable—especially in connection with the section of "Polarity"—who pointed out many things that I surely would have otherwise missed. Dr. W. K. Gregory suggested many points in connection with the biological aspects of the study. Dr. A. E. Parr gave helpful suggestions regarding the distribution of elements in surface patterns. Mr. C. M. Bogert pointed out certain features of reptilian squamation. Capt. J. W. Atz was kind enough to read and criticize the manuscript. Mr. Bernard Nathanson assisted in some of the mathematical calculations.

THE GEOMETRY OF SYMMETRY

EXAMPLES OF SYMMETRY WITH ANALYSIS OF FORM

BEFORE A SYSTEM OF NOMENCLATURE based on abstract physical arrangement by which we may freely discuss objects in relation to this feature of their morphology, is presented, it may be useful first to consider the gross differences between actual physical entities that pass as possessing some degree of symmetry, as well as those customarily excluded from such denomination. Figure 1 presents a number of examples of so-called symmetrical objects drawn from a variety of fields. The maple leaf (fig. 1A) normally passes as a bilaterally symmetrical object. One side is clearly the replica of the other in reverse. That is to say, if a mirror were placed vertically to the page along the axis, the mirror image would reproduce the other half. This indeed would apply to any case of bilateral symmetry considering the object as a plane surface. A rabbit, for example, because of its rounded surfaces shows its bilaterality more readily in a three-dimensional manner. It is evident that here, too, one side is the mirror image of the other (fig. 1B). There is, of course, no fundamental difference between the organizational form of these two examples in regard to their symmetry, the first merely being spread out in a thin sheet, or, in other words, the maple leaf has very little extension in one of the three dimensions. It, too, could be treated as in figure 1B, while the rabbit could be treated as in figure 1A by considering a front view of it as a projection on a plane.

If now we take the outline of a starfish, as in figure 1C, it will be seen that an equivalent mirror image may be obtained about any of the five axes indicated. Thus, a radially symmetrical figure is bilaterally symmetrical for as many times as it has symmetrical parts. If we now take a four-armed "starfish," as in figure 1D, we find that similar axes drawn through each point produce only half as many axes of bilaterality as there are points —two axes and four points. This naturally follows since the points are opposite one another in a straight line. However, we may draw another set of two axes between the low parts of the star, as is indicated by dotted lines, and obtain two more axes of bilateral symmetry. These two sets of axes added together make four axes, which equals the number of similar parts of the construction. There is, however, this difference: figures composed of an odd number of parts have the same number of identical axes of bilaterality, but in figures composed of an even number of parts one-half of the number of axes are of a different order than the other half. Expressed another way, along any axis of the odd-numbered figure the parts on either side of the center are unlike, but in the even-numbered figure they are identical. Even in such a simple figure as a square, which is usually not thought of in connection with such discussions, the same sorts of axes may be drawn, as is indicated in figure 1E. This is naturally true of any equilateral figure. A triangle, as in figure 1F, subscribes to the principles set forth for the five-armed starfish, as it necessarily must do.

The solid crystals of the crystallographers usually present complicated systems of symmetry. For example, an idealized crystal of garnet presents three patterns of symmetry, one for each dimension of space. Figure 1G shows a perspective view and the three projections of such a crystal with three, four, and two axes. The last, of two axes, is similar to a two-armed starfish or a uniform lanceolate leaf, as in figure 1H. Thus the crystallographers are able to refer their particular systems of symmetry separately to each of the three spatial dimensions. They recognize 32 theoretically possible types. This need not delay us here, but will appear again further on in other connections. We may go on directly to another kind of solid symmetry, of which one sees most in treatises on geometry. This kind of solid symmetry does not consider the three-dimensional axes separately but each in reference to the others by virtue of central polyhedral angles. This kind of symmetry is limited by the number of regular polyhedrons possible, of which there are only five. Thus such symmetry must be basically

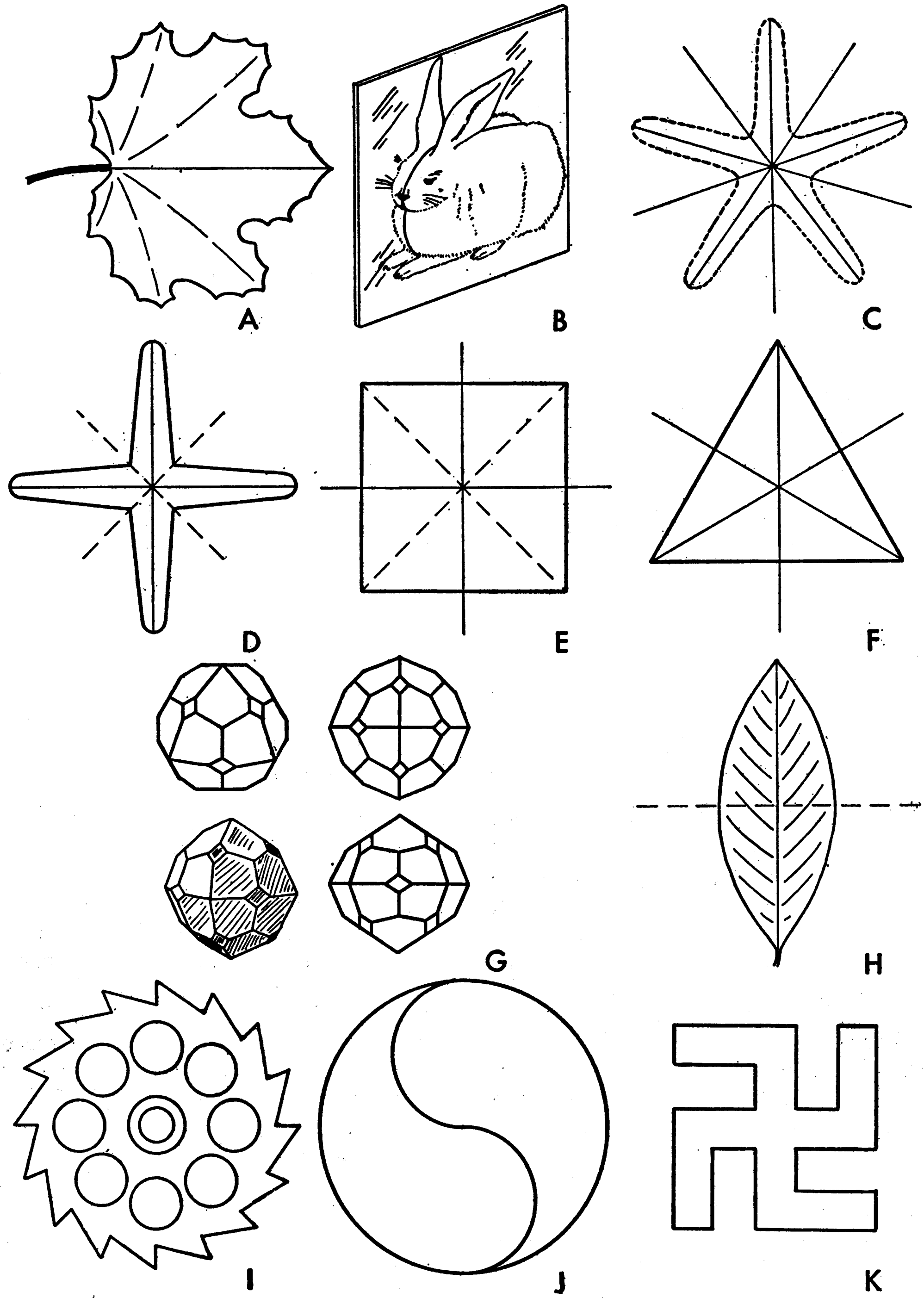


FIG. 1. Examples of symmetrical objects. A. Maple leaf, as a projection on a plane showing first-degree reflective symmetry. B. Rabbit, in perspective showing a three-dimensional object with first-degree reflective symmetry. C. Starfish, as a projection showing fifth-degree reflective symmetry. D. A four-armed "starfish" showing fourth-degree reflective symmetry. E. A geometrical square showing fourth-degree reflective symmetry, identical with that of D. F. A geometrical equilateral triangle showing third-degree reflective symmetry. G. A crystal of garnet in perspective (lower left) and in three projections, showing third-degree (upper left), fourth-degree (upper right), and second-degree (lower right) reflective symmetry, together making up a type of solid compound symmetry. (Modified after Whitlock, 1928.) H. A lanceolate leaf, showing its close approach to second-degree reflective symmetry. I. A ratchet wheel, an illustration from mechanics showing sixteenth-degree of congruent symmetry. J. An ancient oriental design showing second-degree congruent symmetry. K. A swastika, showing fourth-degree congruent symmetry.

designed to conform to the angular requirements of the tetrahedron, hexahedron, octahedron, dodecahedron, and icosahedron. On the other hand, the three-way radial symmetry of the crystallographers is limited in no such manner, but both systems have an upper limit and infinitely surfaced design—a perfect sphere. Likewise, as now should be evident, plane designs culminate in a perfect circle.

To make matters more complicated, there are also designs other than any so far considered which pass in common parlance as symmetrical. These may be included or excluded, depending on one's definitions, but in any case they represent a different but consistent and regular order of arrangement. Figure 1I shows a ratchet wheel, 1J an old oriental mystic design, and 1K a type of swastika. All have similarly arranged parts, but no part is the mirror image of any other. Axes drawn at any place divide the figures into equal halves. These parts are, moreover, truly congruent. If one side is traced and slid over the other and rotated through 180°, the match is perfect.

The differences between the mirror image and the non-mirror image type of repetition of parts may be expressed by thinking of the first as formed by folding one-half up through the third dimension through 180° and the second as formed by rotating through 180° in the plane of the paper. One is generated with reference to the third dimension and the other by reference to the second. Because of geometrical limitations, the use of less than the two dimensions is inconceivable, while more than three requires reference to the fourth dimension. This dimension will be referred to in the Einsteinian sense at another point, but here symmetry is being considered in the older, Euclidean sense. It would thus appear that these two orders of symmetry are all that are possible for strictly geometrical reasons. Also, while the first type includes the possibility of being generated by the method necessary to the second, the reverse is not true. Since the latter have a bias to one side, they may be of two kinds, either right- or left-handed, depending on which surface is uppermost. Expressed another way, as was done by Curie (1884a, 1884b, 1894) and Jaeger (1917), the mirror image of a whole figure will in the first case give an identical object and in the second will give a reversed one—a pair of right- and left-handed objects. This latter is, of course, true of any asymmetrical object, such as a pair of hands. Jaeger (1917) calls this symmetry by congruence "first order symmetry" and reflective symmetry "second order symmetry," basing the terminology on the fact that "reflective symmetry" is also

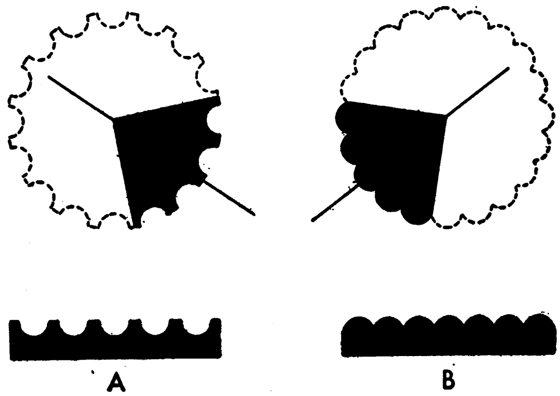


FIG. 2. Ornamentation formerly much used by furniture makers. A. Fluting of sixteenth-degree reflective symmetry frequently used as a fragment of a quarter circle as a fillet and, unrolled, to cover flat surfaces. B. Reeding of twentieth-degree reflective symmetry treated in identical fashion.

"congruent symmetry" but not vice versa. For the present non-mathematical treatment other terms have been used, as is subsequently discussed.

Our definitions having been extended to cover regular arrangements as either mirrored images or congruent parts on either side of an axis or plane, the bars are at once down to other varieties of the duplication of parts. It has been mentioned above that for geometrical reasons there can be only two basic types of symmetrical arrangement; the rest may be most conveniently considered as distortions or modifications of these within the framework already erected.

If, for example, we generate a symmetrical design about a point by the repetition of elements, there is no geometrical reason why we cannot draw that point out into a line. So doing we may have fluting or reeding, as in figure 2, obviously derived from circular designs. This immediately calls to mind the repetitive metamerism of zoologists. It is also similar to the polyisomerism of Gregory

(1934, 1935a, 1935b), and if distorted along the line it is his anisomerism. In such distortions of linear series the axis may not be a straight line, or various influences not within this axis may be at the root of the distortion.

If we permit our initial point to be drawn out into a line, there is no reason from a geometrical standpoint why that line cannot be also moved sidewise to form a surface. Then immediately we obtain an all-over design such as a honeycomb or scales on a fish or a checker board.

Having gone that far, if we move our surface at some angle so as to generate a solid, we then have a three-dimensional entity that shows pattern throughout. One thinks at once of thick tissues with cuboid or polyhedral cells, a pailful of shot or crystal lattices.

It will be noted that in the latter part of this discussion no specific mention has been made of the symmetry of congruence. The details of this will be reserved until later, but it may be pointed out here that it is much more limited in application than symmetry of reflection, evidently because of its basic two-dimensional genesis.

Many students have discussed these relationships in various ways and frequently with considerable mathematical analysis. Perhaps the closest approach to the present attitude towards concepts of symmetry, although with a vastly different treatment, is that of Jaeger (1917). His careful analysis of the various systems of symmetry should be consulted in reference to the many special cases that actually exist in nature or are possible as geometric constructions. He did not, however, attempt to reduce his analysis to a simple system of classification as is here undertaken.

Weyl (1938) in a study of the general aspects of symmetry has examined the nature of surface patterns in considerable detail. Although his approach to the matter is vastly different, his study is evidently the only treatment of this subject covering ground similar to that herein discussed.

A GENERAL NOMENCLATURE OF SYMMETRY

With reference to the preceding introductory parts, we may now frame a series of definitions concerning the differentiation of concepts of symmetry. Following the geometricians, we may best consider plane and solid symmetry separately, beginning with the simpler two-dimensional symmetry of pattern or projection.

It will be noted that the definitions used here are not in complete accordance with dictionary definitions. Possibly a whole series of new words should be created to cover the concepts. For present preliminary purposes, however, an extension of the terms is deemed adequate. It is not implied that these definitions are final or in the best possible usage, being given purely as a guide to a better understanding of the concepts set forth herein.

SYMMETRY: The systematic reduplication of units with reference to a geometrical boundary

- PLANE SYMMETRY: That division of symmetry which treats of the systematic reduplication of plane figures or projections with regard to a point or line in the plane of the figures

REFLECTIVE SYMMETRY: That division of symmetry which shows one part the reverse of the other, as in a mirror image

- AXIS OF REFLECTION: That line in reflective symmetry which divides the figure into two equal but reversed halves
- CIRCULAR SYMMETRY: (Plane symmetry) If there is more than one axis of reflection, all such necessarily intersect at a point which is the geometrical center of the figure
- DEGREE OF SYMMETRY: A measure of the kind of symmetry of a figure, in which the degree number is equal to the number of axes of reflection
  - ZERO-DEGREE SYMMETRY: Said of a figure through which no axis of reflection may be passed. (In ordinary usage this is considered as asymmetry)
  - FIRST-DEGREE SYMMETRY: Said of a figure through which a single axis of reflection may be passed. (In ordinary usage this is considered as bilateral symmetry)
  - SECOND-DEGREE SYMMETRY: Said of a figure through which two axes of reflection may be passed, at right angles

to each other. (In ordinary usage this is considered as a double bilateral symmetry or anterio-posterior symmetry)

THIRD-DEGREE SYMMETRY: Said of a figure through which three axes of reflection may be passed, each separated by 60° from the next adjacent one, and all intersecting at the geometrical center. (In ordinary usage this is considered as radial symmetry of the simplest possible kind)

FOURTH-DEGREE SYMMETRY: Said of a figure through which four axes of reflection may be passed, each separated by 45° from the next adjacent one and all intersecting at the geometrical center

ANY DEGREE OF SYMMETRY: Said of a figure through which one or more axes of reflection may be passed, each at an equal angular distance from the next and all intersecting at the geometrical center. The number of units names the number of the degree of symmetry, and this number divided into 360° gives the angular distance between the axes

N DEGREES OF SYMMETRY: Said of a figure through which N axes of reflection may be passed. When $N=\infty$, the figure is always a circle

ODD DEGREES OF SYMMETRY: Each axis of reflection in a figure of an odd number of degrees passes through different parts of the figure on either side of the geometrical center

EVEN DEGREES OF SYMMETRY: Each axis of reflection in a figure of an even number of degrees passes through identical parts of the figure on either side of the geometrical center, giving half of the axes a different character than the other half in regard to the parts of the figure they cut

LINEAR SYMMETRY: Said of a linear reduplication of reflective symmetrical parts that could be generated by drawing the point of intersection of the axes of reflection of circular symmetry of any degree as a line

SURFACE SYMMETRY: Said of a surface reduplication of reflective symmetrical parts that could be generated by moving a line of linear symmetry at some angle to itself

DISTORTIONS OF SYMMETRY: Since lines and planes are subject to distortion, systems of symmetry based on them may be distorted correspondingly into any deformation possible. In addition to these deformations of the substrate of symmetry, external influences acting directly on the units of symmetry make for other kinds of deformatory modifications

FRAGMENTARY SYMMETRY: Incomplete designs may show a different degree of symmetry from that of the completed figure. Since reduplication is possible in many ways, virtually any figure may be considered as a fragment of some larger and more inclusive construction

CONGRUENT SYMMETRY: That division of symmetry which shows one part as congruent to the other, but not reversed as in a mirror image

AXIS OF CONGRUENCE: A line in congruent symmetry which divides the figure into two equal, but not reversed, halves

CIRCULAR SYMMETRY: Same as under reflective symmetry, substituting axis of congruence for axis of reflection

DEGREE OF SYMMETRY: A measure of the kind of symmetry of a figure in which the degree number is equal to the number of mutually congruent parts

ZERO-DEGREE SYMMETRY: Said of a figure in which no elements of congruence may be found

FIRST-DEGREE SYMMETRY: True symmetry of congruence can exist only in figures of greater than unity because of the basic lateral bias of the figures that go to make them up

SECOND-DEGREE SYMMETRY: Said of a figure composed of two congruent parts

THIRD-DEGREE SYMMETRY: Said of a figure of three elements, each congruent with one another and mutually separated by 60° from one another

FOURTH-DEGREE SYMMETRY: Said of a figure of four elements, each congruent with one another and mutually separated by 45° from one another

ANY DEGREE OF SYMMETRY: Said of a figure through which axes of congruences may be passed and in which each element is separated from the next at an equal angular distance. Their number divided into 360° gives the angular distance between the elements

N DEGREES OF SYMMETRY: Said of a figure with N elements of congruence. This is always a circle, as in reflective symmetry

ODD DEGREES OF SYMMETRY: Since each element in congruence of odd degree is opposite different parts of the figure on either side of the geometrical center, as in reflective symmetry, it follows that no axes of congruence can be drawn

EVEN DEGREES OF SYMMETRY: Each axis of congruence in figures of even degree divides the entire figure into two congruent halves, the axis cutting similar but opposite elements of the figure on either side of the geometrical center. An infinite number can be drawn

LINEAR SYMMETRY: Same as under reflective symmetry, substituting congruent for reflective and congruence for reflection

SURFACE SYMMETRY: Same as under reflective symmetry, substituting congruent for reflective

DISTORTIONS OF SYMMETRY: Same as under reflective symmetry

FRAGMENTARY SYMMETRY: Same as under reflective symmetry

SOLID SYMMETRY: That division of symmetry which treats of the systematic reduplication of solids with regard to a plane or planes in three-dimensional space

REFLECTIVE SYMMETRY: Same as under plane symmetry

PLANE OF REFLECTION: That plane in reflective symmetry which divides the object into two equal but reversed halves

SPHERICAL SYMMETRY: That form of solid symmetry that treats of objects with regard to the duplication of parts based on equal central polyhedral angles

DEGREE OF SYMMETRY: A measure of the kind of symmetry of a solid with mutual reference to the three spatial dimensions

ZERO-DEGREE SYMMETRY: Said of a form through which no plane of reflection may be passed. (In ordinary usage this is considered as asymmetry)

FOURTH-DEGREE SYMMETRY: Said of a form geometrically based on the tetrahedron. (Since the solids in spherical symmetry are based on the regular polyhedrons, of which there are five, such symmetry is likewise equally limited. See under compound symmetry)

SIXTH-DEGREE SYMMETRY: Similar to the above but based on the hexahedron or cube

EIGHTH-DEGREE SYMMETRY: Similar to the above but based on the octahedron

TWELFTH-DEGREE SYMMETRY: Similar to the above but based on the dodecahedron

TWENTIETH-DEGREE SYMMETRY: Similar to the above but based on the icosahedron

N DEGREES OF SYMMETRY: Said of a form through which *N* planes of symmetry may be passed. This is always a sphere

COMPOUND SYMMETRY: Said of solids that show symmetry on more than one of the several planes of projection possible. Each may be treated as a projection on a surface at right angles to the plane or planes of symmetry forming an axis of symmetry. The propositions under plane symmetry then apply to them each individually. (This type of symmetry is regularly found in crystals)

CUBICAL SYMMETRY: Said of a solid reduplication of units that could be generated by moving a plane of surface symmetry at some angle to itself. See under linear and surface symmetry in plane symmetry

DISTORTIONS OF SYMMETRY: Since solids are subject to distortions, it follows that systems of symmetry based on them are subject to the same influences. See under this head in plane symmetry

FRAGMENTARY SYMMETRY: Same as under plane symmetry, substituting form for figure

CONGRUENT SYMMETRY: Same as under plane symmetry

PLANE OF CONGRUENCE: That plane in congruent symmetry that divides an object into two equal but not reversed halves

SPHERICAL SYMMETRY: Constructions impossible in three dimensions because of mutual interference

COMPOUND SYMMETRY: Same as above

CUBICAL SYMMETRY: Same as under solid reflective symmetry

DISTORTIONS OF SYMMETRY: Same as under solid reflective symmetry

FRAGMENTARY SYMMETRY: Same as under solid reflective symmetry

A SYNTHESIS OF THE ABSTRACT CONCEPTS OF SYMMETRY

The formal definitions of the preceding section are listed in table 1 together with their equivalents in other usages. They become less formidable and attain some measure of utility as conceptional tools if we consider the geometrical basis of symmetry synthetically, in which each configuration is looked upon as a figure of generation.

For purposes of simplicity we may start with a figure enclosed by the fewest possible number of straight lines. This, of course, is a triangle. Such figures are classified according to the relative magnitudes of their angles or of their sides as scalene, isosceles, and equilateral. The latter two are already symmetrical figures, but the first is not, all three sides being of unequal length. Although not usually so referred to, all right triangles but one are scalene triangles in which one angle equals 90°. The exception is an isosceles triangle with 90° between its equal legs. Both isosceles and equilateral triangles may also

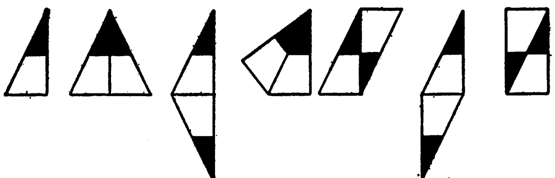
TABLE 1

SYSTEMATIC CLASSIFICATION OF FORM IN REFERENCE TO SYMMETRY

Nomenclature Here Adopted	Current Usage in Various Disciplines
Symmetry	Symmetry (in part)
Plane symmetry	Symmetry (in part)
Reflective symmetry	Symmetry (in part), second-order symmetry
Circular symmetry 0°	Asymmetry
Circular symmetry 1°	Bilateral symmetry
Circular symmetry 2 to N°	Radial symmetry (in part)
Linear symmetry	Isomerism, segmentation, etc.
Surface symmetry	Pattern
Congruent symmetry	First-order symmetry
Circular symmetry 0°	Asymmetry
Circular symmetry 1°	Bilateral symmetry, asymmetry
Circular symmetry 2 to N°	Radial symmetry (in part)
Linear symmetry	Isomerism, segmentation, etc.
Surface symmetry	Pattern
Solid symmetry	Symmetry (in part)
Reflective symmetry	Symmetry (in part), second-order symmetry
Spherical symmetry 0°	Asymmetry
Spherical symmetry 4°	Radial symmetry, tetrahedral
Spherical symmetry 6°	Radial symmetry, hexahedral
Spherical symmetry 8°	Radial symmetry, octahedral
Spherical symmetry 12°	Radial symmetry, dodecahedral
Spherical symmetry 20°	Radial symmetry, icosahedral
Spherical symmetry N°	Sphere
Compound symmetry	Crystallographers' terms
Linear symmetry	Isomerism, segmentation, etc.
Cubical symmetry	Crystal lattices, etc.
ongruent symmetry	First-order symmetry
Spherical symmetry 0°	Asymmetry
Spherical symmetry N°	No construction
Spherical symmetry N°	Sphere
Compound symmetry	No construction
Linear symmetry	No construction
Cubical symmetry	No construction
Special cases	
Distortions of symmetry	Anisomerism
Fragmentary symmetry	Isomerism (in part)

be considered as made up of two right-angled triangles, one on either side of their altitude between equal sides.

If we take a right triangle in which one leg is equal to one-half the other, we clearly have a figure with no symmetry, as in figure 3A. This particular triangle is taken as a starting point merely for purposes of convenience. It will be clear that if we construct on any of its three sides its duplicate, mirror fashion, we will obtain three symmetrical figures (fig. 3B, C, and D). Two will be triangles by virtue of the right angle in the original, and the



A B C D E F G

FIG. 3. Genesis of symmetry from basically asymmetrical elements. The upper portion of each element has been darkened as an aid to identifying its changes in position. This darkening necessarily partakes of the symmetrical nature of the transformations. A. A right triangle with one leg twice the other. Symmetry of zero degree. B. Figure A reflected about its long leg. Reflective symmetry of the first degree. C. Figure A reflected about its short leg. Reflective symmetry of the first degree. D. Figure A reflected about its hypotenuse. Reflective symmetry of the first degree. E. Figure A repeated about its long leg. Congruent symmetry of the first degree. F. Figure A repeated about its short leg. Congruent symmetry of the first degree. G. Figure A repeated about its hypotenuse. Congruent symmetry of the first degree.

third, built on the hypotenuse, a trapezium. It need not confuse us to realize that such a mirror image, including the totality of any figure or object, produces symmetry of the first degree.

It will also be clear that if, instead of turning over a replica of the original right triangle, we place an exact duplicate, with regard to right and left, on any of its sides we may obtain three other figures (fig. 3E, F, and G). These are clearly not symmetrical in the preceding sense nor can any axis of reflective symmetry be passed through them. They nevertheless present an orderly arrangement of parts and what is here called congruent symmetry.

Referring now to figure 4, we may readily see how a reduplication of parts around a point may produce any degree of symmetry desired. Each addition enlarges the area so that finally a circle of infinite diameter would be reached. Except for the "infinitely large" the figures are drawn to scale.

Although he went into no such detail, Whitlock (1928) clearly recognized the basic differences between what we here call reflective symmetry and congruent symmetry. He went so far as to draw rather complex figures of second-, third-, fourth- and fifth-degree symmetry of both and recognized the impossibility of passing axes of reflective symmetry through the latter. If he had carried the matter further he would have very likely arrived at the present concepts. Jaeger (1917) with a different attitude discussed at length many of such complications of crystal form. Frey (1925) published an interesting table showing both reflective and congruent symmetry up to that of the fifth degree as expressed in flowers, for each of which he used appropriate terms. In certain respects his treatment is not unlike that of figure 4, although not carried so far.

If the units, instead of being reduplicated about a point, are reduplicated along a line, or, expressed another way, if the figures are "unrolled," we have linear reflective or congruent symmetry. As this becomes an open series, it should be evident that a line of infinite length would be the geometrical end point.

In a strictly analogous manner a transverse reduplication of such a line produces a surface design, checkerboard fashion, the geometrical end point being a surface of infinite area.

When we reach into the third dimension, affairs seem to become more complicated, but only in the sense of the geometrician. If the figures in figure 3 are thought of as the ends of prisms, or pyramids, their symmetry is retained throughout their length. Symmetry with regard to two dimensions is shown at one end since they are drawn two dimensionally. The third dimension with its axis of symmetry parallel to the plane of the

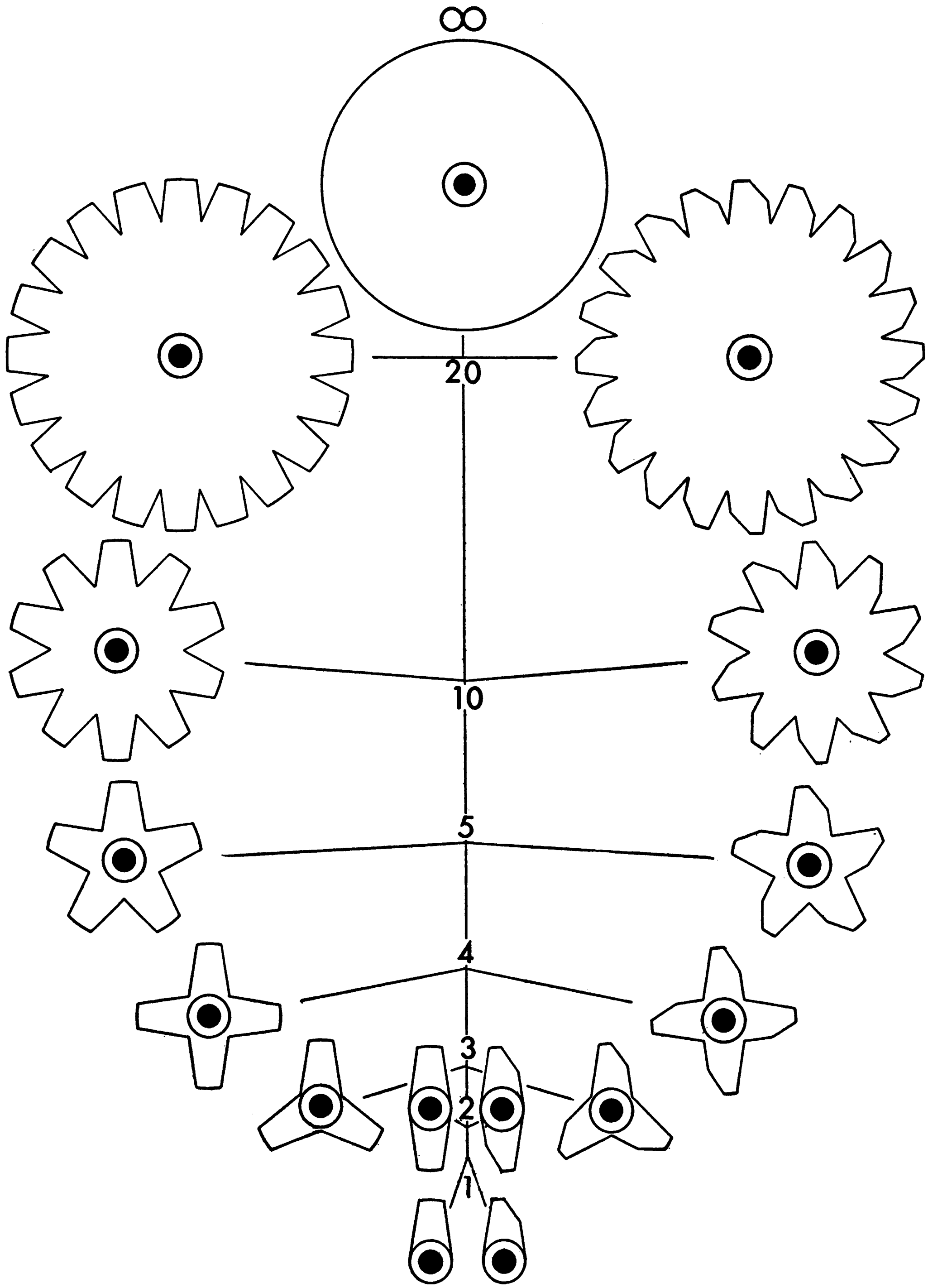


FIG. 4. Diagram illustrating the relationships of various degrees of reflective and congruent symmetry. Drawn to scale except the circle at the top which should be infinitely large. See text for explanation.

paper may show symmetry or not. If, in these figures, the solids based on them are pyramids, the figures show symmetry of the first degree in side view. If, on the other hand, they are taken to represent the ends of prisms with parallel, right-angled ends, and viewed sidewise, the solid is equally divisible by a plane and shows symmetry of the second degree in such a view. When this obtains we have compound symmetry, which in the case of crystals becomes exceedingly complicated but there are no new elements involved. This is actually plane symmetry expressing itself in each of three mutually right-angled planes which represent the three dimensions and in which some element on each plane, also represented in one of the other planes, acts mutually to interlock the figure.

A true reflective symmetry of solids, which we have here called spherical symmetry, is limited to each of the five regular polyhedrons possible, and congruent symmetry is not possible because its deflected bias makes its limited interrelations collapse. This should be evident from the foregoing. On the faces of any of the five regular polyhedrons, reflectively symmetrical designs or pyramids may be constructed involving designs of great complexity. The nature of some of these and their infinite possibilities are discussed by Lesovre (1946).

A solid generated by reduplicating a surface symmetry produces a massive effect and is actually more common in a state of nature than might at first be supposed. Its relationship to the rest should be evident.

The distortions to which all these forms may be subject are hardly within the geometrical limits of this paper but will be taken up in the biological application, including that very evident natural phenomenon, spiraling.

Fragmentary portions of symmetrical designs are abundant in nature and in artifacts. If, for example, we take the so-called sunburst of certain period furniture we have a design of first-degree symmetry. Obviously if it were carried around a full circle it would, in this case, be one of sixteenth degree. (See fig. 5.) The Japanese flag is such a figure of eighth degree, except as the rectangular form of the flag limits it to the second degree. Although the whole figure of our sunburst is second degree, clearly each element is reflectively symmetrical with each of the others. Considering other items from the same source, prior to 1775 fluting was a popular decoration for furniture, such as grandfather clocks,

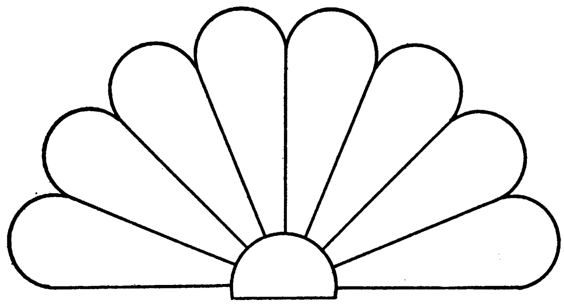


FIG. 5. A sunburst as used by furniture makers. This, a fragment of sixteenth-degree symmetry, is bilateral as a whole, while each element is reflectively symmetrical in the first degree with each of its fellows.

etc., and was subject to both fragmentation and distortion. On a flat surface it became linear symmetry and on columns circular, fragmented commonly into half and quarter circles. After 1775, it gave way to reeding, which then went through similar fragmentations. (See fig. 2.) From this we derive the corollary that any fragmentation of a figure in circular symmetry, with due regard for the axes of reflection, produces a figure that as an entity possesses only first-degree symmetry regardless of the size of the fragment or the original degree of symmetry shown by the entire figure.

ON THE NATURE OF SURFACE PATTERNS

Since the crossing of series of parallel lines delimits an all-over pattern of quadrilaterals, it is useful to consider first the consequences of such a meshwork of lattices as a matter of plane geometry. If two such series of parallel lines be mutually equidistant so as to intersect at any angle, the areas marked off by them form a series of equilaterals mutually adjacent. If the two sets of lines are at right angles the quadrilaterals will be squares, otherwise diamond-shaped figures. If these lines now be considered as pivoted at each intersection, we have a geometrical construction very like a "lazy gate." The angles may then be changed by any amount, and, while alternate angles equals 180° and the other equals 0° each.

Before the significance of this, for present purposes, is discussed, it is necessary to provide another geometrical proposition. Since it is possible to construct a regular polygon of any number of sides from three to N and to

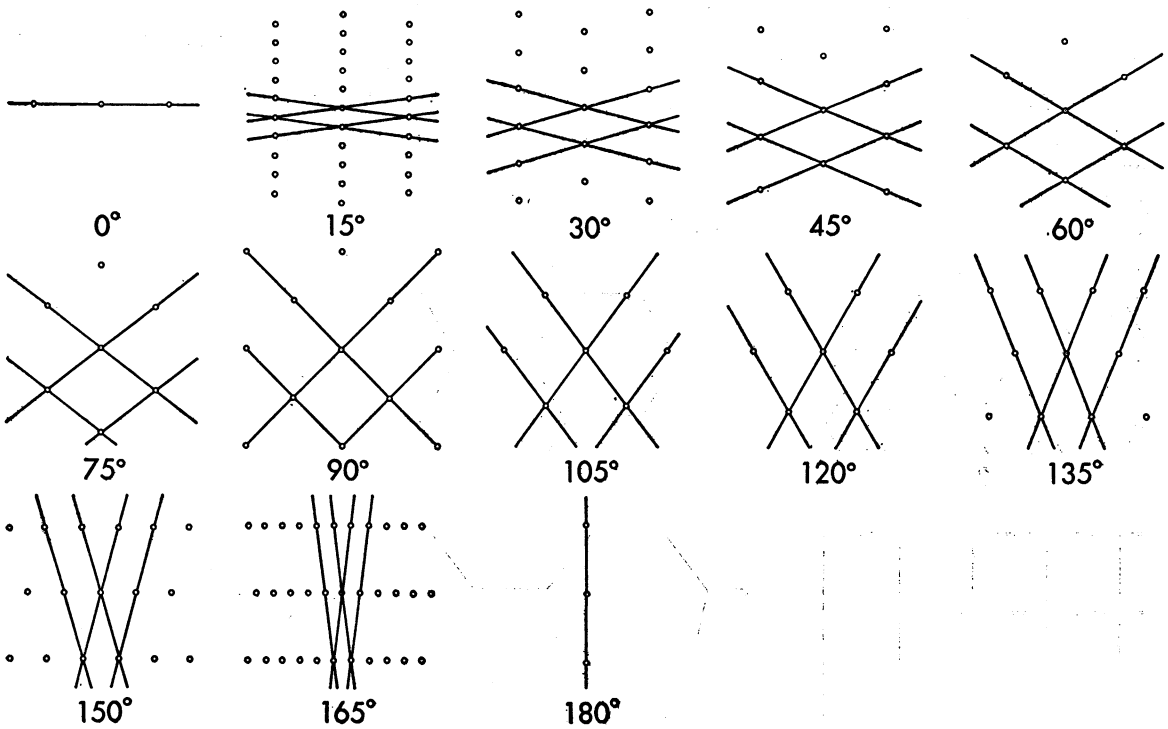


FIG. 6. Patterns formed by two pairs of equally distant parallels intersecting at various angles, in steps of 15°, from 0 to 180°. The points of intersection of the parallels are indicated by small circles including all the equidistant parallels included in the area covered.

the area of the quadrilaterals increases or decreases, the lengths of the mutually equal sides remain constant. Such transformations for several angular measurements, in 15° steps, are shown in figure 6, in which only two pairs of the intersecting lines are indicated, the shifting positions of the other intersections being indicated by small circles. It is clear from this that there is a regular decrease on either side of the 90° intersection to the 0° intersection in which all lines of the lattice are identical, appearing as a single line, vertical on one side of 90° and horizontal on the other, and in which the "quadrilateral" is represented by a line two times the length of one side and in which one set of spread them over a surface so that they have mutually common sides, a series of patterns, as shown in figure 7, may be arrayed. From this it may be demonstrated that of all the regular polygons so deployed only three provide complete occupancy of the surface, i.e., the triangle, the square, and the hexagon. All the others by any arrangement necessarily leave areas of other shapes between them. These are indicated by black areas in the figure.

Between the three kinds of polygons which provide complete coverage a peculiar relationship exists. It may be seen by inspection that the set of triangles may be transformed into a set of hexagons by removing certain lines, i.e., a hexagon may be considered as composed of six equilateral triangles. The set of triangles may be transformed into a grid of two sets of intersecting parallel lines by removing any one set of homologous sides of the triangles. The quadrilaterals thus formed have alternate angles of 60° and 120°. Conversely, the grid of parallel lines at right angles, forming squares, may be so shifted that the quadrilaterals have alternate angles of 60° and 120°, as has already been indicated in figure 6. The introduction of another set of parallel lines at 60° to the two already present returns to the equilateral triangle condition. Similarly the hexagonal arrangement may be returned to the triangular condition by the continuation of the six sides of each hexagon.

Since in each of these transformable grids the intersections are determined by straight lines, it follows that such a surface, however warped or distorted, will retain these points along geodesic lines, and all the intervening area will be marked off into polygons of three,

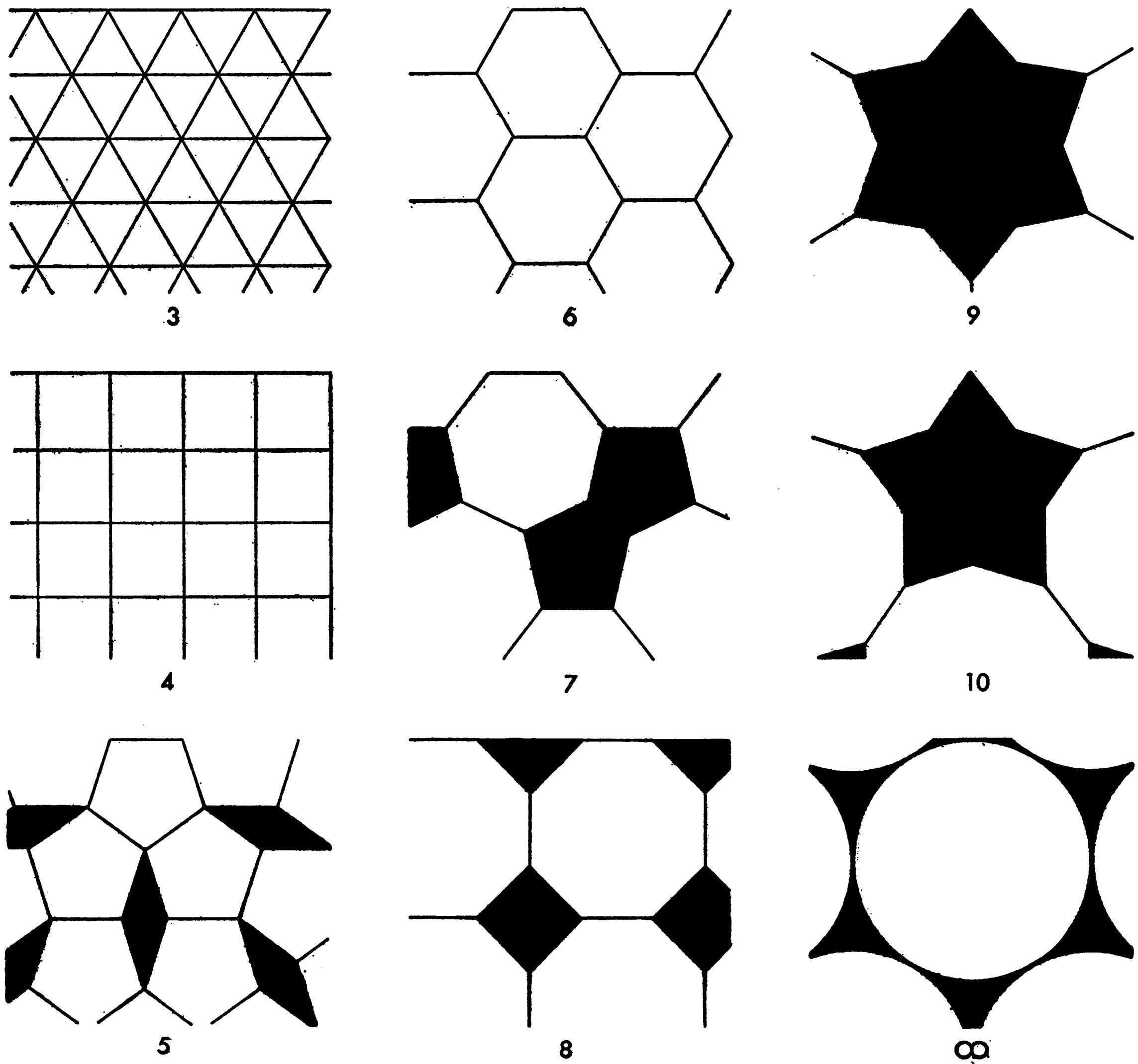


FIG. 7. The coverage of an area by regular polygons of from 3 to N number of sides. The black areas indicate portions of the surface which remain uncovered in certain cases. The length of the sides is equal in all cases except for N.

four, or six sides. As already indicated, any other regular polygonal arrangement requires the interspersion of other shapes. Thus far, consideration has been given only to grids of all equidistant parallel lines. By altering the distances between one set of parallel lines, other than regular polygons are produced. Figure 8A, B, and C shows such a condition with one set of crossing parallels of equal distance, one of one-half the distance, and one of two times the distance of the alternate set. Since these values have a factor in common, it is possible to consider these as having appropriate parallels, omitted or interlarded as the case may be. If values are chosen in which the distances between the parallels have no factor in common, in order to treat them conveniently, as above, it is necessary to consider the values as factors of their product, with an appropriate number of parallels omitted and then to proceed accordingly.

Thus far, only parallel lines have been considered. Obviously other constructions are possible, and they lead to an infinite variety of relationships which are summarized in the remaining part of figure 8. Either one or both sets of crossing lines may be divergent. The first case, illustrated in figure 8D, obviously leads to graded and asymmetrical quadrilaterals except in certain special cases of angular selection. The second, not illustrated, is similar and sufficiently obvious.

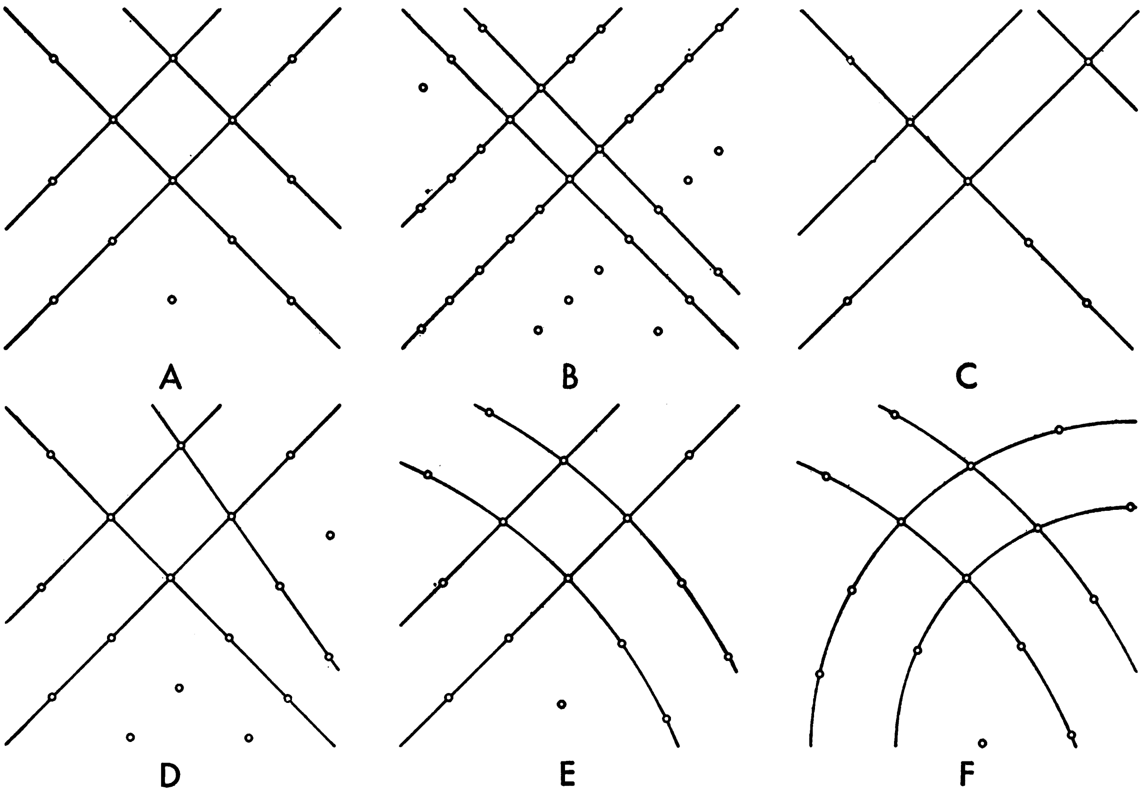


FIG. 8. Patterns formed by two pairs of lines of special relationships. A. Two sets of parallels, both equidistant. B. Two sets of parallels, one one-half the distance of the other. C. Two sets of parallels, one two times the distance of the other. D. One set of parallels and one set of divergent lines. E. One set of parallels and one set of concentric arcs. F. Two sets of concentric arcs.

With the introduction of other than straight lines still further complications arise. The case of a set of straight lines and one set of curved is shown in figure 8E and of two sets of curved lines in figure 8F. In the illustrations concentric circles have been used, but

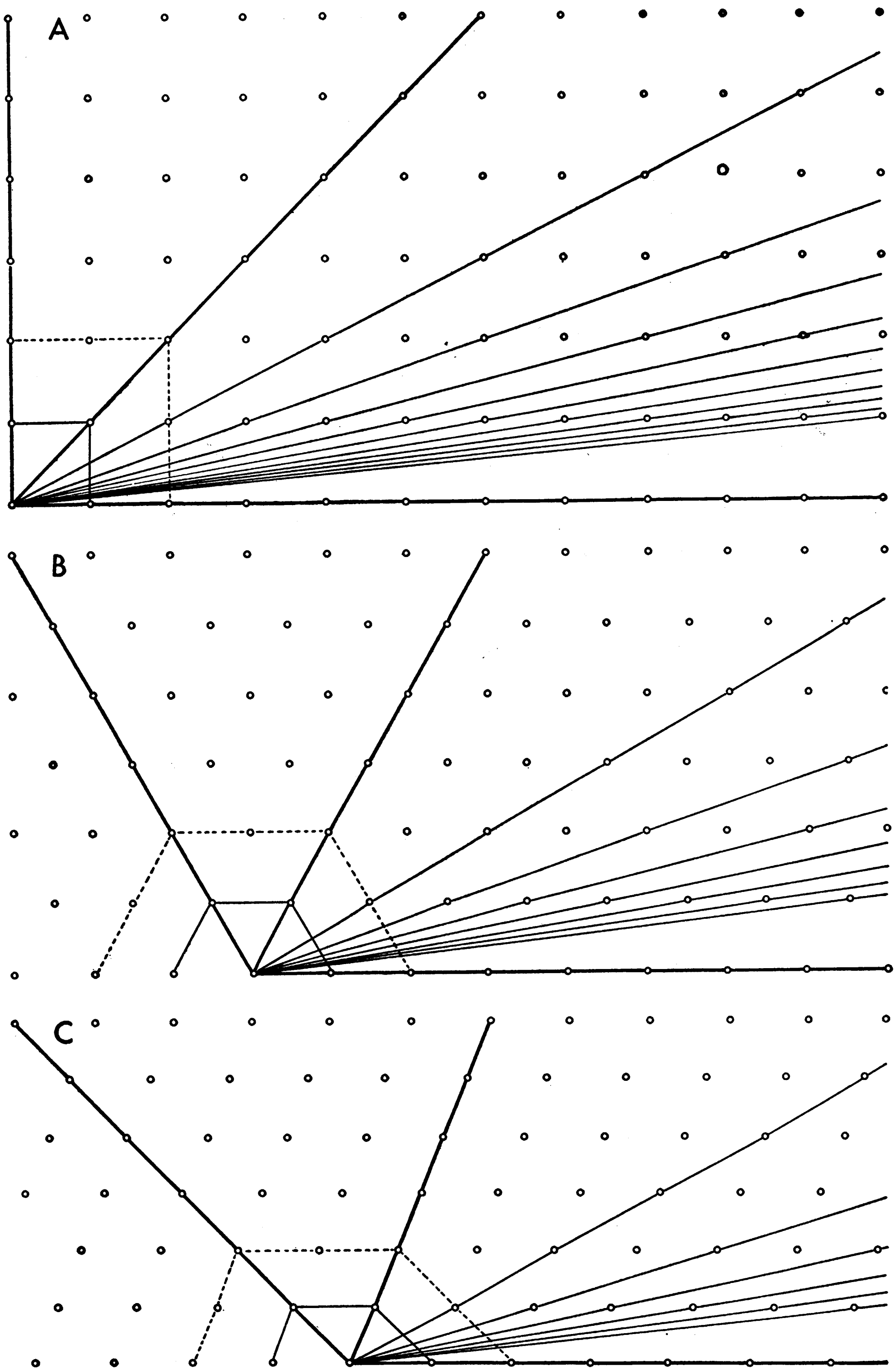


FIG. 9. The relationships of prime ratios and factors in three arrangements of grid intersections. A. Intersection at 90°. B. Intersection at 60°. C. Intersection at 45°.

obviously curves of any order could be employed. These will suffice for present purposes, but it should be obvious that all these possible combinations of geometrical arrangement are infinite in detail. It is evident, moreover, that those based on other than two sets of parallel lines would not have their intersections lying on mutual geodesics throughout. In special cases certain geodesic lines could be found connecting series of non-adjacent intersections, but they would be few in number and would in fact merely represent curves drawn through certain points on what could be thought of as primarily a grid of parallels.

If the intersections of the simple crossing parallels be plotted out as points for the three types (actually two since hexagon equals six triangles), as is done in figure 9, it becomes evident that the real difference between them is the angular difference between 90° and (60° or 120°) which equals 30° in either case. It so happens that these two arrangements (fig. 9A and B, respectively) represent the common conventional types for the spacing of plants in corn fields. If these diagrams are considered as representing corn fields and it is recalled how in walking or driving past a well-ordered corn field a large number of passageways between the plants radiate in all directions from the observer, which as he moves constantly shift and open up a seemingly infinite number, a peculiar feature of such all-over patterns develops. In each of the grids of figure 9 the primary "files of corn plants" are indicated by a heavy line, that is, a line connecting the nearest points in a straight line. Lighter lines connect the "next to nearest" and so on. In the illustration one-half of those in one quadrant are shown radiating from one point. It is this network of rows, or rather passages between them, that is so notably evident in a field of corn. The primary, secondary, tertiary, and even quaternary are usually entirely evident in such a planting, but those of higher order are naturally harder to find and tend to disappear in the foliage. It is to be noted that in either the 90° or 60° grids such series are present. Actually this particular feature is present in any other angle of intersection, as is shown in figure 9C for that of 45°, the asymmetry of such systems not interfering with this feature. Furthermore, the notable difference between the 90° and 60° grids shows especially clearly in these diagrams. In the first one any point has the four nearest points equidistant from it, whereas in the second any point has six such equidistant points owing to their relocating in swinging from 90° to 60°. Other constructions, such as that of 45°, can have only two such points.

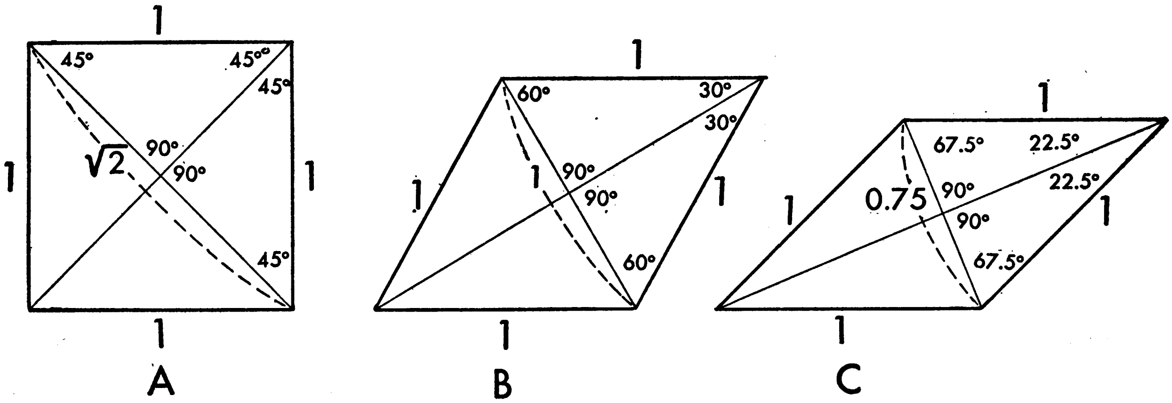


FIG. 10. The relationships of the angles and dimensions of one quadrilateral under transformation. A. From 90° grid. B. From 60° grid. C. From 45° grid.

If ratios, beginning with 1 to 1, are arrayed in systematic order as in table 2, those that are prime to each other may be indicated by italics. By comparison with figure 9 it then becomes at once apparent that the rows indicated are those that include the points that have identical numerical ratios and may be expressed as rows of similitude. Stated another way, the quadrilaterals that may be constructed on each successive unit distance from the point of origin are similar, "magnified" figures.

Perhaps an even simpler way of visualizing these relationships is to consider the quadrilaterals and the triangles involved in such transformations, as is done in figure 10, where the three cases are considered as simple geometric figures with their equal and unequal sides and angles indicated.

Thus far these figures of intersection have been considered merely as all-over patterns. If now an axial orientation be brought in, still other peculiarities develop. Taking the base line as a horizontal and rotating the pattern through angular changes, a series of patterns may be developed, as shown in figure 11. Triangles have been drawn on these patterns to give a simple measure of the numerical differences encountered, and the angular values are given in table 3. Figure 11 indicates a position with the axis at 45°. Counting from any point downward to the same horizontal along each of any two intersecting lines, it is found that the distances are equal, or the same number of intersections are passed. The two legs of this triangle thus bear a 1/1 ratio to each other. In a like manner each of the other arrangements provide for other ratios, 1/2, 2/3, 3/5, and 5/8, until the last (fig. 12) in which the triangle disappears as such, with one angle equaling 180° and the other equaling 0°. The relationship to that of the "corn row" diagrams of figure 9 and table 2 of prime ratios is clear. Figure 13 shows a comparison of a series of such axes reaching up to a 5/8 ratio and a second set normal to the first which refers to the pattern of complementary angular divergence to the first.

TABLE 2

A COMPARISON OF RATIOS, PRIME AND FACTORIAL

(1- 1)	*2- 2*	*3- 3*	*4- 4*	*5- 5*	*6- 6*	*7- 7*	*8- 8*	*9- 9*	*10-10*
(1- 2)	(2- 3)	3- 4	4- 5	5- 6	6- 7	7- 8	8- 9	9-10	10-11
1- 3	*2- 4*	(3- 5)	4- 6	5- 7	6- 8	7- 9	8-10	9-11	10-12
1- 4	2- 5	*3- 6*	4- 7	(5- 8)	6- 9	7-10	8-11	9-12	10-13
1- 5	*2- 6*	3- 7	*4- 8*	5- 9	6-10	7-11	8-12	9-13	10-14
1- 6	2- 7	3- 8	4- 9	*5-10*	6-11	7-12	(8-13)	9-14	10-15
1- 7	*2- 8*	*3- 9*	4-10	5-11	*6-12*	7-13	8-14	9-15	10-16
1- 8	2- 9	3-10	4-11	5-12	6-13	*7-14*	8-15	9-16	10-17
1- 9	*2-10*	3-11	*4-12*	5-13	6-14	7-15	*8-16*	9-17	10-18
1-10	2-11	*3-12*	4-13	5-14	6-15	7-16	8-17	*9-18*	10-19

The italic figures are all multiples of the respective prime ratio at the extreme left to which they correspond. Note that these figures proceed to the right in series which bear an angular relationship similar to that shown in the corn-field example.

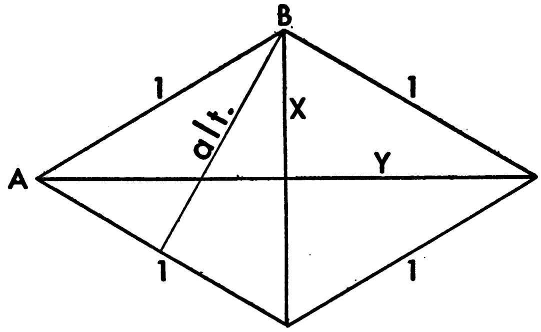
The figures in parentheses represent the terms of the Fibionacci series and serve to indicate the relationship of that series, together with the *sectio aurea* to the present table of ratios.

From these considerations it should be clear that such ratios could be infinitely extended, and in selecting such series, certain restrictions appear in those prime to each other. Those not prime to each other simply imply magnification, as already indicated. If we proceed from left to right in table 2, i.e., to progressively higher ratio values, we find that in avoiding factorial ratios we arrive at such series as 1/2, 2/3, 3/5, 5/8; or 1/3, 3/4, 4/7, 7/11, etc., which are obviously expressions of the famed Fibionacci series, which has most recently been discussed at length in other but similar connections by Thompson (1942). Since ratios such as the above may be expressed as common fractions, it is convenient for the purpose of clarity to plot such a series graphically, as is done in figure 13. Incidentally this is a graphic way of indicating the manner in which this series approaches its value for its *N*th term 0.61803 . . . , which is the *sectio aurea* of much mystical interest to the ancients. Various values for the cor-

TABLE 3

VALUES FOR DIMENSIONS AND ANGLES OF VARIOUS QUADRILATERALS

Sides = 1
Angle A opposite diagonal X (vertical)
Angle B opposite diagonal Y (horizontal)



Angle A	Angle B	Value of X	Value of Y	$\frac{X}{X}$	Altitude or Area	Remarks
0°	180°	0.0000	2.0000		0.0000	
15	165	0.2611	1.9829	7.5948	0.2598	
30	150	0.5176	1.9319	3.7324	0.4999	
				3.1416		$Y/X = Pi$
36	144	0.6180	1.9021	3.0776	0.5877	$X = \frac{\sqrt{5}-1}{2}$
37°46′	142°14′	0.6473	1.8922	2.9232	0.6180	Alt. $= \frac{\sqrt{5}-1}{2}$
45	135	0.7654	1.8478	2.4141	0.7071	
				2.2360		$Y/X = \sqrt{5}$
60	120	1.0000	1.7321	1.7321	0.8660	
				1.4142		$Y/X = \sqrt{2}$
75	105	1.2175	1.5876	1.3039	0.9664	
90	90	1.4142	1.4142	1.0000	1.0000	X and Y both $= \sqrt{2}$
105	75	1.5876	1.2175	0.7676	0.9664	
				0.6180		$Y/X = \frac{\sqrt{5}-1}{2}$
120	60	1.7321	1.0000	0.5773	0.8660	
135	45	1.8478	0.7654	0.4142	0.7071	
142°14′	37°46′	1.8922	0.6473	0.3421	0.6180	Alt. $= \frac{\sqrt{5}-1}{2}$
144	36	1.9021	0.6180	0.3244	0.5877	$Y = \frac{\sqrt{5}-1}{2}$
150	30	1.9319	0.5176	0.2685	0.4999	
165	15	1.9829	0.2611	0.1312	0.2598	
180	0	2.0000	0.0000	0.0000	0.0000	

Indeterminate Values

$\frac{\sqrt{5}-1}{2} = 0.61803\cdots$ *N*th term of Fibionacci series

$\sqrt{2} = 1.41421\cdots$ Gnomonic ratio

$\sqrt{5} = 2.23606\cdots$ Gnomonic ratio of square

$C/D = 3.14159\cdots$ *Pi*

responding angles and dimensions of the varying quadrilaterals are given in table 3, the significance of which will appear in the discussion of actual surface patterns as the scales on the side of a fish. Table 4 gives the Cartesian values for the various lattice angles, which are illustrated in figure 14. It is evident that they are merely the sine and cosine of one-half the angle A of table 3 or one-half the sine and cosine of angle A. Table 5 gives the mean proportional between various prime numbers and special values concerning gnomonic relationships. Table 3 gives the values of the Nth term of the Fibionacci series, gnomonic values, and *Pi*, a discussion of which, along with the other tabular values and constants, appears again in the discussion of squamation.

Another matter which comes up in such studies involves a consideration of figurate numbers, gnomons, and the logarithmic spiral. Referring to figure 9, it is evident that either the triangular or the hexagonal numbers are suggested by diagram B and the square numbers by A. Starting from the center of reference, first a solid line and then a dotted line have been inserted to connect the members of the second and third terms of such series. Taking the squares indicated in A we have the square numbers:

1, 4, 9, 16, 25, 36, 49, 64, etc.

Taking the triangles in B we have the triangular numbers:

1, 3, 6, 10, 15, 21, 28, 36, etc.

Taking the hexagons in B we have the hexagonal numbers:

1, 7, 19, 37, 61, 91, 127, 169, etc.

Actually all three of these series may be found in either configuration of points. When it is considered that one may be transformed into the other by simple angular change, the reasons for this should be evident. It is merely because regular squares, triangles, and hexagons catch the eye that there seems to be

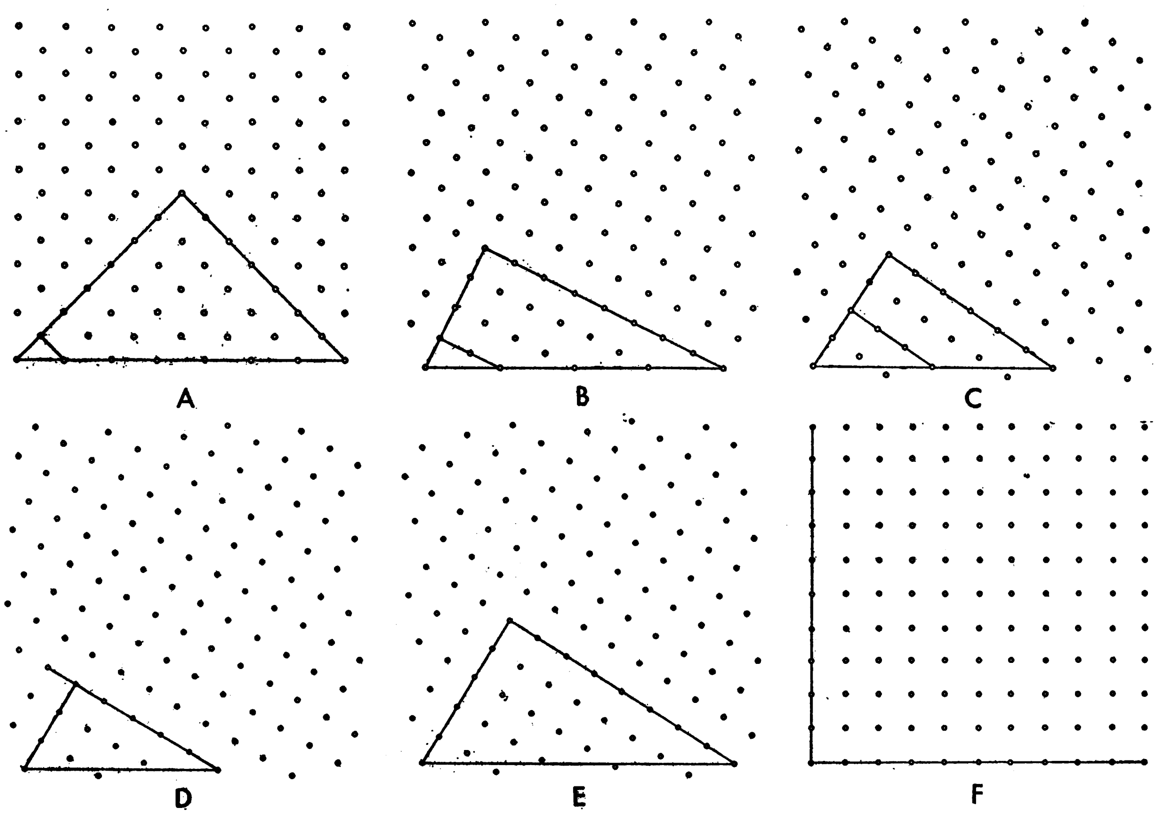


FIG. 11. Grids rotated about a horizontal axial line in steps of various ratios. A. 1/1. B. 1/2. C. 2/3. D. 3/5. E. 5/8. F. 0 or infinite.

separation. Examination of figure 9C, where none of these polygons are regular, should make this clear. The other figurate numbers, such as the pentagonal series, or the stellate numbers, may likewise be found as well as others. These, however, do not show the same simple gnomonic relationship, which is non-technical discussion of the nature of the figurate numbers.

Since the numbers in these series bear a gnomonic relationship to each other, it follows that their geometrical representations must be gnomons, as can be easily established by simple inspection, no matter what angles

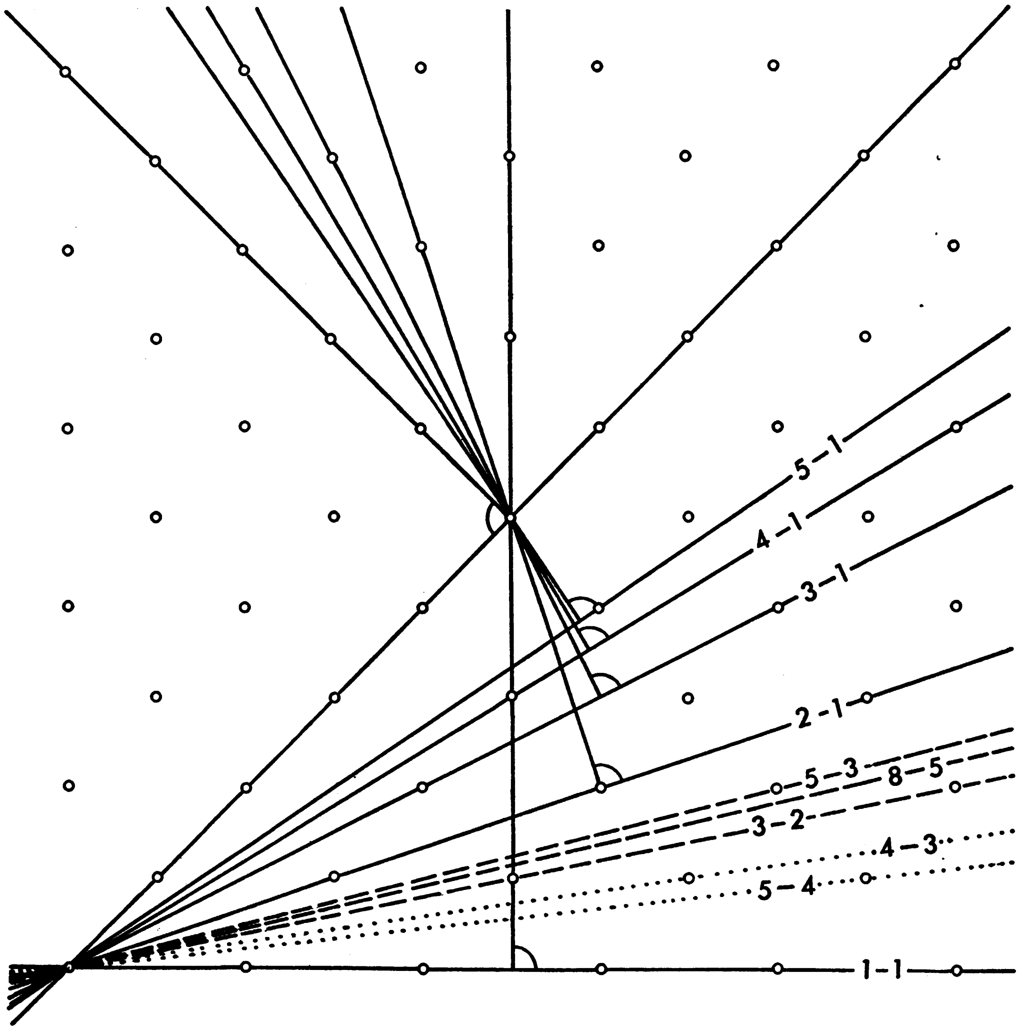


FIG. 12. Axes rotated across the face of a grid in steps of various ratios, also showing a second set of axes normal to the first, which mark the grids of complementary degree.

related to the fact that only squares, triangles, and hexagons give all-over coverage in such an arrangement as is indicated in figure 7. Further discussion of this would carry us too far afield from present purposes. Hogben (1937), however, gives an instructive exist between the originating grids. Furthermore, since the homologous points on successive gnomonic figures lie on an equiangular spiral, it follows that such a series of spirals may be found on the appropriate points on such a grid. Thompson (1942) shows such relationships in an interesting series of diagrams involving the use of squares, triangles, and hexagons, but arrived at from an entirely different approach. The gnomons and the derivation of logarithmic spirals based on the grids here used are indicated in figure 15.

One each is based on a triangle, a quadrilateral, and a hexagon. Only the triangle is regular, being an isosceles triangle of 45° at its apical angle and 22.5° at each basal. Its slight departure from the equilateral construction is evident.

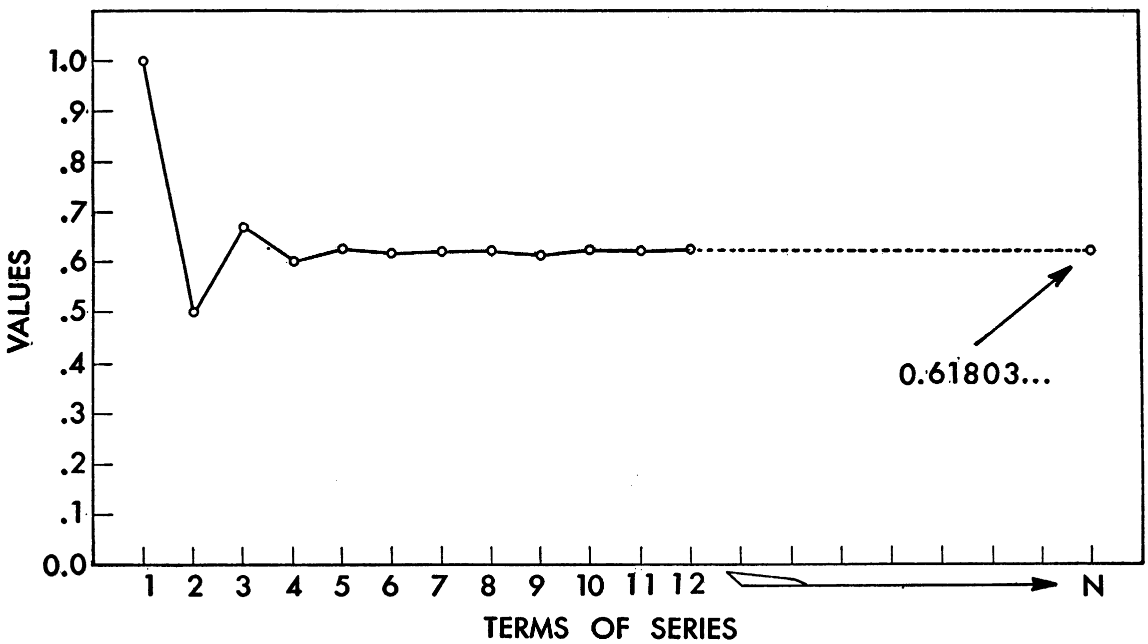


FIG. 13. A graphic representation of the Fibionacci series. The terms numbered consecutively to N represent the ratios 1/1, 1/2, 2/3, 3/5, etc. The Nth term is shown where actually the twentieth term, 6765/10946, should be placed. The Nth term is represented by 0.61803 · · · , the twentieth term by 0.61712 · · · .

The gnomons and their equiangular spirals indicated by solid lines are those based on the square, triangle, and hexagon, using the sides of the respective figures and their multiples to derive the curve. These in themselves give a measure of the nature of the opening up of the grids in passing from polygons based on 60°, 90°, and 120°. The dotted spiral in the square grid, A, is based on the diagonals of the squares and possesses the identical gnomonic properties. The two curves are identical. The dotted spiral of the triangular grid, B, is based on quadrilaterals as in A. The spiral, of course, indicates the distortion of the initial squares, if such it be considered, and is clearly a curve of another order. All the curves shown in the 45° grid are dotted, since none can be based on a regular polygon.

It should be evident that an endless variety of such constructions is inherent in such grids, just as we have seen that in them there also is present an infinite number of "rows" that may be delineated, as is shown in figure 10. Clearly if our line of vision took the path of a logarithmic spiral instead of following a straight course, such spirals would be evident in a corn field, and the straight files would be no more evident than the spirals are under customary conditions. Thus it becomes evident that such constructions, and still others could be devised, are rooted primarily in what physical constants are able to impress themselves on our sensory and mental selves.

To elucidate further the loci of points on such grids, figure 16 shows a number of constructions based on the three angular distances that have been employed for purposes of illustration. The left-hand figure in each shows that the loci of the nearest point to any other includes two in the 45° grid, six in the clearly why all bear gnomonic relationships. The relationships of the quadrilateral and its axes, indicating the disappearance of one in the 90° grid, are evident.

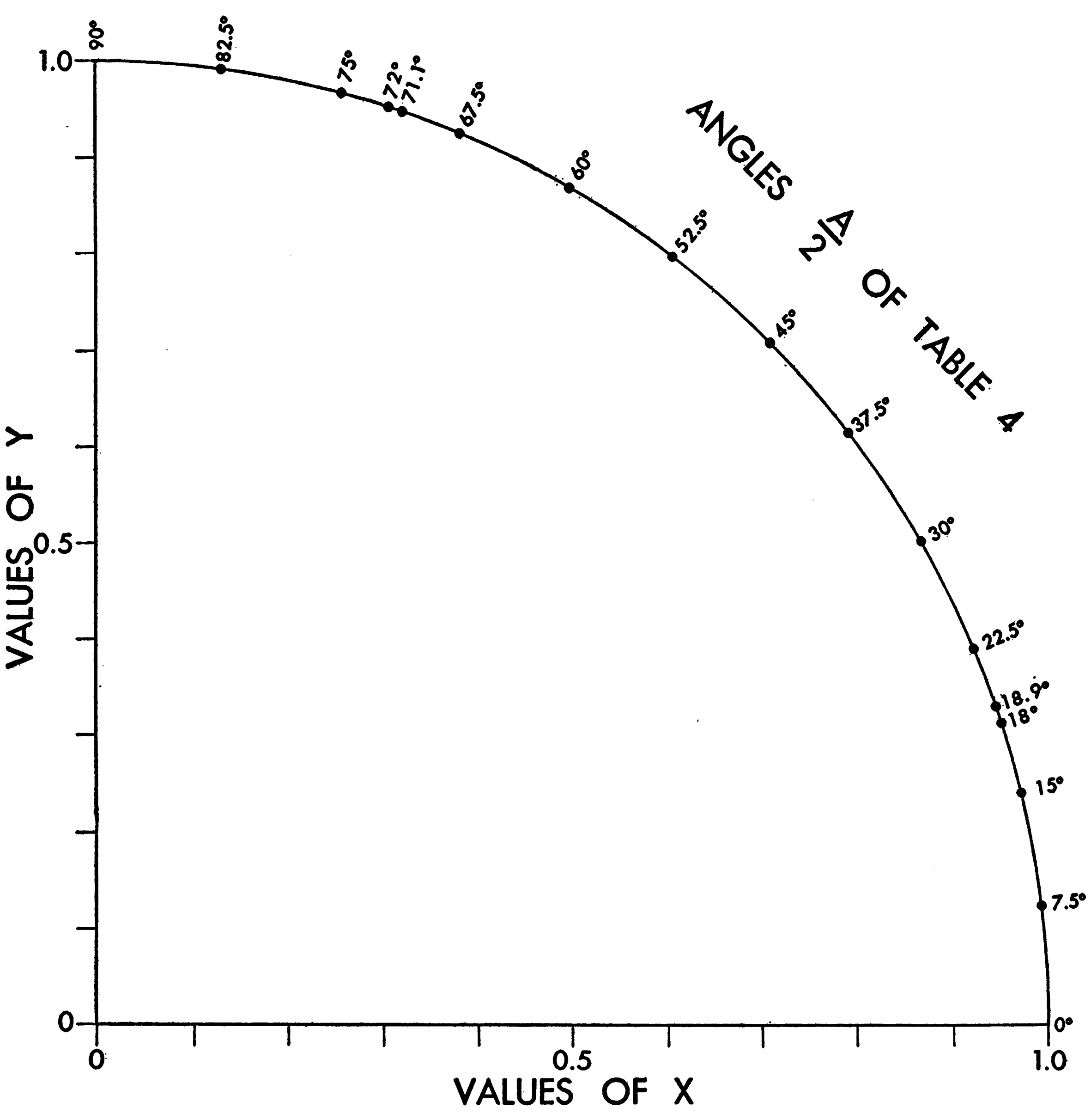


FIG. 14. Diagram of the Cartesian values for the data of table 4.

60° grid, and four in the 90° grid. It is only in the two special cases of 60° and 90° that more than two have a common locus from one point. The right-hand figure in each shows an extension of this relationship and indicates

In such studies one must always be on guard to distinguish biological influences as distinct from the purely mathematical properties of space. This is not always as easy as it might seem, since organisms are restricted

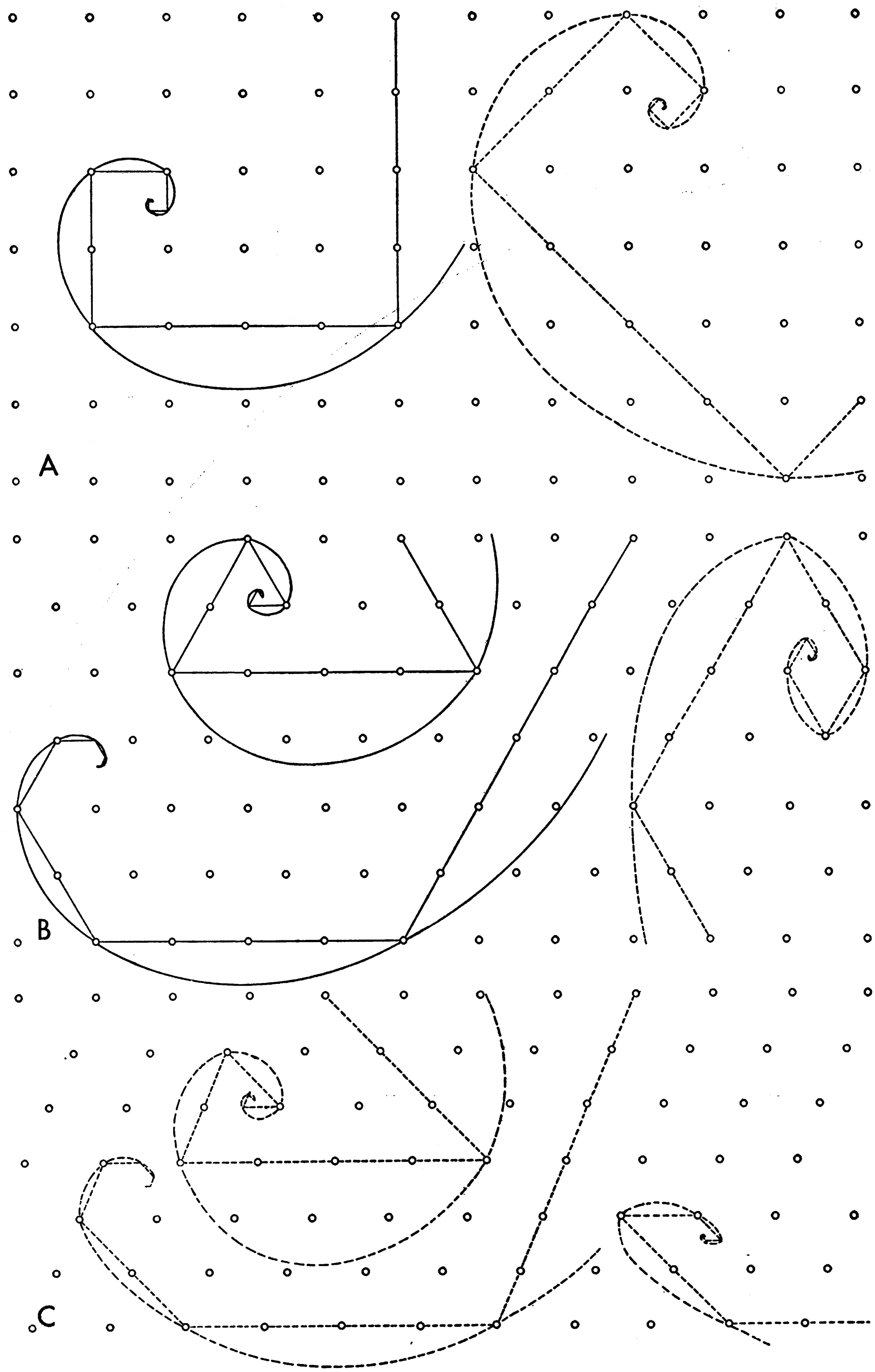


FIG. 15. Gnomons and equiangular spirals in three arrangements of grids. A. Intersecting at 90°. B. Intersecting at 60°. C. Intersecting at 45°.

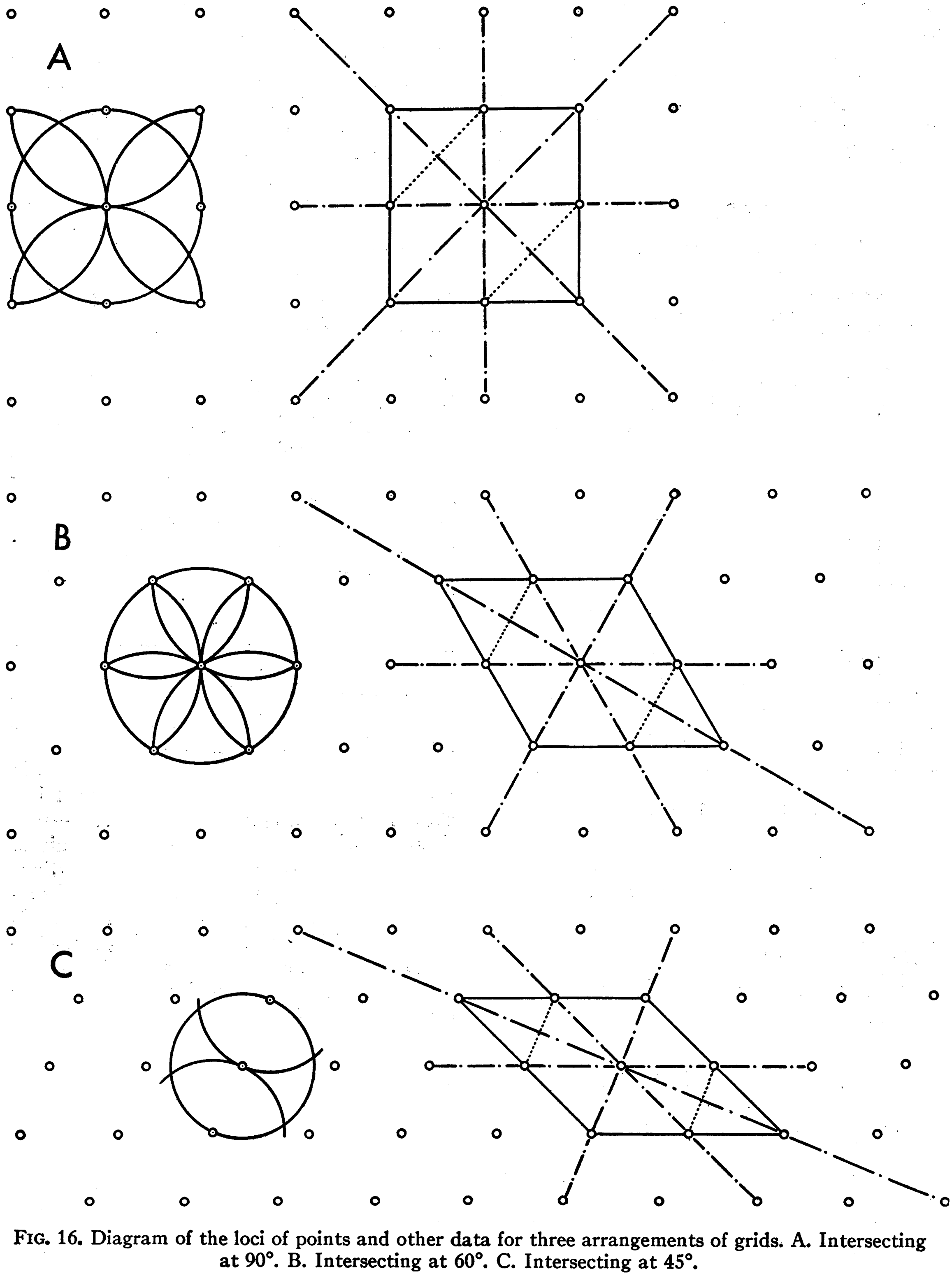


FIG. 16. Diagram of the loci of points and other data for three arrangements of grids. A. Intersecting at 90°. B. Intersecting at 60°. C. Intersecting at 45°.

to the limitations of mathematical ratios. If, for example, an organic object is spherical, it perforce expresses all the relationships of diameter, area, volume, etc., based on the constant *Pi*, or if it increases equally all around, or adds to itself at one end, it necessarily follows some gnomonic relationship,

TABLE 4

CARTESIAN VALUES FOR VARIOUS LATTICE ANGLES

Angle A	Value of X	Value of Y	Angle $\frac{A}{2}$
0	1.0000	0.0000	0
15	0.9914	0.1305	7.5
30	0.9659	0.2588	15
36	0.9511	0.3090	18
37°46′	0.9461	0.3239	18.9
45	0.9239	0.3827	22.5
60	0.8660	0.5000	30
75	0.7934	0.6088	37.5
90	0.7071	0.7071	45
105	0.6088	0.7934	52.5
120	0.5000	0.8660	60
135	0.3827	0.9239	67.5
142°14′	0.3239	0.9461	71.1
144	0.3090	0.9511	72
150	0.2588	0.9659	75
165	0.1305	0.9914	82.5
180	0.0000	1.0000	90

$$Y = \left(\tan \frac{A}{2}\right) X + b$$

$$R = 1$$

$$X = \cos \frac{A}{2} \text{ and } Y = \sin \frac{A}{2}$$

The left-hand column of angles is that of the quadrilateral and is the same as that of angle A of the diagram in table 3.

and the logarithmic spiral comes into the physical relationship. Thompson (1942), in discussing gnomons, stated it tersely as follows: " . . . it follows that in the spiral outline of a shell or of the horn we can always inscribe an endless variety of other gnomonic figures, having no necessary relation, save as a mathematical accident, to the nature or mode of development of the actual structure." It is indeed one of the objects of the present study to separate, in so far as possible, the purely mathematical characteristics of space from the peculiarities of the morphological expressions of organic activity.

Another aspect of surface pattern involves topological concepts. An excellent résumé of the subject is given in Thompson (1942). The present contribution, on symmetry, can add nothing to that subject from a basis of present concepts, except to note the bearing that topological studies have on what appears to be expressions of symmetry that have not been fully realized in a geometrical sense. As the eye contemplates an object that appears to be expressing some simple, geometrically symmetrical design, it frequently happens that the object is "marred" by a consistent and recurring "irregularity." Clearly all of these are not mere fortuitous "malformations." The cases of a segmenting egg or soap bubbles in a dish for reasons of physical requirement are not symmetrically disposed in the geometrical sense herein discussed but show a partitioning concerned with an establishment of the minimum area per unit of volume which leads to stable configurations which may or may not show features of simple symmetry. In such cases it is frequently even more difficult to separate simple mathematico-physical concepts from the biological, involving as it does some of the more abstruse concepts of topology.

ON THE NATURE OF SOLID PATTERNS

As Thompson (1942) has given a very full and extended discussion of the nature of space-filling solids, together with the partitioning of space, it is unnecessary at this place to go into these matters in much detail. It suffices for present purposes to call attention to the relationships of these solids to the plane figures discussed in connection with surface patterns. The well-known tetrakoidekahedron or "14-hedron" is the solid with plane faces which presents a minimum of surface for its volume. Glaser (1945) gives an extended discussion on the manner in which this solid fills space and indicates the large variety of patterns and formations that it may be caused to take. This figure is bounded by 14 faces, six of which are squares and eight of which are hexagons, and presents 36 edges, all of which are necessarily equal. It is no geometrical accident that these faces include all the polygons giving all-over coverage on a plane, as is indicated in figure 7.

Other space-filling figures and their peculiarities show similar relationships. Thompson (1942), in discussing the "Archimedean bodies" and the work of von Fedorow, wrote, "All of these figures, save the hexagonal prism, are related to and derivable from the

TABLE 5

MEAN PROPORTIONALS BETWEEN PRIME NUMBERS

$a:b::b:c$

$\frac{a}{b}=\frac{b}{c}$

$b^2=ac$

$b=\sqrt{ac}$

$b^2=ac$

$\frac{b^2}{a}=c$

First Term	Mean Proportional		Third Proportional
1	1.414	$\sqrt{2}$	2
1	1.732	$\sqrt{3}$	3
1	2.000	$\sqrt{4}$	4
1	2.236	$\sqrt{5}$	5
1	2.449	$\sqrt{6}$	6
1	2.646	$\sqrt{7}$	7
1	2.828	$\sqrt{8}$	8
1	3.000	$\sqrt{9}$	9
2	2.449	$\sqrt{6}$	3
2	3.1622	$\sqrt{10}$	5
2	3.7416	$\sqrt{14}$	7
2	4.2426	$\sqrt{18}$	9
3	3.4641	$\sqrt{12}$	4
3	3.8729	$\sqrt{15}$	5
3	4.5825	$\sqrt{21}$	7
4	4.4721	$\sqrt{20}$	5
4	5.2915	$\sqrt{28}$	7
4	6.0000	$\sqrt{36}$	9
5	5.9160	$\sqrt{35}$	7
5	6.3245	$\sqrt{40}$	8
5	6.7082	$\sqrt{45}$	9
1	0.919	$\sqrt{0.036041}$	0.036041
1	0.61803	$\sqrt{0.381967}$	0.381967
1	1.414	$\sqrt{2}$	2.000000
1	2.236	$\sqrt{5}$	5.000000
1	3.047	$\sqrt{9.274119}$	9.274119
1	3.1416	$\sqrt{9.76945}$	9.76945
1	3.851	$\sqrt{14.6304}$	14.6304
1	4.667	$\sqrt{21.780889}$	21.780889
2	5.000	$\sqrt{25}$	12.500000
3	8.000	$\sqrt{64}$	21.333333
1	1.772	$\sqrt{3.1416}$	3.1416

cube; so we end by recognizing two principal types, cubic and hexagonal." He was referring to the whole polyhedron, but we have already shown, in considering the faces alone as polygons, that there is a very definite relationship between a cubic face (square) and the hexagon by way of equilateral parallelograms made up of two equilateral triangles. Thus we may consider the entire series as derivable from the cube or square, or perhaps preferably from a line of unit length variously reduplicated in simple prime numbers, three being the fewest possible that can enclose a surface and four appearing, instead of two which is impossible, as the smallest even-numbered figure. Five appears like three as a true prime number, but six may be considered either as composed of six sets of three or three sets of four.

THE BIOLOGY OF SYMMETRY

SYMMETRY IN ORGANISMS

HAVING SET FORTH A SCHEME for the general handling of the concepts of symmetry, we may now consider its implications when applied to biological phenomena, which was the basic reason for the foregoing excursion into geometry. While plants and animals have been considered as either asymmetrical, bilateral, or radial, it should now be evident that with the present classification we would refer them to a more refined set of terms expressing similarities and differences in a finer, and we hope clearer, sense.

It is at once apparent that externally animals for the most part show symmetry of the first degree, a relatively very few of zero degree, and, grading from the exceedingly common type of first degree, we find fewer of second degree, third degree, and so on. Superficially it seems that there is a tendency for the fifth degree to be disproportionally numerous (see Jaeger, 1917). Again, at the other end of the series, the complete expression (∞ degree of symmetry) or its approximation is common. A statistical study of the number of animal forms in relation to the degree of symmetry expressed would be of considerable interest. Congruent symmetry in animals is relatively rare. Considering plants, asymmetry is rare and so is first-degree symmetry, but the higher degrees are relatively abundant, and congruent symmetry is notable. Here again a statistical approach would be of interest. These remarks, of course, apply to the whole structure only.

If we examine parts, we find a most complex situation in which asymmetry, reflective symmetry of various degrees, and congruent symmetry become inextricably mixed. An attempt to find a rational basis for this leads us into a poorly explored field, and all that we can hope to do at this time is to suggest possibilities.

If, for example, we consider man in his superficial aspects, we note that as a unit he shows symmetry of the first degree. If we contemplate one part of him, say his hand, it is clear that it is thoroughly asymmetrical, although his two hands are mirror images of each other. Considered alone each digit is strongly marked with first-degree symmetry. The iris, on the other hand, shows a high degree of symmetry, if the pattern of flecks in it be considered of a degree based on the flecking and its outline of infinite degree. Internally man is again a hodgepodge of symmetry and its lack. Although generally spoken of as being asymmetrical internally because of the conspicuousness of certain unduplicated elements, many are in fact duplicated in exquisite detail, and the majority of parts of even the asymmetrical arrangements are symmetrical unto themselves.

For comparison we may consider the parts of plants. A typical pine tree is built on a multiple degree of symmetry, its degree depending on the species. The fruit, however, has a clear development of congruent symmetry. Figure 17B shows this in the end view of a pine cone. Many of the Compositae show a similar arrangement of their flowering heads. A sunflower shows reflective symmetry around the outside of the flowering head and double, but unequal, congruent symmetry within it. Certain diatoms are fully congruently symmetrical, while others are equally reflectively symmetrical. Some arrange themselves in colonies around a center, approaching circular symmetry, while others arrange themselves along a line forming linear symmetry. This shows nicely the relationship of the two types, as the form taken results from the shape or mode of attachment rather than the form of the individual diatoms themselves.

The scale patterns of fishes may represent a surface of congruent symmetry, although the scales themselves may be reflectively symmetrical objects; as overlaid by their fellows the pattern is not infrequently congruently symmetrical. (See fig. 17D.) Univalve mollusks—which may be considered as forming shells that are a distortion in two planes of a linear symmetry or of a radial symmetry which did not quite meet but rather overslid itself as it came around to its starting point because of the large diameter of the primary whorl—usually show sculpturing or markings of a congruent symmetrical kind.

Such illustrations are all about us (a few others also are shown in fig. 17), and the reader may pick his own. When fitted into the present scheme the unity of the basic concept becomes apparent.

Thus far nothing has been said of the possible importance of this basis of "design" in nature. Given a unit of whatever kind, symmetrical or not, as a building block (and it makes no difference whether molecules, cells, or other units are thought of), certain arrangements must follow on their reduplication which is a common feature of living and non-living processes alike. Just as we took a triangle for the illustrative purposes of figure 3, so may any other item be taken. The arrangement of its duplicated part has certain definite limitations which determine the kind of structure that will result. They may be arranged either around a point, in a line, over a surface, or through a solid, and they can all be alike or mirror images of each other. ***There are no alternatives.*** These arrangements are exactly what we have used in determining

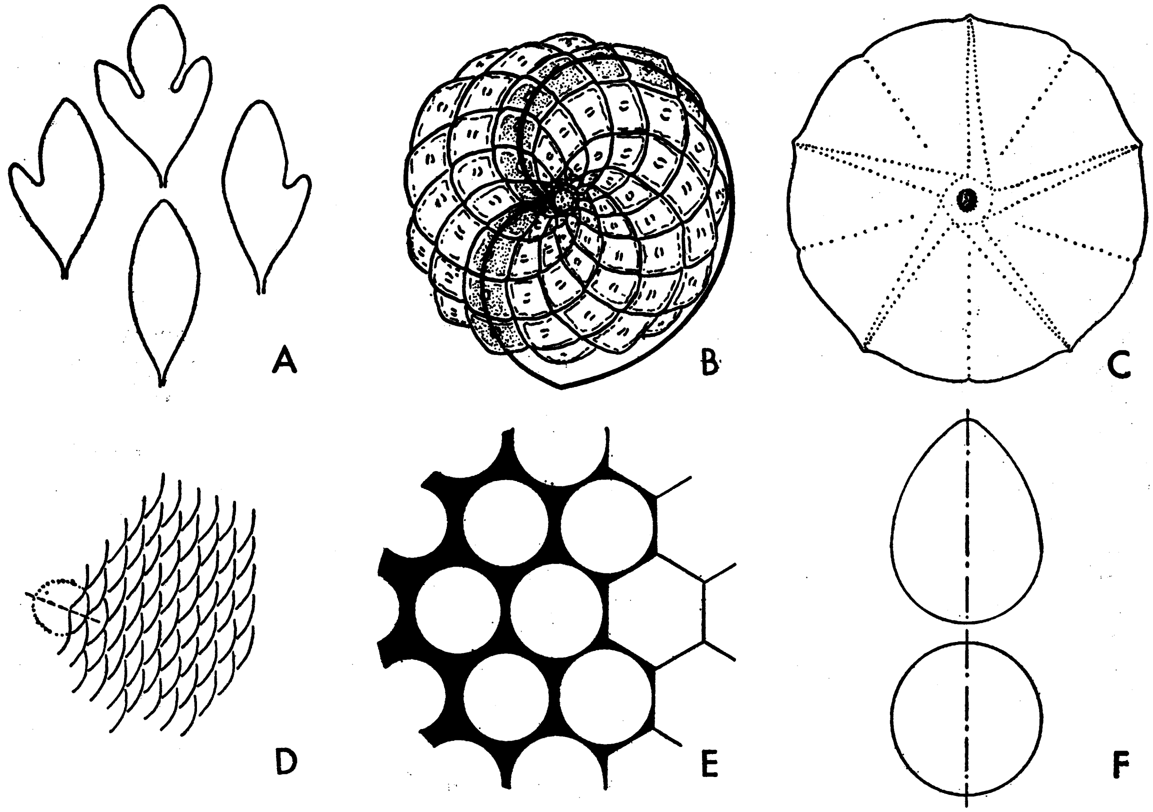


FIG. 17. Various examples of special cases of symmetry as found in natural objects. A. The four types of sassafras leaves, *Sassafras officinale*, Nees, thumbless, right-handed, left-handed, and double-thumbed. All taken from a single branch. B. End view of a cone of ***Pinus palustris***, showing 13° and 8° of congruent symmetry, right- and left-handed, respectively. The heavy lines are true logarithmic spirals. C. Cultivated morning glory blossom, *Convolvulus*, showing 5° congruent symmetry based on the folds that are involved with the system by means of which the flower opens and closes. D. Scale arrangement on the side of the fish *Dorosoma*, showing congruent symmetry spread out over a surface built up of reflectively symmetrical units. E. Nested circles and hexagons. From left to right regularly spaced circles are increased in size until they are in contact, from which condition they pass on into hexagonal outlines. This condition of transition may sometimes be found in honeycombs, especially near the edges. F. Side and bottom views of a falling drop, showing its transverse symmetry of N degrees and its symmetry of 1° in the axis of polarity.

our understanding of symmetry. Consequently, it should not be surprising that illustrations of each can be found from nature with little difficulty.

Given this primary basis, two things follow which should be able to account for the observed differences in symmetry among objects. One is that the resulting structure must be able to work or it will collapse. The other is the wide variety of materials (building blocks) which organisms find available.

If an organism can survive sitting still and cementing itself to the substrate, as an oyster, there would seem to be little reason why it should be limited to building itself into a particularly restricted symmetrical body unless there is an innate physical tendency for organisms in the direction of symmetry. The asymmetries of such objects may be referable to asymmetries of the environment rather than to a looseness of building pattern in the organism. The rearing of such organisms in a "symmetrical" environment should be instructive. On the other hand, if mobility is of value, symmetry of the first degree must be invoked because of streamline necessity. Only the first degree of symmetry is useful in this connection and it must be from right to left, that is, symmetrical about the sagittal plane. Dorsoventral symmetry could conceivably be of value to a truly pelagic fish, and indeed they do tend to approximate it, but all fast-moving animals must have some recourse to a horizontal plane, and this calls for a dorsoventral differentiation. Even pelagic fishes exist within a gravitational field, although they may have no direct contact with the water's surface or the bottom and live below the penetration of light. Either the basic particles are able to arrange themselves in some appropriate manner or the organism fails.

In plants the locomotor problem does not enter in the same sense as the above, and there would be seemingly little mechanical drive toward a first-degree symmetry. There are many reasons, however, why a higher degree of approximated symmetry (and frequently it is a very rough approximation) would be of use to a vegetative growth. Even slow-moving animals, echinoderms, coelenterates, etc., are apt to take on this feature. However, the beautiful designs of leaf outlines with their elaborate bilateral symmetry are not passed over so easily. One can see why a leaf should show symmetry of the first degree rather than some other. In the first place, its function calls for presenting one surface to the light; obviously for mechanical reasons it could not so use both simultaneously. Therefore, one should not expect symmetry in that direction. Since it is attached at one portion to form organic union with the plant, there is a proximal and a distal end which would naturally tend to be different, although in some lanceolate leaves there is surprisingly little difference. Consequently, there is only one possible plane left in which symmetry could express itself to any marked degree—and it most certainly does. For this there seems to be no really valid functional explanation. There are enough exceptions to this growth pattern to rule out the supposition that it results from some obscure need which we have not been able to recognize. Certainly exposed surfaces of photosynthesizing material could be almost any conceivable shape, and actually they are, but predominantly of very definite first-degree symmetry, which would appear to be rooted in the necessary attachment at one end. Actually in leaves attached on the under surface there is a strong tendency towards a circular form, as in water lilies, etc.

The answer to this puzzle would seem to lie further back. One does not seek for an explanation, in the present sense, for the shape of snowflakes, but they, too, are elaborately symmetrical and myriad in form. Since we can see no strong reason for any particular leaf shape, may we not have a similar condition here? Given a certain set of materials and no particular urge to reduplicate parts in any particular way, could this not be merely owing to the forces of arrangement, expressed in a single plane? Thus leaves would be considered as possessing first-degree symmetry because of physiological need, but shaped within that plane by the mechanics of arrangement of their component parts, of course as controlled by the processes of heredity. Suggestive in this connection is the leafage of the sassafras tree which is of four kinds (fig. 17A). Two are symmetrical and two asymmetrical. These latter are reflectively symmetrical in regard to each other. The whole group is similar to a left hand, a right hand, a hand without a thumb, and a hand with two thumbs. These grow on the same stem of a single plant and are usually scattered about through the entire foliage. Sometimes a tree may hold a predominance of one or the other of the symmetrical leaves, but I have yet to see one that does not have at least one leaf of each kind. Examples have been found with a large bias to each of the four types, but in a small plot of ground each type of bush was about equal in number. It would seem that the elements which go to make up these leaves are susceptible to two basic arrangements, tending to make intermediates which are halfway between the two and either right- or left-handedly asymmetrical. Even more striking are the leaves of *Gossyipium* in which there is a wide genetic variance as well as a marked ontogenetic one. (See, for example, the outlines of climax leaves shown by Stephens, 1945a, 1945b, 1945c.)

Similar to the leaves of sassafras but modified by functional differences are the asymmetrical chelae of many decapods. This, too, would engender another way of looking at the first-degree symmetry of most animals, as there is only one plane in which underlying structural symmetry can express itself, the ones that happened to be first degree getting away in a straight line in a locomotor sense, while those of a higher degree still seem to be trying to "march off in all directions at once."

Palmate leaves, furthermore, may be thought of as basically symmetrical in degree equal to their number of parts, distorted primarily by the stem attachment. Pinnate leaves may be thought of as a further distortion of the same thing or as simple linear symmetry. Since one can be generated by unrolling the other, the differences would seem to be more superficial than fundamental.

THE PERCEPTION OF SYMMETRY

Since the perception of symmetry is finally based on the limitations of the sensory apparatus—usually the eye, and the brain to interpret its reports—the environment determines to a considerable extent the recognition of symmetry. At a sufficient distance any object so decreases in visual size that it is reduced to a mere point. Thus symmetry and asymmetry can be considered as identical at infinity. Since natural objects never completely fulfill abstract mathematical definitions, at lesser distances symmetry or its lack usually depends on the closeness of measurement, visual or instrumental. This, however, in no way invalidates the repetitive arrangement of parts as a basic principle, its crudity of approximation being quite another matter not in the least associated with the underlying principles of geometrical order. The effects of symmetry, as perceived, on the observer have been discussed at length by Heymans (1896) and Mach (1902) and reviewed by Jaeger (1917).

THE INFLUENCE OF POLARITY

The foregoing mention of the appearance of symmetry, real and perceptional, is by way of introduction to the concepts to be developed concerning the biology of symmetry. The illustrative descriptive matter appears not to have any very substantial reasons for so being, until one considers the entire matter in reference to the basic nature of the directions imposed by elements of the environment and of the activities of the organism. Thus if we consider the environment as a field highly polarized in various manners and the individual organisms as more or less polarized in regard to their necessary basic activities and behavior, acting within this field and limited by the strictures imposed by it, it is possible to develop a rational approach to the basic nature of the aspects of symmetry as displayed by organisms. It is to be noted that in the section devoted to the geometry of symmetry there was no mention of field of force, the constructions being considered without regard to environment, as in the ordinary abstractions of the geometer.

Polarity may be defined for any system as follows: If such a system has no planes of symmetry except those which meet in a given line, that line is a polar axis of the system. Thus a sphere is symmetrical with respect to every plane through its center and has no polar axis. A nail has one polar axis from head to point and is symmetrical to every plane passing through this axis. An ax has two mutually perpendicular polar axes—one from haft to head, the other at right angles to this through the edge—and is symmetrical with respect only to the plane including both these axes. A scythe has three mutually perpendicular axes and no plane of symmetry.

Polarity of the Environment

All environmental features possessing direction and extent are considered as displaying polarity in present connections. Some are definite, uniform, and consistent and grade into those which vary, are irregular, intermittent or present under certain circumstances only. Some are primary and direct, while some have their effects on organisms in a secondary or tertiary manner. Features of absolute size of the organism become involved in the matter as well as the volume and mass of the organism in reference to those of the surrounding medium.

Gravity represents a vertical axis which pervades all environments. This polarity affects an organism directly through the gravitation of its parts and indirectly by providing horizontal surfaces of solids and fluids. As all physical objects in the environment are under the same influence, these, too, have secondary vertical axes, e.g., rainfall, the settling of dust, falling leaves, and so forth.

Other axes of polarity, such as the inclination of the sun's rays, the direction of water currents, prevailing winds, and so on, may be constant, variable, regularly recurrent, or irregular. Such polarities as these may be expected directly to influence the form of immobile organisms, such as rooted plants and sessile animals, but their effects on mobile organisms capable of turning about a vertical may be expected to cancel out so far as direct effects on structure are concerned but in its stead have influence on the immediate behavior of the organism.

Polarity of the Organisms

As already indicated, objects may or may not have a polar axis. Since organisms are, by and large, symmetrical constructions with less than an infinite number of axes, the nature of the polarization displayed by them may be examined. It becomes quickly apparent that the polarizations displayed are functions of their particular organic systems, the biologic functions of which in turn determine the nature of the polarization. For example, an organism with a respiratory system will necessarily have a polarity unless it breathes through apertures symmetrically placed on its surface. The same will hold true for a digestive, reproductive, or other system. Other morphological items will similarly involve polarities as specialized functions are developed. A mobile organism will have preferred direction of motion, as by walking, flying, or swimming, or even by being windborne, as in the case of a dandelion seed.

Since it is obvious that any polarity whatsoever limits the very nature of the symmetry of an organism, it is evident for the very initiation of such construction that the degree of symmetry attainable by any but the simplest of organisms is sharply restricted. Herein evidently lies one of the earliest directives of evolutionary progress, rooted in simple three-dimensional geometrical possibilities.

Polarity induced directly by gravitation will be least important in aquatic organisms in which the gravitational force is balanced by hydrostatic pressure, as compared with organisms of comparable size on land or living at the bottom or surface. Among the latter two there will be the indirect effect of the horizontal bottom or surface, while those on land have found no structural way to balance importantly the effects of gravity and atmospheric pressure by static means. In other words, no land animal has been able to develop an aerostatic condition such as is illustrated by a blimp. The direct effect of gravitation may also be expected to be less on very small aquatic organisms, i.e., organisms in which weight is so small that the internal hydrostatic pressure is much less than the internal pressure due to surface tension. With the surface tension and density of water the weight would have to be much less than 2 mg. for the gravitational influence to be negligible, if not offset by external hydrostatic pressure. Organisms dwelling on the surface of the land will have generally an indirectly induced gravitational asymmetry from this fact. Also we may expect to find an absence of marked polarity or an approximation to spherical symmetry only among very simple organisms, generally of small size. That we do is too patent to require extended discussion.

Among organisms having a gravitational polarity and having any high degree of functional specialization, at least two axes of polarity are to be expected unless either functional organs are symmetrically placed or the axis of functional polarity is coincident with the gravitational axis. The starfish is an example of the first sort. The mushroom, in which the nutritive axis coincides with the gravitational, is an example of the second. Perhaps certain jellyfish are examples also of the second sort. These have a preferred direction of swimming, but its axis coincides with the line in the structure which is the gravitational axis when the animal is resting.

Mobile creatures, among the higher forms, will generally have at least two perpendicular polar axes, the gravitational axis and the motor axis. Consequently such organisms cannot possess more than one plane of symmetry (the sagittal section), viz., the plane including these two axes. Moreover they cannot possess even one plane of symmetry unless all their other polar axes, such as those of respiration and digestion, lie in this same plane. Since many organisms at least approximate bilateral symmetry, it may be concluded that most organisms approximate the highest order of symmetry permitted by their environment and their possession of such faculties as reproduction, respiration, and digestion.

Viewed from such a standpoint it would appear that we may consider organisms as tending to assume or start from a spherical form with no polar axis. The change from this condition is evidently induced primarily by the influence of living in a field composed of a variety of polarized forces. The organism's own particular system of polar axes is dependent on these field influences, and their behavior depends upon what they must do in order to survive under the interaction of their own polarity and that of the fields of influence. Huxley and de Beer (1934) have discussed at length the influence of the polarity of the environment on that of developing eggs from a different viewpoint, and Child (1941) summarized his axial gradient concepts. Both these discourses are clearly related to the present views.

The principles of spiral growth, as set forth by Thompson (1942), refer to different growth speeds in snail shells in the various dimensions which are, in the present connection, a matter of distortion of a primary cylinder. That this shell is not basically a cone is because that geometrical form in itself is a distortion of a cylinder, resulting from the increasing diameter of the contained organism. However, as elaborated upon by Huxley (1932), the conic form is only distorted into a spiral by differential growth speeds. Since a cone built on the same basis as a cylinder is equally symmetrical, it is only when it becomes twisted into a spiral that it may be spoken of as a distorted symmetry as here understood. The mathematics of spiral growth has most recently been discussed in considerable detail by Lison (1940, 1941).

Grüneberg (1935), in discussing the basic causes of asymmetries in animals, presents a classification of asymmetries as to their origins which is quoted below.

I. Entirely endogenous asymmetries
   a. Asymmetries of genes or chromosomes
   b. Asymmetries of the substratum
II. Entirely exogenous asymmetries (environmental asymmetries)
III. Asymmetries caused by the interaction of intrinsic and extrinsic factors

It should be clear that this tabulation would be equally applicable to symmetry, as well, by merely substituting that word for asymmetry. Considered in reference to the foregoing discussion of polarity of both organism and environment, it should also be apparent that the same tabulation may be considered as a list of the conditions in regard to polarity by substituting that word. Thus this simple list may be expanded to cover the whole field of the interaction of the external and internal forces concerned with symmetry or its lack and with polarity.

Hubbs and Hubbs (1945) discuss at length asymmetry in fishes, ranging from the extremely asymmetrical flounders to minor variations in forms that ordinarily pass as symmetrical, and consider the matter in reference to tendencies for such asymmetries to be biased to the right or left. A large bibliography is given concerned with this aspect of departures from symmetry.

THE MORPHOLOGY OF ORGANIC SYMMETRY

The Organism as a Whole

After having discussed in general terms the nature of organic symmetry, we may examine these features from a standpoint of how they are expressed in organic structures, considering only the totality of the individual.

Generally speaking, plant growths, such as commonly displayed by the higher forms, have in their totality of form less regularity in the details of symmetry than the higher animals. For example, the number and disposition of the members, branches, and twigs of a maple tree are much more variable from specimen to specimen than are the members of a dog, or man. Probably more of this superficial difference is connected with the basic difference between sessile organisms and motile ones than with any other single item. Thus a sessile organism shows its response to the common polar field in terms of permanent growth which does not necessarily have any very precisely fixed pattern. A motile creature must be more definite in its architecture in order to be satisfactorily motile, but in turn shows its response to the polar field by prompt and large motor responses, which are impossible for a sessile organism. It has frequently been noted that sessile animals often show marked plant-like features in this regard. Moreover this very fact of indeterminate growth characteristic in plants, considering them as a whole, makes a discussion of them in the present connection more difficult than of the more definitely designed animal forms.

The various phyla of animals may be considered in regard to the type of symmetry that they display. Aside from Protozoa and their colonial aggregates, most animal phyla exhibit a fairly definite type of symmetry, being either bilateral (first degree, as here used), as in the case of the chordates, annulates, arthropods, and so on, or of a higher degree ("radial symmetry" of somewhat varying degree) in such as the Echinodermata and Coelenterata. That there are exceptions and that the larval forms often show differences in respect to their degree of symmetry preclude the listing of any simple arrangement by phyla and again emphasize the grand mixture of systems of symmetry to be found both in phylogeny and ontogeny.

The Symmetry of Organic Parts

It is obvious that any part of an organism may be treated, in regard to its symmetry, in an identical fashion with the above treatment of the whole organism. Parts could be conveniently listed according to their homologies. Although it is clear that symmetrical parts tend to retain their symmetry and asymmetrical parts their asymmetry even when their functions have changed widely, many exceptions to this general proposition exist. The features of it are sufficiently evident to obviate discussion covering a wide field. Sufficient data on the subject of the squamation of fishes are given under that head to serve as illustrative material of the wide scope of organic possibility opened by the combination of varied symmetrical systems and their interactions in a single organic unit.

THE INTRODUCTION OF TIME

Since the objects under discussion exist in time and have a past history, unlike a geometrical construction, the element t involves their nature and existence and variously modifies the entire concept. Thus the two features of growth and motion differ from form, per se, in being primarily conditioned by *t*. This may be summarized in the following terms.

1. Symmetry or its lack in any object or group is a function of the magnitude of the measuring device used, as already indicated in discussing the perception of symmetry.

A. Any asymmetrical mass may be found to contain symmetrical elements if small enough units be chosen, finally reaching molecular arrangement.

B. Similarly if it is large enough (or remote enough) so that the irregularities disappear, finally reaching a point at infinity.

2. Symmetry is rooted in molecular arrangement, which is a dynamic condition and is further rooted in mechanical necessity where motion is involved (and organization where growth may be considered as motion). Thus machines, animals, plants, crystals, and geological formations necessarily display evidences of symmetry. It is of interest in this connection, too, that Needham (1943) in an illuminating discussion of organic evolution and thermodynamics pointed out that in certain systems, at least, pattern appears with increasing entropy and that chaos in the sense of symmetry does not necessarily follow on progress from a less probable to a more probable state. Schrödinger (1945) develops a similar thesis, arriving at the thought that life is a process of avoiding decay to equilibrium by extraction of "order" from the environment.

3. The motion of objects likewise betrays symmetry comparable to the static symmetry of solids as radial, lineal, and surface symmetry, etc. All of this results from repetition in its various aspects and is another way of expressing Spencerian "wave motion." Thus a weight on a string being swung in a circle may be said to show radial symmetry of the *N*th degree as a figure of generation. The string breaks and the symmetry is changed to one of lineal symmetry (a straight line tangent to the circle) distorted by the influence of gravity into a parabola.

The Symmetry of Growth

Since organisms show various modifications in the nature of their growth, it follows that such features of animal transformation must be considered in connection with the maintenance of symmetry or its modification or destruction. If growth is regularly proportional, part for part, the original symmetry is maintained, that is, if only isogonic growth is involved the large animal may be looked upon as simple magnification of a smaller. However, if there is heterogonic growth, the changing proportions may or may not alter the nature of the symmetry involved. For example, in the case of a fish in which the jaws become longer with age, as in some species of *Tylosurus*, the animal maintains its bilateral symmetry, but no longer is a large fish the simple magnification of a small one. Such changes are exceedingly common and probably always present to some degree when any great range of sizes is encompassed. Probably true isogony is rare or actually absent, if sufficient refinement of measurements be made. In any of the more advanced forms of animal life, the appearance of isogony is probably only a matter of relatively slight and slow heterogonic relationship, only approaching true isogony as a limit. See Huxley (1932) and Thompson (1942) for extended analysis of such matters. Waddington (1933) and Needham (1934a, 1934b, 1936) discuss aspects of extensions of such growth relationships to the chemical ground plan of organic development.

Heterogony may, on the other hand, change the nature of the symmetry in a quantitative sense. Thus differential growth areas may cause the development of double spines where there was originally one. In organisms of more than first-degree symmetry this frequently leads to doubling the number of radially arranged parts and so doubles the degree of symmetry.

There are a variety of borderline cases which lead to further complications. The narwhal, which may serve as an example, starts life with paired tusks. By heterogonic growth one tusk far outreaches the other, so that relatively the one fails to make an external appearance. The fast-growing member shifts to a central rostral position, thus changing the animal from a form with symmetrically paired tusks to one with a single median member. First-degree symmetry is thus maintained in an over-all sense.

Illustrations might be found in nearly any growing structure, including the essentially spiral nature of plant growth, as discussed by Schuepp (1938). If there exists a large basic pattern of uniformity in such changes among any considerable series of plants or animals, much more work must be undertaken to uncover the basic trends and regularities. As in many such matters, at the present stage it appears there is a large mixture of general basic trends with particular generic or specific details, in keeping with the general tendencies of "heritage" and "habitus." There has been much work done on the nature of spiral growths; see, for example, Zimmerman (1893), Coleman (1912), Hambidge (1920), Duerden (1934), Preston (1939), Silen (1942), Thompson (1942), and Condra and Elias (1944).

Thompson's (1942) interesting Cartesian transformations of both symmetrical and non-symmetrical objects and their relations to the present discussion are obvious. If the object is of first-degree symmetry, that line of the grid which happens to fall on the axis of symmetry remains a straight line if the object retains its symmetry, as is clearly indicated by the transformations of Thompson shown for the carapaces of brachyurans. On the other hand, if an object of zero-degree symmetry, such as the lateral view of the avian pelvis during its transformations, no coördinate retains its rectilinear character. This is also true of the lateral view of Thompson's horse skull transformations, while a dorsal view of the same transforming skulls would retain a median straight line. This may all be considered sufficiently self-evident, but it may be worth pointing out that where transformations include the warping of a former straight line, an indication is present of a change in function involving a reference to some single-sided influence, as when an evenly fusiform fish becomes flattened on the bottom or top surface in reference to some plane above or below it.

If we consider the properties of symmetry as existing in time, which of course they do, we may then discuss them in terms of the fourth dimension, *t*. It may be sufficient to point out in this connection that such linear symmetrical objects as the proglotids of cestodes continually being added to at one end and lost at the other represent an extent of linear symmetry in the fourth dimension equal to the total number of segments produced in the life of the process. Lillie (1922) goes so far as to consider reproduction to be definable as "discontinuous growth," a concept distinctly pertinent in this connection. It is obvious that this kind of indefinite extent in time is possible only where the symmetry is an open system. In the complete, closed systems shown by circular symmetry and spherical symmetry, this kind of dimension in time is possible only with a change in the size of the elements involved. Growth, as of a starfish, after the pattern has formed is one of mass of tissue, not of degree of symmetry. Growth in this direction could be accomplished only by binary fission of each arm or the interlarding of new arms. This increase in degree of symmetry does actually occur in some coelenterates, *Craspedacusta*, for example.

The modern concept of the origin of vertebrates from the echinoderms of the crinoid group, if acceptable, represents an interesting transfer from a symmetry of the fifth degree to one of the second degree by immediate distortion. If, by way of illustration, we take some elongate design of several degrees of symmetry, say, for example, a lily, and press it carefully between the pages of a book, we have an object of second-degree symmetry which was previously of some higher degree. It is thus possible for a unit to change completely the superficial aspects of its symmetry by such a simple item as a bit of compression. Since acceptance of this origin of the vertebrates would have them derived from organisms showing fifth-degree symmetry, one wonders if it could be in any way associated with the fact that the terminal appendages of the tetrapods tend to have basically a five-degree symmetry variously distorted or fragmented. For a discussion of the origin of vertebrates from echinoderms, see Gislen (1930), Gregory (1934, 1935b, 1936), and Smith (1943).

Such transformations as above indicated are not alone to be found in the field of evolutionary speculation, for there are many living animals which undergo changes even more profound in their individual ontogenies. For example, the starfish starts out life as a larva of second-degree symmetry, giving no hint in its early days of the fifth-degree symmetry of the adults.

Such considerations naturally lead to a discussion of what was the primary symmetry of the earliest living things and what is primary symmetry and what are secondary transformations of it. Further studies by the electron microscope should enable a thorough working out of such matters in reference to virus forms as asymmetrical protein molecules or symmetrical combinations of opposite isomers or larger groups. However, since they are thought of as autocatalytic agents, it follows, by the nature of catalysis, that their basic activity is continually distorting whatever degree of symmetry they may show in a resting state. In other words, here life activity is being carried on with so few elemental building blocks that its very activity involves a continuing mutilation of the outline of the unit.

Passing on to things of which we make an optical appraisal, we immediately find organisms, bacteria, for example, showing for most part a well-organized symmetry of outline: rods, balls, etc. As soon as we come to cells, protozoans, or metazoan elements, we find symmetry of a further organized kind fully present. Incidentally, if the skewness of the protein building blocks were important to the partial asymmetry of the higher metazoans, it would seem likely that many of the smaller protozoans and bacteria would show an even more marked degree of this kind of modification. Actually such skewed structures are relatively rare at these lesser size levels. In the Protozoa we find all manner of various types of symmetry, as reference to any book illustrating various species will show.

The Symmetry of Motion

One of the most striking cells which superficially would seem to have no reference to present considerations is the amoeba. These wandering and amorphous cells are, however, no more characteristic of the Protozoa than they are of mammals, since all animals, except only the non-amoeboid Protozoa, are in part composed of such cells. These cells in their locomotor efforts distort themselves into all manner of forms not in the least symmetrical. In the resting form they are, however, apt to be symmetrical in some degree, presumably because of surface tension effects. Actually the kind of asymmetry the amoeba shows, while usually not so considered, is not dissimilar to the kind that man himself shows when in locomotion. Taking a man in the full stride of a walk, it is impossible to pass a plane of symmetry through him. Obviously the word symmetry, as ordinarily used in reference to animals, then, means that the aspect of an object, either man or amoeba, may be symmetrical if properly arranged, and it is present in both when the two are in what may be said to be a "resting" position. High-speed animals, such as birds and fish, moving through fluid media, must maintain symmetry of form to a certain degree because of streamline necessity while moving at their faster paces.

Locomotor asymmetry, because of its basic rectilinear nature, averages about the organism in question in a symmetrical position, so that considered in time the symmetry of a moving animal may be discussed in terms of the fourth dimension. The reduplicative poses recur in time, which, when reduced to two dimensions, form a track on a plane surface that is what we here call linear symmetry. A swimming fish shows this in an especially pretty fashion (see fig. 47 of Breder, 1926, or refer to the tracks left by any normal animal).

The incompleteness of symmetry also puts in an early appearance, as witness the arrangements of vacuoles, nuclei, etc., in Protozoa, and carries right on through the series, in a similar dynamic sense.

ORGANISMS AS GRAPHS OF FORCES

If a further analysis of the matters so far discussed be attempted, such analysis inevitably gravitates to a graphic treatment of form and the forces involved. Before entering this field certain general considerations, not so far discussed, are essential and are given in the following section.

General Considerations

That the basis of symmetry in organisms is not of any special attribute of livingness should be evident. Any question of this nature is readily answered by reference to inorganic structures that have been produced by a variety of investigators, such as Overbeck (1877), Traube (1878), Monnier and Vogt (1882), Herrera (1908, 1919), Leduc (1910, 1911), Lillie (1917), Rosett (1917), Stansfield (1917), Hatschek (1918, 1924), and Lillie and Johnston (1919), to mention only a few. De Beer (1924) discusses these structures in reference to organic development. These students have produced various physico-chemical reaction products which in some cases resemble living structures in form and behavior to a remarkable degree. The important item in present connections is that the morphological resemblances result principally from such artificial structures showing similar aspects of symmetry to those shown by various animate structures.

Conspiring to produce symmetrically disposed physical parts are such phenomena as surface tension, streamline influences, polarized fields, differential diffraction, molecular structures, osmotic pressure, and so on. As pointed out by Thompson (1942), the principles of minima and maxima in regard to films under the influence of surface tensions have been discussed at length by Steiner (1838) and Jaeger (1917); the effects of pressure on closely packed bodies have been discussed by Tutton (1911), Matzke (1927, 1931, 1945), Hein (1930), and Lewis (1933a, 1946). The geometry of the Fresnel diffraction patterns has been most recently studied by Kathavate (1945). Conrad (1946) discusses the mathematics and development of soil structure approximating hexagonal prisms.

Lewis (1923) expresses this thought as "... nature is ill at ease—restless—in the presence of asymmetry," which is actually a somewhat fanciful way of saying that a large number of physical forces interact to direct the development of both inorganic and organic entities towards an orderly or symmetrical arrangement. His discussion (Lewis, 1933a, 1933b, 1946) of the polyhedral shapes of cells gives a very clear exposition of the nature and results of some of these forces. The mechanics of pebble formation (Rayleigh, 1944) and the conditions leading to their various shapes are also pertinent in connection with a consideration of forces tending towards the production of symmetrical bodies. Chesters (1945) showed that porcelain balls in a ball mill under certain conditions tended to become cuboid. The behavior and the effects on the individual items going to make up aggregates even in the case of inorganic groups may be complex enough, but in the case of animal aggregations lead to profound modification of their behavior rather than physical form. Breder and Halpern (1946) discuss at some length the inorganic effects of aggregation as compared with the organic.

In recent years much has been made of the influence of the basic asymmetry of the protein molecule and its influence on the architecture of organic structures. (See for example Duerden, 1934, and Sleggs, 1939.) The latter finds a basis for reduplication in the manner in which protein lattices may be superimposed, from which he deduces a most ingenious and interesting theory of morphogenesis involving a concept of organic form as derived from a moiré of staggered lattices. If this theory can be established, it would give a more fundamental reason for the ubiquity of organic symmetry than any herein set forth, although they, in themselves, would appear sufficient. This view, in theory at least, should be resolvable by recourse to an application of the Fourier series. Whatever may be the significance of the form of protein molecules in the larger life forms, its influence is evidently at least frequently masked by massive influences. The remarks of Needham (1936) and Northrop and Burr (1937) are pertinent in these connections. (See also Gulick, 1939, and especially Child, 1946.)

In those animals that show a conspicuous bias, such as snails, there are genetic variants which show the reverse; that is, a species of right-handed snails will frequently have a genetic strain that is left-handed throughout. Ludwig (1932, 1936) reviews the whole field of dextral and sinistral forms. The genetics of the mollusk *Limnaea* and others in reference to the inheritance of right- and left-handed individuals is discussed by Harrison (1921, 1925, 1945), Sturtevant (1923), Crampton (1924), Boycott, Diver, Garstang, and Turner (1930), and Goldschmidt (1938). Gause (1939) in discussing the operation of this phenomenon writes:

"It may be supposed that the direction of the spiral is determined by some substance which is labile in the sense that it is able to undergo inversion of configuration with comparative ease. Such an idea is due to Koltzoff (1934) and to Needham (1934), who wrote that it is possible that the origin of dextrality and sinistrality in the eggs of certain snails, which later appear in the direction of spiral twist of their coil, is due to sterochemic properties of the protein molecules composing them. At present these relations are very obscure, and it seems essential to record accurately which physiological properties of dextral and sinistral spiral forms of organisms are identical and which are not. Such analysis is a necessary step in the attempt to comprehend the mechanism of morphologic inversions."

The organism *Bacillus mycoides*, which grows in colonies in which the radiating "arms" bend and branch all in one direction, was studied by Gause (1939). These colonies are consequently objects of congruent symmetry as here used. Usually these colonies grow sinistrally, that is, counterclockwise, but occasional dextral colonies appear. Gause found that these two growth patterns were hereditary in that on a given medium subcultures always resembled the parent stock. By varying the isometric characteristics of the growth promoting substances in the media, Gause concluded that the basic physiological properties of both right- and left-handed forms were the same and that the chemical basis of the phenomenon was not due to inversion of the basic protoplasmic system but to differences in some secondary substances determining the cellular form.

Castle (1936a, 1936b) considers the origin of spiral structures in *Phycomyces* as due to the interaction between turgor and elastic forces within the cell membrane and not as concerned with the theory of spiral growth based on peculiarities of molecular architecture. He presents an interesting model of spiraling under forces which may perhaps be considered as analogous. The reversal of the asymmetry of *Physalia* in reference to prevailing winds, as pointed out by Woodcock (1944), is an especially pretty case where there is evidently a functional value to be attached to such a mirror image reversal.

This brief consideration of symmetry in regard to various living systems should serve to show that it is impossible to postulate any particular basic pattern of symmetry, and that considered with regard to the geometrical portions of this paper it becomes evident that in living systems, which are reduplicating parts because of need or accident, any one of a wide number of reduplicative arrangements may put in an appearance and in fact switch sharply from one degree to another by very simple adjustments. However, as living forms became well established and relatively fixed by the very complication of their increasingly complex system of organs, it becomes more and more difficult for slight adjustments to modify the whole organism. Bearing on this is the view of Gregory (1924) of an increasing "loading of the dice" of chance which implies less and less possibility of fundamental modifications as complexity increases. Even so, each vertebrate egg starts out with external symmetry approximating the *N*th degree, and a single cell division, the first cleavage, transforms it to one of the second degree where it remains. The sphere is a solid of minimum surface and is automatically assumed because of surface tension, etc. This may be thought of as at the root of the underlying force which gives organic units a start with virtually infinite symmetry and which has within it all possibilities of the lesser degrees of symmetry. The immediate forces that cause changes from this to some definite lower degree are those which go to make it possible for living systems to display such a myriad of forms.

Trigonometric Functions

Thus far these concepts have been discussed only with reference to simple geometrical principles. If now the principles of trigonometry and analytic geometry be brought to bear, a variety of items become entirely clear that have not been brought up as yet in the simpler foregoing treatment. For example, harmonic motion is so deeply rooted in the environment that it should not be surprising that much can be detected in organisms that reflect response to this condition, which follows of necessity with a field uniformly pervaded by a force such as gravity. The classical example of the pendulum is probably as good a starting point as any. Here we have a quantity moving regularly from maximum to minimum and back again under the influence of gravity alone. Such a condition is expressible by the general equation,

$$y=a \sin bx$$

where y equals displacement of the pendulum, x equals time, a equals the maximum value of y, and b is a constant determined by the physical characteristics of the device. This formula and its derivatives appear again and again in connection with a wide variety of natural phenomena, including such things as ocean waves, a spider dangling on its thread, the swing of the human leg. The relationship of the parts of all such mechanisms is found in the common diagram basic to all trigonometric considerations, such as is shown in figure 18A. Point p travels in the direction of the arrow in a circular path of radius, r, at a constant speed. The normal projection of the point p on a diameter of the circle, as q, correspondingly moves back and forth along this diameter in accordance with the motion of p. From elementary trigonometry it is evident that, for unit radius, the line p-q is the sine of the angle q-o-p and the line q-o the cosine. The graphic representation of such harmonic motion is indicated in figure 18B which is a graph of

$$y=\sin x$$

The curve of the sister equation

$$y=\cos x$$

is identical with it except that it is displaced along the x axis so that where the sine curve reaches a maximum the cosine curve is halfway between crest and trough on that axis. In this case the constants a and b each equal 1. Changing a serves to increase or decrease the amplitude of these curves, and changing b affects the wave length. Not only is this basic equation useful for pendulums, reciprocating steam engines, levers, and other simple mechanical contrivances, either man-made devices or organic systems, but it is also basic to any understanding of the wave motions of physics such as sound waves, alternating currents, and the entire electromagnetic series from Hertzian to Roentgen rays. Other modifiers brought into this equation enable it to express all manner of complicated phenomena, which, as will be developed, have distinct bearing on the morphology of growth and the present concepts of symmetry.

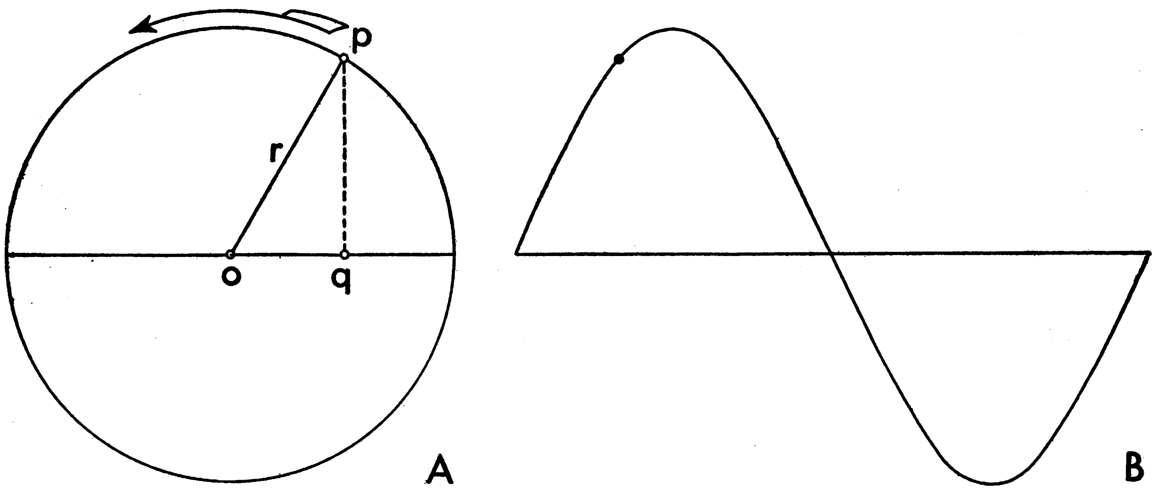


FIG. 18. Diagram of the simple sine relationship and its projection. A. The development of the primary trigonometric ratios. B. The trajectory of the point p as moving along a straight line.

Returning to the pendulum, a real physical pendulum differs from the ideal one so far considered in that unless continually supplied with energy, as in a clock, it slowly comes to a position of rest. The graph of this shows such a curve with a constantly decreasing amplitude but with a constant wave length.

Leaving this consideration for the present, it is pertinent that some mention of the nature of graphs be made at this time. If the usual coördinates, the rectangular Cartesian system, in which the x and y axes are at right angles to each other, are used, curves such as have been under discussion will be presented as shown. If some other angle than 90° be employed, appropriate changes occur in any curve based on them. The construction may be thought of as being compressed after the fashion of the arms of a pantograph and is indicated in figure 19A and B. Any other transformation involving diverging or curved lines may be employed, as shown in figure 19C. If the y coördinate lines cross at a point and the x coördinate lines are made circular with their concentric centers at the focal point of the y coördinates, the well-known and useful polar coördinates result in which the distances from the center are measured along the y axis, and the x values become the angular distances between the y coördinates and are then usually expressed as θ, as shown in figure 19D. It is to be noted that this type of transformation is not the same as the ordinary algebraic method of changing curves expressed in rectangular coördinates to polar coördinates in which

$$x = r \cos \theta$$

and

$$y = r \sin \theta$$

or

$$r = \sqrt{x^2 + y^2}$$

and

$$\theta = \text{arc tan } y/x$$

Thus far these have all been considered as on a plane surface. Naturally they can be applied to a curved surface, convex or concave, with distortions of the ordinates which are along neither x nor y. A common case of this sort is shown by the meridians of longitude and parallels of latitude used on a terrestrial globe. The ordinates of longitude are all great circles, while those of latitude are not, except only for the equator. The significance will appear later in a specific connection.

Further than this, solid "graphs" in which a z axis is introduced may be used and are naturally not expressible easily on a sheet of paper since they involve three dimensions. Distortions of this and the introduction of time and non-Euclidean space and concepts of relativity would lead us far afield from the application of such graphs to organic design.

Thompson (1942) applied a typical Cartesian grid to various animal forms and then, on related and somewhat dissimilar forms by drawing through homologous points similar coördinates, he obtained coördinate systems distorted in a regular manner as compared with the original. He admitted that the mathematical treatment would be difficult and pursued the matter no further. It served to indicate clearly, however, that such transformations proceed in a regular systematic manner and that in evolutionary terms the modifications were not merely capricious, but were moving according to coördinated mechanical and other restraint, however complicated that may be. Few have pursued the matter further, and no one has attempted to break the concept down to more understandable terms. While it is true that any transformation from one grid to another will show a change, and so any grid may be taken as a starting point, it does not necessarily follow that the selection of one is as useful as of any other. With this in mind it should be worth while to explore the possibility of selecting an initial grid which bears some reference to the order of symmetry expressed by the form under consideration. Generally, Cartesian grids have been used as a starting point, although Breder (1944, 1945) used polar coördinates for such a special purpose.

If we consider some object, such as an earthworm with its long axis of symmetry and which expresses what has here been called linear symmetry, there are obvious reasons why, in expressing it graphically, it be referred to a right-angled grid. On the other hand, such a form as a starfish with no linear symmetry but with circular symmetry of a certain degree clearly belongs in treatment to a grid of polar coördinates. It is just this that has led to the breaking down of symmetry into so-called bilateral and radial types, but it is to be especially noted that this is between circular and linear symmetry (between a circle and a straight line) and not between circular symmetry of the first degree and all for purposes of analysis. If, rather, we consider the form in question as the graph and then attempt to find the "invisible coördinates" implied but not showing visible exist-

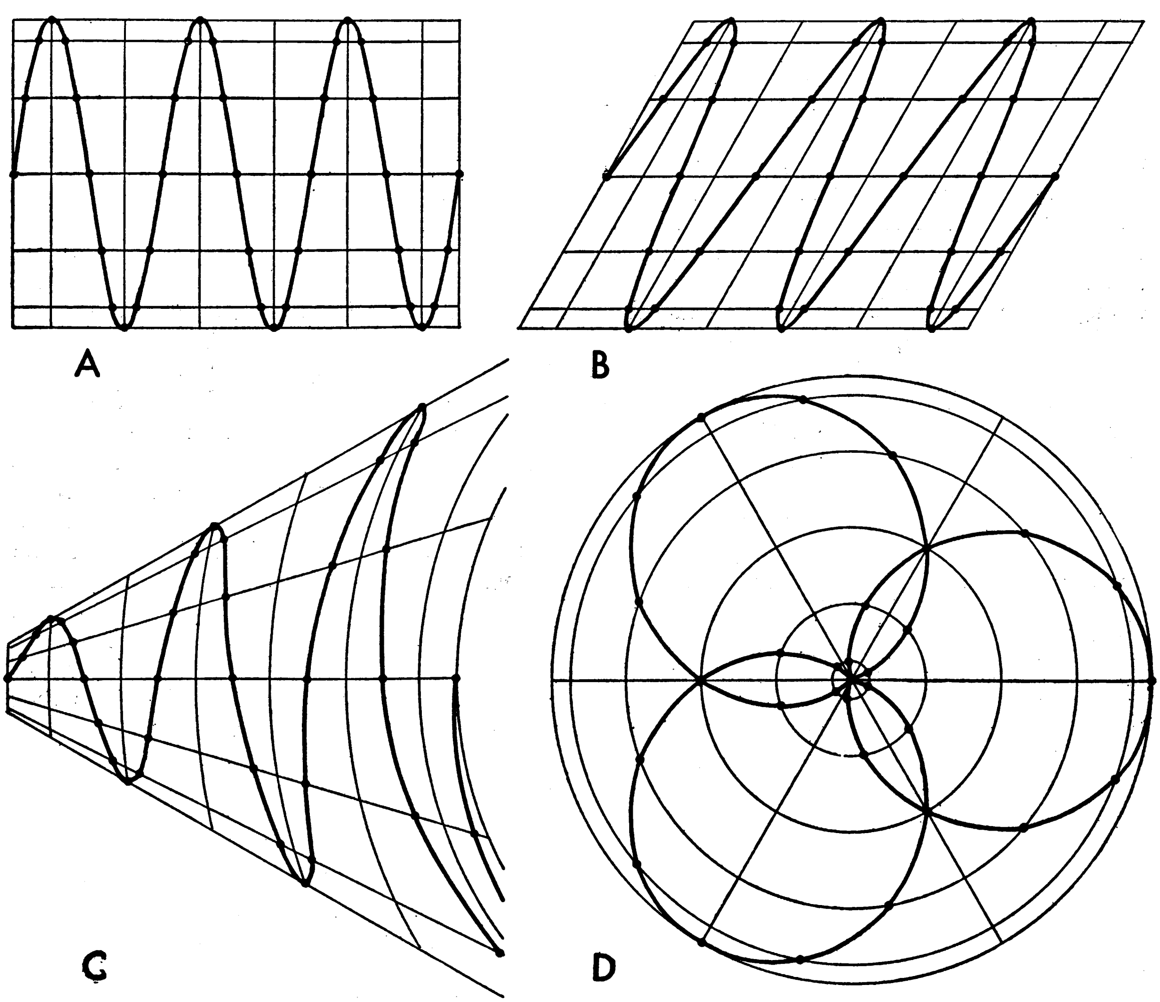


FIG. 19. Transformations of the sine curve. A. In the original form with rectangular (i.e., right-angled) coördinates. B. With coördinates intersecting at other than 90°; 60° in this case. C. With coördinates one set of which is radial and the other concentric about two different points. D. With coördinates one set of which is radial and the other concentric in respect to a single point, i.e., polar coördinates.

other degrees. What is here called circular symmetry of 1° may be equally well represented by either a Cartesian or polar grid.

Viewed from a slightly different angle, there is every reason why organic units should be looked upon as being graphs of the forces involved. This is related to, but not identical with, the views of Thompson (1942). He took a form and drew an arbitrary grid about it ence by studying the symmetry of the system and any other usable characteristic of the system, the suitable grid should, at least theoretically, become evident. In simple cases this is readily done, and in fact Thompson himself has indicated a number in other connections as well as their derived equations. From this it should follow that the study of morphology in passing from a descriptive and comparative stage would tend to become analytical to the extent to which it is able to view its material in terms of graphs and equations representing the summation of the forces involved. This it will probably not be able to do until it frees itself from the use of such terms as "homologous" in referring to actual structures of considerable complication. Only by limiting such terms to mathematical abstractions can one avoid the continual confusion which has surrounded them.

When once the form can be expressed by an equation and comparisons made between shifts in various mathematical constants as expressive of evolutionary or ontogenetic changes, we shall have a tool of considerable merit. For example, in the current genetic studies of the shape of cotton plant leaves (Stephens, 1945a, 1945b, 1945c) and of cucurbit fruits (Sinnott, 1935, 1944), even now it should be possible to consider these genes as representing various constants in the equation descriptive of the form and whether they are substitute terms or modifiers (in both the genetic and mathematical sense) of it.

If growth is conceived of as a movement in time and the various proportional changes as changing ratios, certain features of growth phenomena may be studied from a standpoint of their geometry, apart from the strictures of the demands of life processes, by recourse to certain mechanical aids. If we think of a line as "growing," as a pencil moves along the surface of a paper, it is at once obvious that it may show both growth (increases in length) and modification (angular change). A pencil in the hand of a man is capable of producing the most complicated figure of which he can conceive and execute, which may be symmetrical or not. In this sense the product may be thought of as the totality of the neural activity which actuates the pencil, and that it may be exceedingly complex should not be surprising. Freeing the pencil of the direct influence of man, and his past conditioning, by purely mechanical means it is possible to construct other complicated products derived directly from very simple geometrical relationships.

Such simple constructions as a straight line, a circle, an ellipse, etc., may be combined by purely mathematical or mechanical means with resulting constructions that are complicated in a degree that would hardly be anticipated. That certain of these features have a direct bearing on the problems in hand will be subsequently shown.

A variety of such equations has been worked out by various students, often closely approximating the form of various radially arranged flowers. (See, for example, the work of Grandus, 1728, Lartigue, 1930, or Thompson, 1942.) Other biologically more remote curves have been the preoccupation of pure mathematicians from early times. (See, for example, Möbius, 1886a, 1886b, and Loria, 1902, 1911.) Decheverns (1894, 1900) devised an interesting but complicated machine for producing curves of special characteristics bearing on these matters. The province of kinematics is largely devoted to such matters, with the emphasis on the locus of a point under various influences and restrictions. In the course of the present studies much of this large literature was explored in a search for treatment of a family of curves that developed in present considerations. Since no recognition of this group or its basic equation has been found in either recent or ancient literature, it is discussed at some length herein because it happens to be expressive of a rather large number of simple forms that appear in natural objects under a wide variety of conditions and situations. It was basically derived from a consideration of the form of eggs, although it is far from limited to such structures. The work of Mallock (1925) and Schönwetter (1930) is without bearing on the present approach. Thompson (1942) has a chapter on eggs, but does not attempt to consider an equation expressive of them. Although the locus of certain points inherent in certain kinematic systems is expressed by the equations in question, kinematicians have apparently not studied this particular element since their efforts tend to be directed to other matters.

The graphic representation of pure harmonic motion has already been discussed, and figured in figure 18, and on a stationary paper is seen to trace a straight line. If a similar arrangement be considered, but in which the line c intersects the extremity of the radius r and also any point such as o_1 at all times, as is shown in figure 20, this line c has a reciprocal motion as r revolves uniformly. A point on this line such as d has its locus on such a figure as is shown by the dotted line in figure 20, which in this case is egg-shaped, and is symmetrical about line b connecting the center of the circle o and the point o_1. By varying r, b, and c, a wide variety of figures may be produced, as is shown in figure 21. It can be shown that these are descriptive of many natural conformations in addition to the obvious egg, including such

$$e = r \sin\theta = d \sin\phi$$
$$f = r \cos\theta$$
$$k = d \cos\phi$$

Then erecting a perpendicular from e through the point on d marking the value of c, the following relationships are found:

$$\phi = \phi_1$$
$$a = c \sin\phi_1 = c \sin\phi$$
$$h = c \cos\phi_1 = c \cos\phi$$

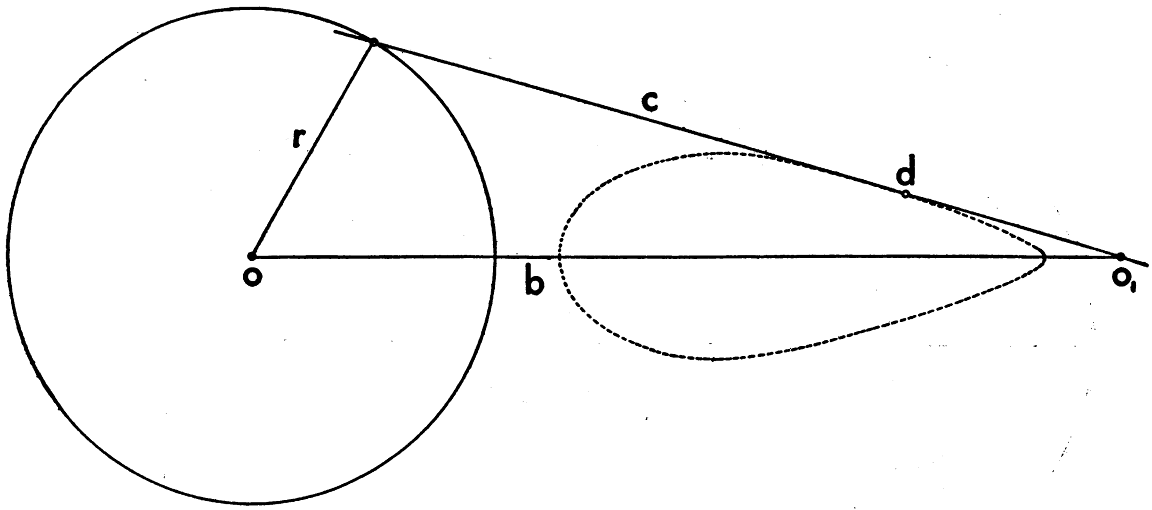


FIG. 20. The geometry of the egg-shaped curve. See text for explanation.

structures as beans, kidneys, leaves, the cross section of many fish bodies, fruits, and so on.

The mathematics of the system is not very involved as is demonstrated below. In the triangle of figure 22A, derived from figure 20, let

- r = radius of the circle
- b = distance from the center of the circle to a point
- d = a line connecting that point with r on the circumference of the circle
- c = the distance from the intersection of d and r on the circumference of the circle to a point which is on the locus of the egg-shaped figure
- θ = the angle of r with b
- ϕ = the angle of d with b
- ω = the angle of r with d

Then erecting a perpendicular from b through ω, the following relationships are found:

Transferring this figure to a system of Cartesian coördinates with θ at the origin and b on the X axis, as in figure 22B, the following relationships are found:

$$X = f + h$$
$$Y = e - a$$

Therefore, from the above relationships,

$$X = r \cos\theta + c \cos\phi$$
$$Y = r \sin\theta - c \sin\phi$$

The values necessary to solve the equation that need be known, since they are the only ones that determine the nature of the figure, are b, c, and r. θ is assigned any or all values, and the corresponding values of ϕ may be calculated.

In polar equations the expressions may be represented by

$$\rho = \sqrt{(X - (c+r)^2 + Y^2)}$$
$$\tan\theta = Y/(X - (c+r))$$

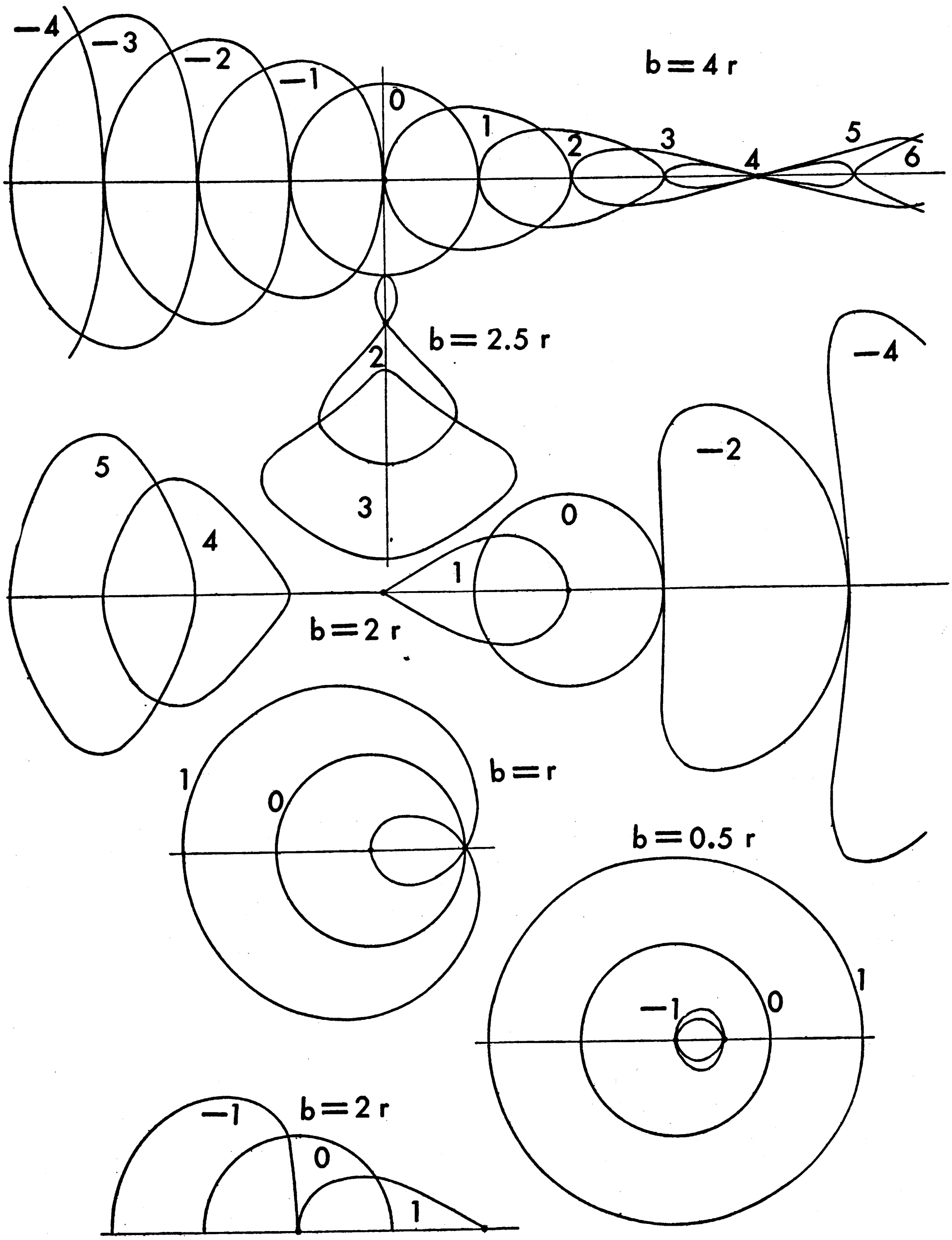


FIG. 21. Variations and relationships of the egg-shaped curve. Values for b in terms of r are indicated for each construction. Values for c are indicated within or adjacent to each figure.

which places one end of the egg-shaped figure at the pole. Omitting $(c+r)$ leaves the figure in its original position.

If, then, for example, the paper on which the egg-shaped figure is being drawn is moved at a uniform rate along a straight line, a wave form is produced which differs from the sine curve of figure 18B only by the amount in which the egg varies from a straight line. Other modifications of this curve of considerable complication may be obtained by introducing additional or curvilinear motions to pattern characteristic of many organic activities, a spiral will be produced, the nature of which is determined by the speed of the turning paper in reference to the speed and acceleration of the radially moving pencil. If the pencil is not moving along some radius but along some other line not passing through the center of gyration, modifications of the spiral result. If the acceleration is in the nature of an exponential, then the equiangular spiral and gnomonic relationships, already discussed, put in an appearance. It is this

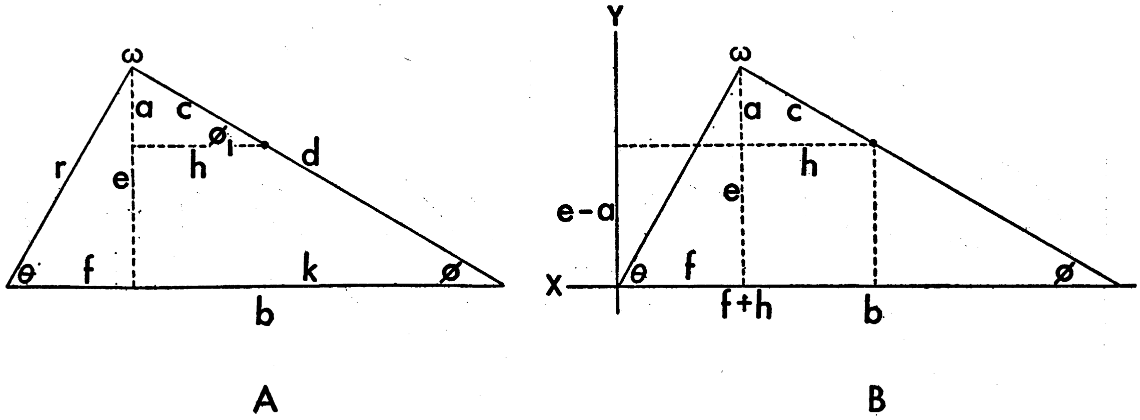


FIG. 22. The derivation of the equations for the egg-shaped curves. A. The basic geometry as based on figure 20. B. Introduction of Cartesian coördinates.

the paper. If, for example, a circular motion is provided, a whole series of related figures of striking difference may be produced, beginning with a simple circle, in which case the paper rotates and the tracing point has *o* motion, and in present terminology represents a figure of an infinite degree of symmetry. In this connection it may be noted that circles may be described by many inorganic natural activities in addition to those described in connection with surface tension and similar simple physical attributes of matter. Such include rain drops falling vertically on soft mud, broken sand dune grasses blowing around the erect portion of the stem as a center, lunar and terrestrial craters, and so on. Returning to the pencil and turning paper, it is obvious that if any motion, regular or otherwise, be imparted to the pencil other outlines than those of a circle will result. If the pencil moves radially in a straight line, while the turntable revolves, another simple relationship that Huxley (1932) expresses as the law of constant differential growth by

$$y = bx^k$$

in which x equals the magnitude of an animal as determined by a standard linear measurement or by its weight minus the weight of the organ concerned, y equals the magnitude of the differentially growing organ, and b and k are equal constants. This relationship he found to hold for considerable periods in comparing the growth rate of certain parts to the growth of the whole body.

If, on the other hand, the pencil is arranged to move through a cycle instead of continuously in one direction, still other configurations result. If harmonic motion is imparted to the pencil while the turning paper revolves, some interesting results may be obtained by adjusting the various constants involved. Likewise a circular path, an ellipse, or the egg-shaped figure may be so applied.

The infinite variations that may be applied to these are dependent purely on the values given to the constants involved in the equations expressive of them, which basically include only the relative speeds, distances, directions, and accelerations of the component elements involved in the "growth" of the number are to be considered, and since the factors are all capable of being expressed in a mechanical construction, i.e., speed, distance, direction, and acceleration, a machine was devised to facilitate such studies. The machine is shown in plate 15, and some of the typical settings of which it is capable are indicated in figure 23. Its relation to harmonic motion and the egg-shaped figure is evident from this diagram. Some of the figures drawn by this device are shown in figure 24, together with the equations for them. These are all of a simple order in which the symmetry is not greater than the fifth degree. A comparison of the figures with their data shows that the determining factor in this is the nature of the ratio of the revolutions of the turntable

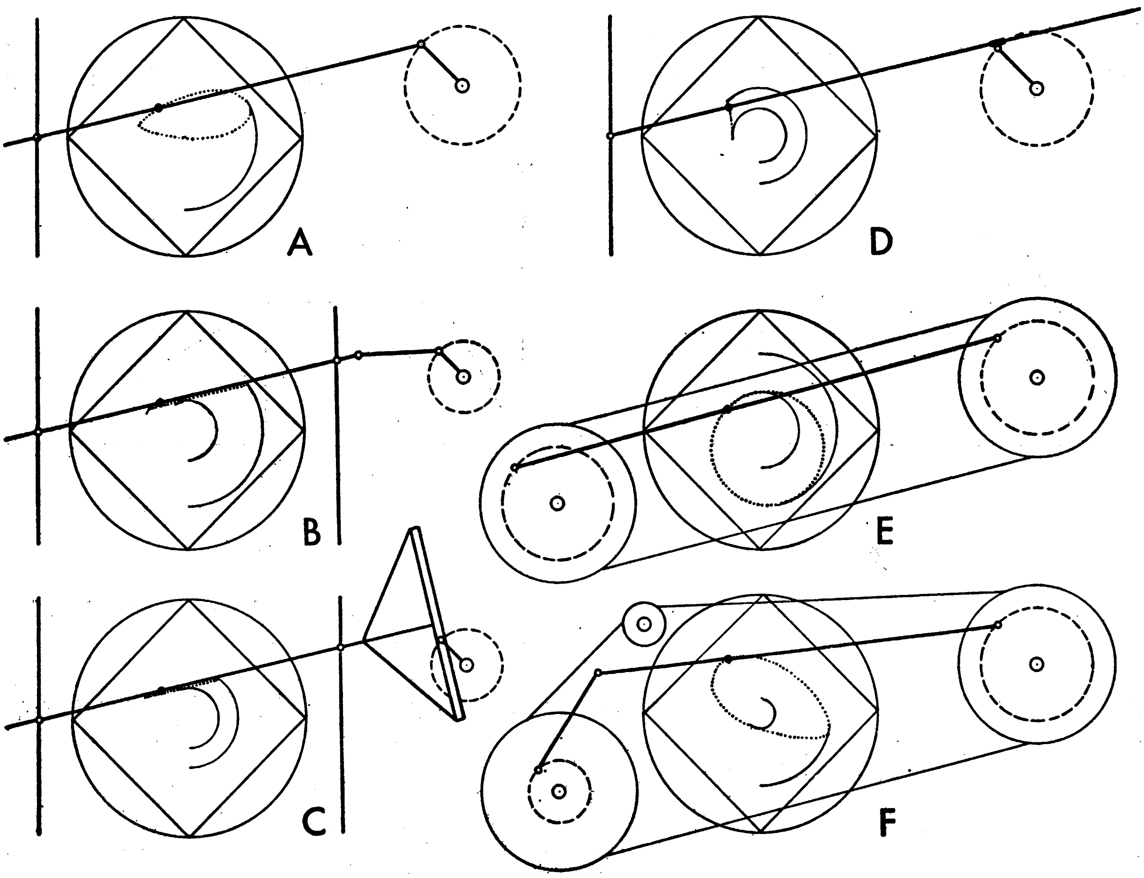


FIG. 23. Various settings of the sine machine. A. Setting for the egg-shaped curve. B. Setting for a modified harmonic. C. Setting for pure harmonic. D. Setting for a circular arc. E. Setting for a circle. F. Setting for a modified egg-shaped curve. The dotted line represents the trajectory of the tracing point as it appears when the rotation of T equals 0. The solid arcs indicate the size of the circle that limits the design both exteriorly and interiorly.

constructions. One of the most impressive parts of these features is the small amounts of change in a single factor that will produce fundamental changes in the nature of the resulting pattern.

THE SINE MACHINE

Since the construction of such patterns from equations is an obviously laborious and time-consuming task, if any considerable to that of the cycles of the tracing point. The higher this value the greater the number of parts before the tracing part returns on itself. If these numbers are mutually incommensurable, the design fills in solidly, and the degree of symmetry is infinite.

There is no intention to go deeply into the mathematics of these figures in the present contribution. The pure harmonic relationships are sufficiently evident and are the same as equations that were worked out years ago by students of analytic geometry and that are generally familiar. Below, a few of the simpler ones are listed, together with the ratios of the revolutions of the turntable, T, to the cycle of the harmonic, D. These are given with one end of the harmonic line touching the center of gyration. When otherwise disposed, modifying factors appear.

T	D	Equation	Figure
0	1	$\rho = r$	Straight line
1	1	$\rho = r \sin \theta$	Circle
1	2	$\rho^2 = r^2 \sin 2\theta$	Lemniscate
1	3	$\rho = r \sin 3\theta$	Trifolium
1	4	$\rho = r \sin 2\theta$	Quadrifolium
1	5	$\rho = r \sin 5\theta$	Quinquefolium
2	1	$\rho = r \sin \theta/3$	Limaçon
3	1	$\rho = r \sin \theta/4$	"Double" limaçon
4	1	$\rho = r \sin \theta/6$	"Triple" limaçon
5	1	$\rho = r \sin \theta/8$	"Quadruple" limaçon

For other motions of the tracing point the equations become more involved. For example, the egg-shaped equivalents of the above

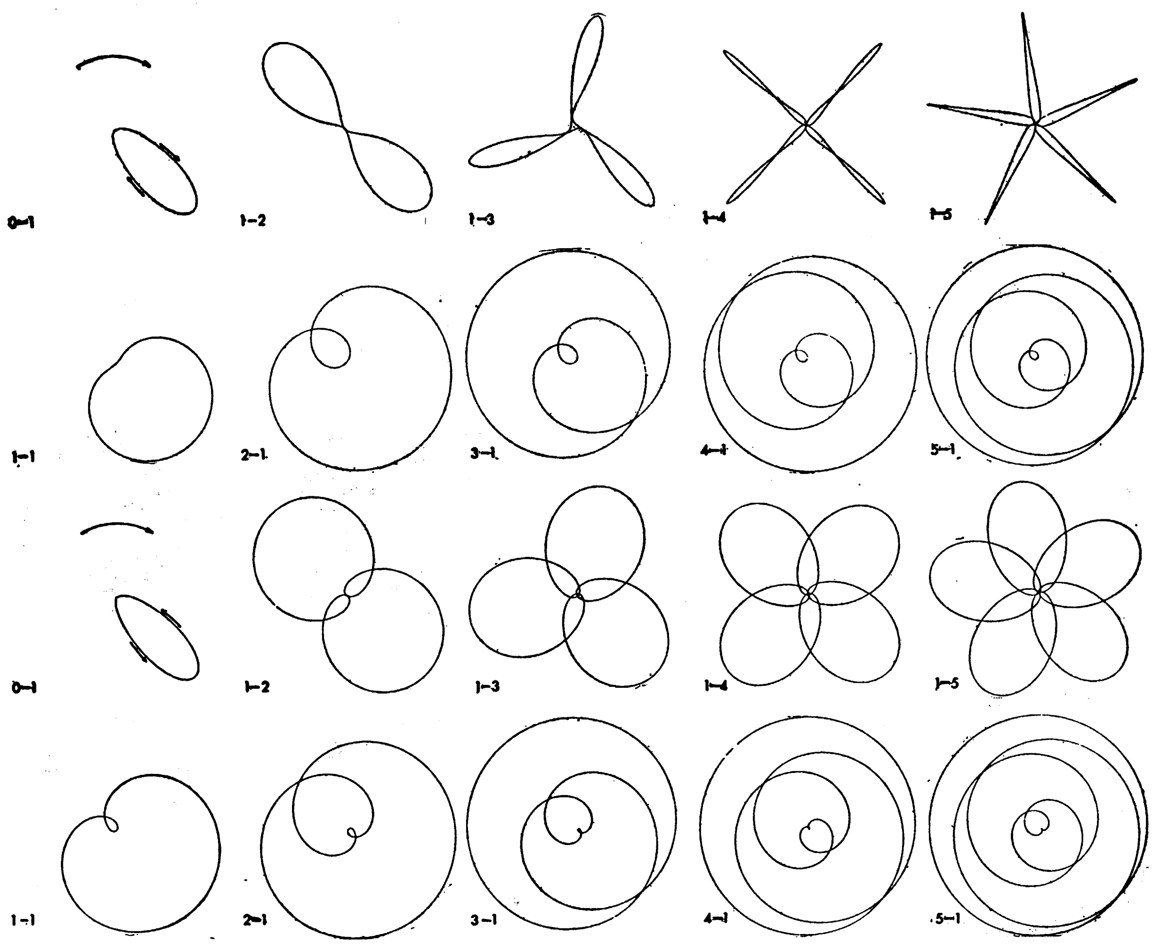


FIG. 24. Simple machine-drawn figures. The ratios of T and D are indicated in each design, T being given first. The first 10 designs show results with direct drive and the rest the same ratios with reversed drive.

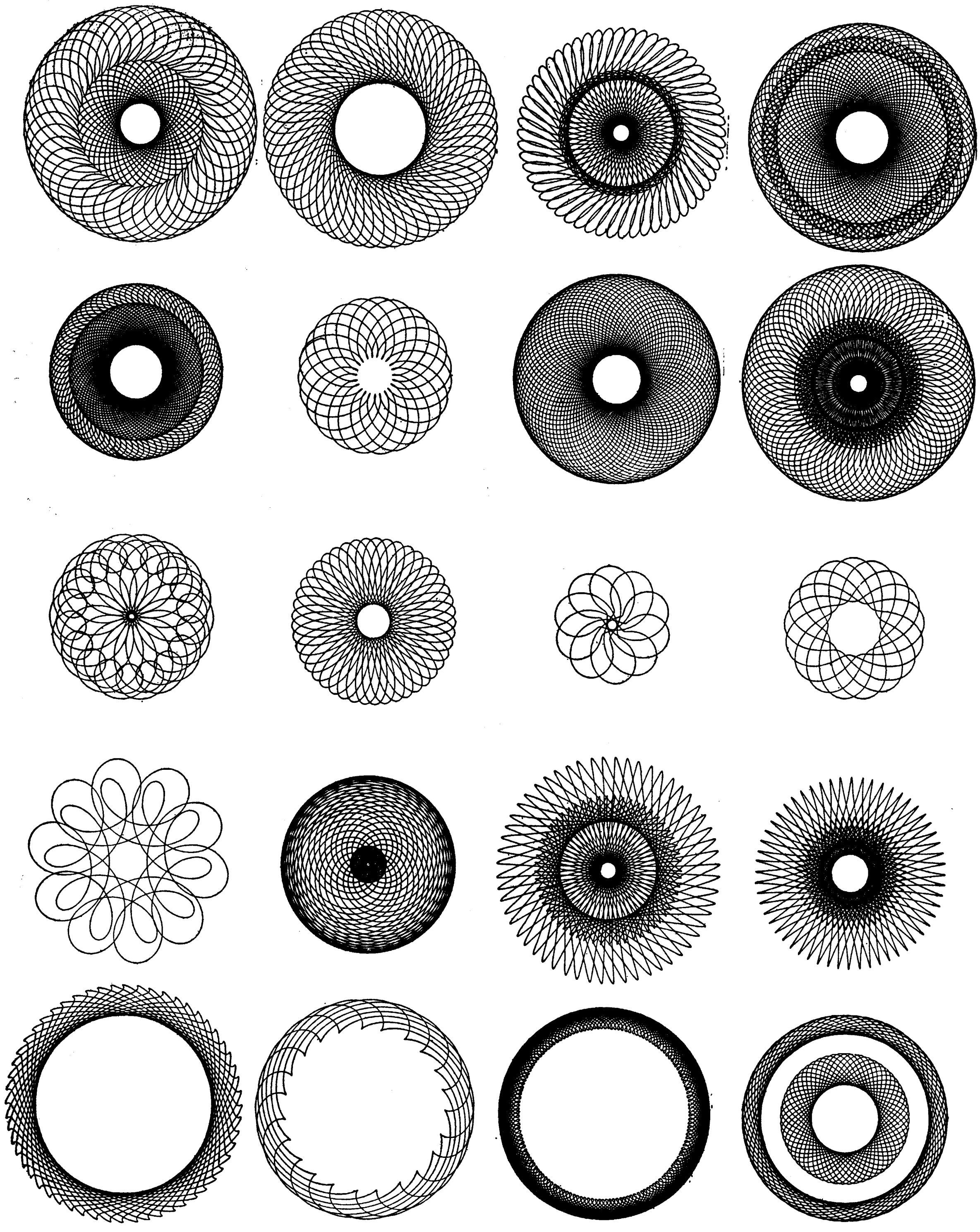
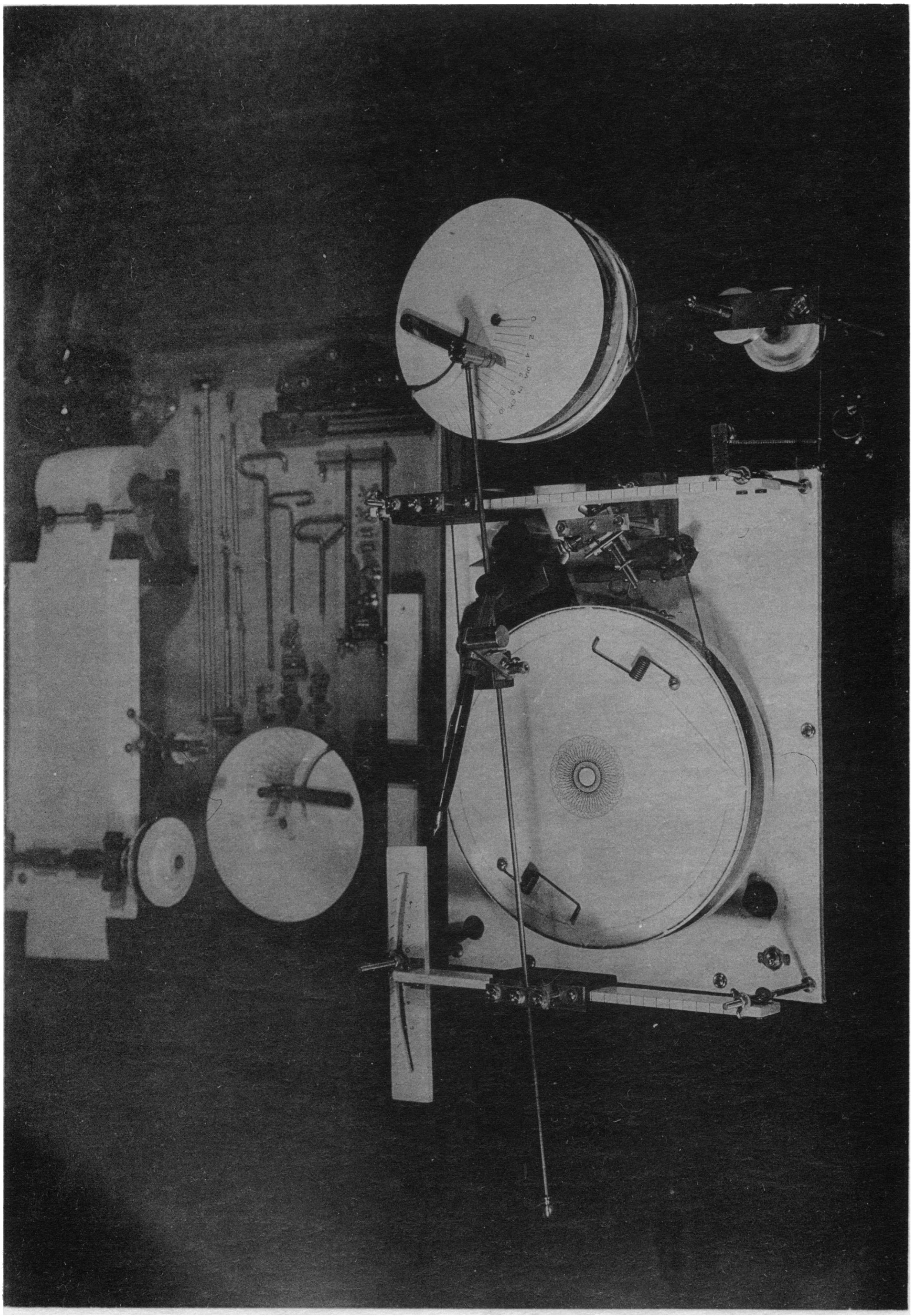
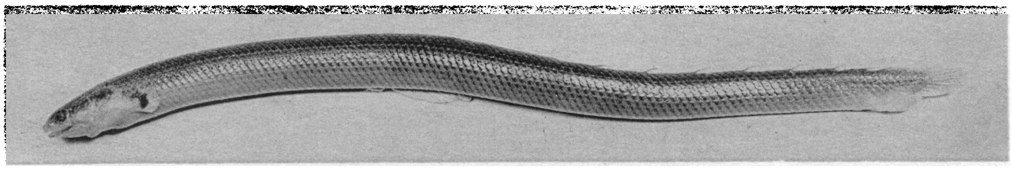


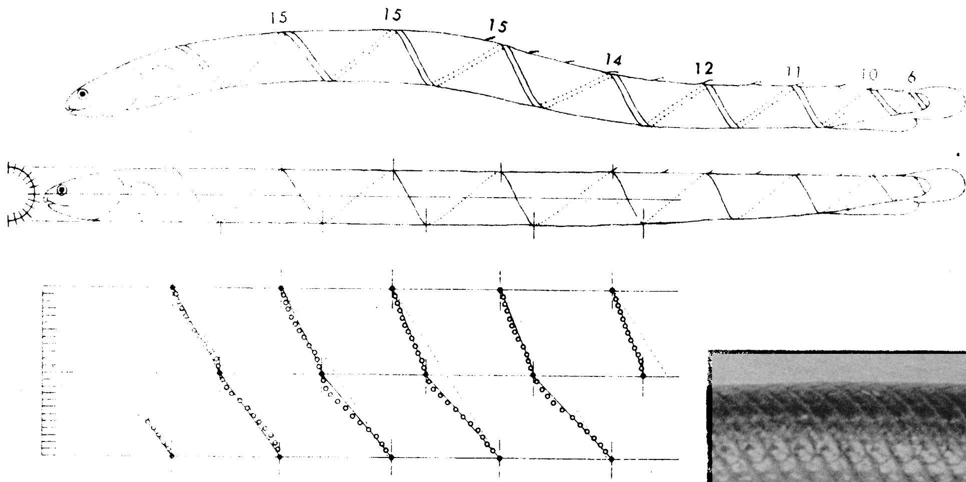
FIG. 25. A selection of various machine-drawn designs based on higher ratios than those shown in figure 24.



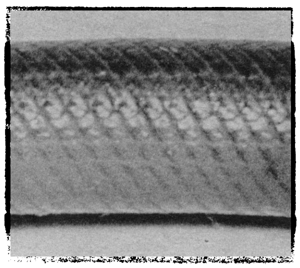
Sine machine showing the entire device, with extra parts for various settings



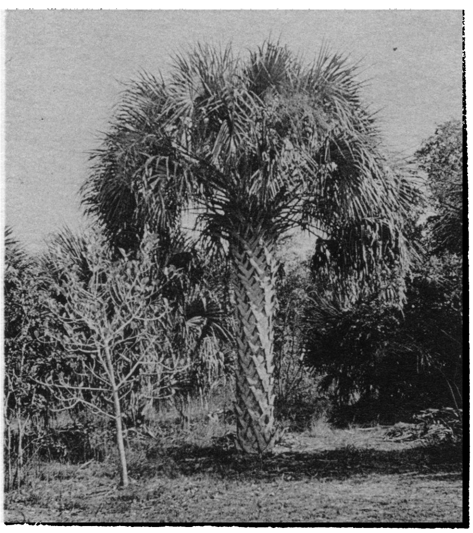
1. Photograph of a *Calamoichthys calabaricus* (Smith), of 19.5 cm. standard length



2. Graphic analysis based on above photograph. Upper outline indicates the winding of a single row of scales with the numerical values of the rows. The middle outline indicates the same outline straightened out and with the scale row indicated as a single line. The lower diagram indicates the cylindrical portion of the fish unrolled. The dots mark points of reference in this reconstruction. The central horizontal line is the midventral line, while the upper and lower meet along the back. The dotted lines connect consecutive points on the back and represent the geometrical geodesic. The solid lines connect dorsal with ventral points and indicate change in angle at this point



3. Photograph of cylindrical portion of fish



4. Photograph of *Sabal palmetto* with the dead leaves removed, showing the basic geodesic nature of their attachment

5. A closer photograph of *Sabal palmetto*, indicating the nature of the stalk attachment

Analysis of geodesics on nearly cylindrical objects are modified appropriately by the equation already given for that figure.

Curves of this nature drawn by the machine are shown in figure 24. The first 10 of these correspond to those equations given for pure harmonic motion, but are appropriately modified by the above considerations and resemble those of pure harmonics quite closely because the basic egg is not very broad. In fact the pure harmonics can be considered as the end point of the egg-shaped series in which the egg is compressed to a line or in which its breadth equals 0. These figures, both those based on pure harmonics and those based on the egg-shaped figure, have considered T and D as revolving in the same direction, i.e., both clockwise or both counterclockwise. If they are moved in opposite directions instead, in the case of pure harmonics, the same identical figures result, but such is not the case of the egg-shaped figures because the egg has breadth and the tracing pen is moving up one side and down the other in reverse order. The figures so produced are also shown in figure 24, from the eleventh on, and correspond accordingly to the first 10. The machine very simply produces these by crossing the belt which connects the two shafts. In manually plotting such curves the same result is obtained by giving negative values to θ.

Other modifications of such constructions which may be mechanically rendered by the machine with various settings as suggested in the diagrams of figure 23 run through essentially similar sets of comparable figures. In other words various families of curves may be drawn by the device which are clearly related, according to the settings of T and D, if the other possible variables are permitted to remain constant, each modified from its counterpart only by the amount of difference in the form of the figure produced by the reciprocating element. All, except that of pure harmonics, have two sets depending on whether the revolutions of T and D are in the same or opposite directions. This has distinct bearing on animate structures, for while harmonics are abundant in animal growth and motion, it is much more common to find that the harmonics are not pure and are modified in manners not dissimilar to those shown by the machine-made curves.

In the constructions under consideration

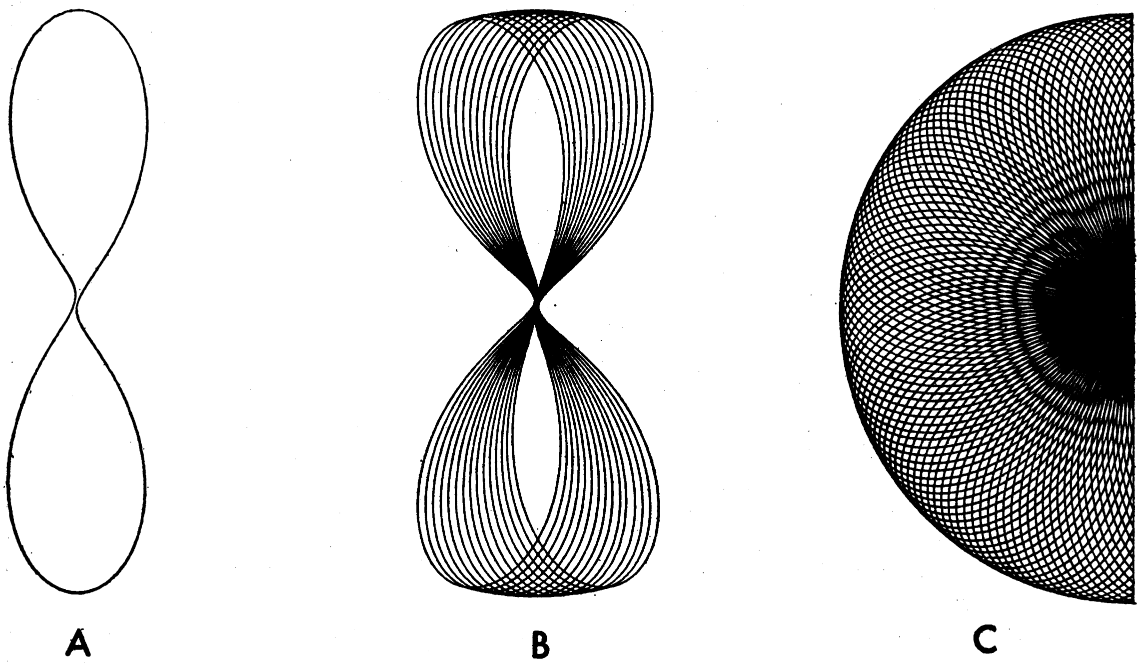


FIG. 26. A. The lemniscate when D/T equals 2/1. B. The same when D/T equals 2.006/1 but not carried to completion. C. One-half of design D/T equals 2.006/1 carried to completion.

simple ratios between T and D have been used, reaching up only to 5/1 and 1/5. If higher ratios are employed, very elaborate and ornate constructions may be produced, of infinite variety. An illustrative selection of such is given in figure 25. They all reduce to modifications of the basic formulas already discussed. In all, the tracing point eventually returns to its starting point except as already indicated, when D or T is incommensurable, in which case the figure goes on to infinity and produces a solid circular disc filled in completely. The interesting point in present connections is that a very minute change in the ratio of D and T will produce a great change in the pattern. If, for example, the simple lemniscate of figure 26A, based on T equals 1 and D equals 2, is ever so slightly modified so that D, instead of equaling 2 equals 2.006, the figure does not return on itself for a long time, and instead of a simple double loop a complicated pattern results. Such a case is shown in figure 26B and C. By gradually increasing the value of D from 2 to 3 a whole series of complicated patterns may be produced, returning to a simple construction only when 3 is precisely reached and the trifolium results. Such a series runs through infinitely complex series with incommensurables appearing between any two of commensurable values. The same is, of course, true for the entire numerical series, the ratio of D and T determining the nature of the design.

Variations of other constants in the equations go through different but approximately analogous series in which slight changes produce enormous changes in the character of the design at certain critical points. For example, if the value of c is changed, while the other constants are held at one value, a series may be produced similar to that of figure 27. As the point of the egg passes to either side of the center of gyration, the figure changes fundamentally, but well out to either side the nature of the comparatively slight changes is apparent. Such matters are similar in the other constants, the magnitude of the changes being proportional to the variation of a given constant.

The point of this is simply that in such a system there is a series of critical geometric values which produce tremendous changes in the resulting structure, although the change in these determining values is exceedingly small. In actual practice with the machine, even with its relatively few possible variables, it was found rather more difficult to avoid passing such a critical value in making adjustments than in finding them. Thus such a system is seen to have the rather remarkable properties that in making large changes, such as from an egg-shaped form to a circle, parallel families of designs of minor differences result, while within any one family of such designs, complete transformations of pattern result from microscopic modifications. Through these large changes induced by slight shifts, return is always made to simple systems where prime numbers of small size are involved, which brings us back to the corn-field patterns of figure 9 and the prime factors of table 2, in which the same features are seen to be expressing themselves in a different pattern.

Since many natural objects closely approximate such designs, which was pointed out long ago by Grandus (1728) for flowers and has since been discussed in various ways by many more recent students, a few of whom are noted in the bibliography, it is no longer necessary to undertake to prove that such mathematical regularity is the common property of organic form, as has been most abundantly shown recently in the treatment of the subject given by Thompson (1942). Thus the question may be posed as to why so many natural forms show such simple relations of what here are reduced to T and D, when it is possible to produce all manner of complications by slight changes in these two factors. Actually the more complex conditions are also to be found, but the simpler ones have been more extensively considered by students, presumably because they are amenable to simpler mathematical treatment. For example, within the Compositae very high orders of symmetry are to be found. Considered in terms of the machine equations it would seem that a simple, few-petaled flower could pass immediately to a complex, many-petaled one by a very slight shift in the values of what forces involved could be represented by D or T. Not only could transition be made from a few-petaled condition, but also transition could be made from a simple center to a central disc or head as is shown in some of the designs of figure 25. Related to this is the condition in the squamation of fishes where large-scaled fishes may be closely related to minute-scaled fishes, a matter which is discussed at length subsequently.

closely related to forms with huge scales. Thus the condition which would be eliminated would differ widely with each item and group considered.

The whole field of animal form could be examined from such a standpoint, bringing in the problems of teratology, including such things as twinning, polydactyly, and so on. Referred to linear symmetry, the questions

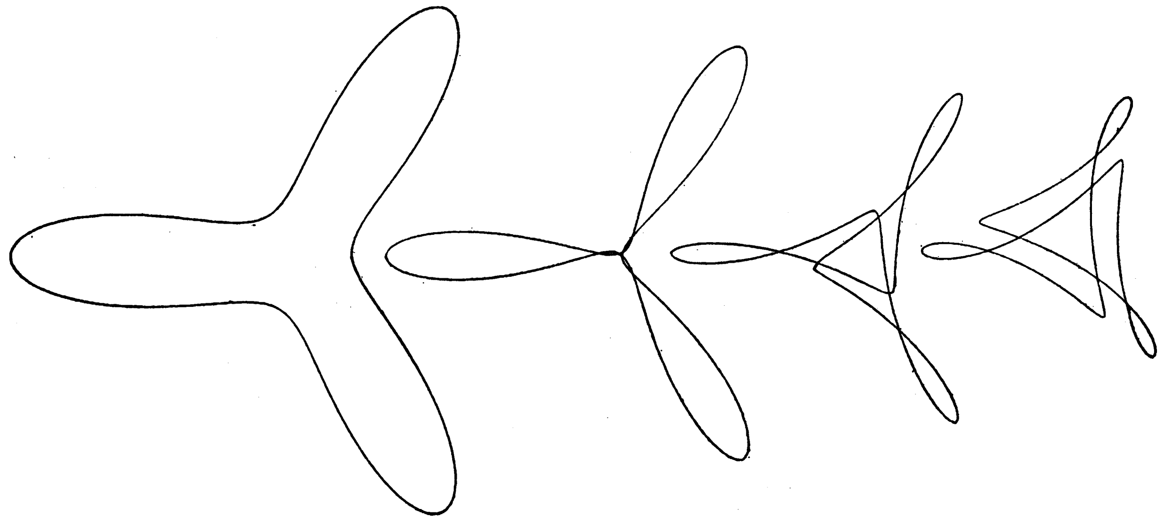


FIG. 27. Changing designs with slight changes in *c*, in which *D/T* equals 3/1 and all other values remain constant.

of metamerism bring up the possibility of reducing Gregory's anisomers and polyisomers to growth constants in terms of mathematical expressions.

From these considerations it should be evident that these related forms are displaying in a more complicated organic fashion what may be called a "principle of imperfection" where a simple factorial relationship between growth forces "slips" to a relationship of a higher order which, as has been shown both mathematically and mechanically, is induced by a micrometric "misalinement" of the controlling influences. If such is the case, the surviving forms would be those which are not lethally modified and which represent nodal points in such a series. If this is a sound thought, it is easy to see why some forms would be readily eliminated. For example, an incommensurable relationship in the Compositae is impossible, for instead of a petaled design of high order a uniform disc results in which the details become infinitely small. On the other hand, such a condition in the squamation of fishes would result merely in nakedness which is common in some fishes, often

Another matter that it seems possible such an approach might help illuminate includes some of the broader aspects of evolution such as the disputed question of macroevolution and microevolution. Considering the designs evolved by the machine, we have what might be considered a model of macroevolution and microevolution but in which there are several families of designs, each of which goes through similar kinds of changes but each within itself produces sharply differentiated types which are largely parallelisms of those in other groups. Considering the simplicity of the mathematics involved and the mechanical simplicity of the device as compared with the forces involved in organic structures, both physical and chemical, the very fact that it is even possible to attempt to trace such an analogy impresses the writer that it is exceedingly unlikely that such resemblances as may be found are purely accidental and of no deep-rooted significance. Since we can show by purely mechanical means that variations in types of designs can be influenced by very minor or by large changes to produce either large or small modifications, and since these interact upon each other, it should perhaps not be surprising that students of organic form have produced theories of evolution (organic change) in which on one hand small, continual modifications have been proposed while on the other large saltations have advanced. Currently many students, e.g., Simpson (1944), have tried variously to reconcile or combine both views which in a purely mechanical sense are not mutually exclusive.

In addition to the foregoing concerned with form and evolution, this "principle of imperfection" would seem to have application in connection with animal behavior. For example, the dogfish, *Mustelus*, searching for food by process of olfaction, tends to describe figures that are close to the lemniscate in outline, but because of imperfections in it do not cover a simple figure-of-eight track but actually completely cover large areas in a manner not unlike that of the tracing pen of the machine similar to that shown in figure 26C. With one nostril occluded, the dogfish swim in spirals with the open nostril on the concave side. These paths may be comparable to a litus or some exponential and again because of imperfections cover a large area. An attempt to plot such tracks produced by hungry dogfish in a uniform environment should be illuminating.

Here, indeed, would seem to reside part of the appearance of independence of animal behavior. Being neither completely tied to a given path, as is a train on a track, nor moving fully at random, as do Brownian particles, organisms responding to various drives by "appropriate" reactions of greater or less accuracy would be expected to show variations, both individual and temporal, as a consequence of imperfections in behavioristic symmetry.

The Design of the Sine Machine

For those who may be interested in the design of the machine that has been discussed, the following details are given. The general appearance is indicated in plate 15, and some of the possible arrangements are shown in figure 23.

The turntable, T of the equations, was mounted on the platen of an electric phonograph, and the motor of that device supplied the entire power for operation. The turntable consisted of a piece of maple 10 inches in diameter on which pulley grooves were turned with diameters 9, 8, 6, 5, 4 inches. On a common base, to the right, were mounted two vertical shafts with ball thrust bearings. On these could be mounted pulleys of various diameters, depending on the ratio of D to T desired. The second of these shafts, which acted as a countershaft, made it possible to obtain a wide variety of ratios by using this as intermediate. On top of one of these shafts was mounted a flat disc on which was placed an adjustable crank arm on a bar pivoted near its edge. Thus the radius of D could be varied from 0 to the radius of the disc which was calibrated for convenience.

At the extreme left was mounted a transverse calibrated bar on which rode a clamp supporting a pivot for the rod which carried the pen. The distance from this pivot to the center of D represents b in the equations. This arrangement produced the egg-shaped curve and is indicated in figure 23A. The pivot consisted of a short length of steel rod with countersunk holes in each end into which were set two pointed steel screws, on which bearings the rod freely rotated. A hole was drilled transversely through the rod, into which fitted the element connecting the pivot with the crank arm. At that end of the rod a collar was mounted. A clamp holding a good fountain pen was mounted on this rod so that the pen could move in a vertical plane. This was provided with a weight sufficient to provide writing pressure. Spring clamps on the turntable held squares of paper in place. This could accommodate squares of 7 inches. The accuracy of the machine, of course, is dependent on the quality of the machine work involved in these moving parts. The cross bar supporting the pivot was adjustable as to height and could swing radially at one end for purposes of accurate alinement.

A second cross bar was provided between

T and *D*, enabling the employment of other curve forms. In these cases the rod bearing the pen had a straight-line motion between the two pivots, as shown in figure 23B and C. The first employed a radius rod as in a steam engine connecting with the crank arm, as shown in figure 23B. The second employed a slotted cross head, as in figure 23C, and this alone provided pure harmonic motion.

case an idle pulley must be provided to prevent the belt from interfering with the pen's movement.

Many other arrangements, limited only by one's imagination, can be provided by this device, but for present purposes these illustrations are sufficient.

In addition to these basic features, an electrical control was built into the machine

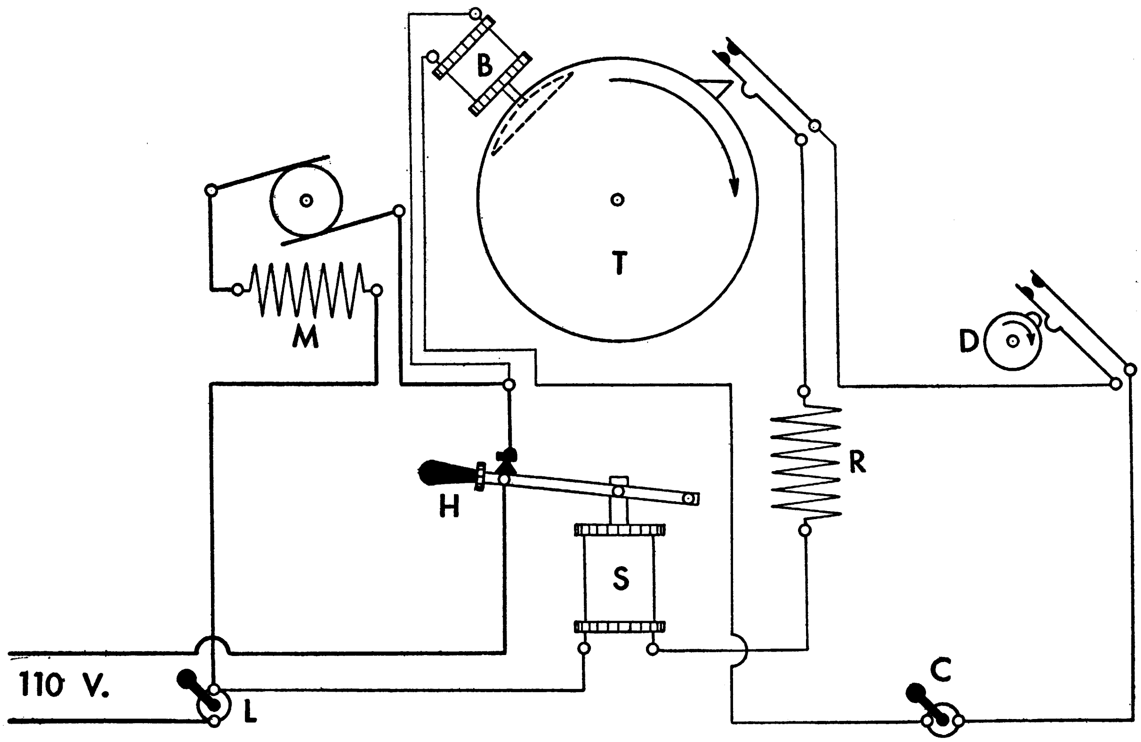


FIG. 28. Electrical control circuit of the sine machine. See text for explanation.

By anchoring the pen-bearing rod on the pivot, as shown in figure 23D, and providing a collar attached to the collar on the crankpin so that it would travel back and forth on the rod, arcs of circles could be produced by the pen. By providing a second rotating disc with an adjustable crank arm and connecting the two by a belt, the pen would produce circles, as is indicated in figure 23E. The diameter of the two pulleys and the setting of the crank arms must be exactly the same. If not, as in figure 23F, a joint must be provided in the rod; egg-shaped curves are again reproduced, but they vary from those produced by the simpler arrangement. In this

so that when it was once set in operation it would stop when the design was finished. This obviated the need for watching the machine come to completion of the design, which in certain cases is not always easy to judge, and enabled the machine to be run at speeds far beyond the point of optical fusion. Control of speed was provided by adjusting the speed control of the phonograph motor so that it could be run as fast as the load on the motor would permit down to the slowest motion at which the motor would operate, so that, when desirable, it was possible to study the growth of the design at very slow speeds.

The automatic stop feature was possible

because in any given case the revolutions of *D* and *T* come to the same relative positions to each other when they have completed one full cycle and are about to begin over again. The electrical circuit is shown diagrammatically in figure 28. The letters in the following description refer to that figure. Single small projections were provided on *D* and *T*, each of which closed a small contact. A toggle switch, *C*, was provided to cut out these contacts. With this switch open the machine was started with the *D* and *T* contacts closed, i.e., with the projections so adjusted that both bore on the spring finger of their respective contacts. Then after the machine had started and the projections had moved away from the contacts, allowing them to open, the cut-out switch, *C*, was closed. Thus the circuit controlled by *D* and *T* would remain open until the two respective contacts were closed simultaneously, which could not happen until the full cycle had been gone through, at which time the design is completed. When this happened a selenoid circuit breaker, *S*, which was controlled by the *D* and *T* contacts, cut the current from the motor, and a selenoid brake, *B*, clamped against the turntable, preventing coasting of the turntable and overrun of the design. As the motor was operating on 110 volts, a resistance, *R*, was employed to reduce the current that operated the control feature to about 18 volts.

After the circuit breaker had cut off the power, it was necessary to reset this switch manually. This was operated by a small lever, *H*, projecting from the left of the case. When this feature was not desired the toggle switch at the front of the case, *C*, cut out the entire control mechanism. The motor, *M*, was worm-geared to *T*, and the switch, *L*, cut off the supply line.

ON THE SQUAMATION OF FISHES

THE GENERAL BASIS OF SYMMETRY having been discussed at length, it may be useful to examine one of the more complicated evidences of such phenomena.

Most fish scales are symmetrical objects where produced remote from the distorting influences of fins or other eruptive structures. Whether they are or are not symmetrical individually, they group to form a surface pattern of symmetry as already discussed (see fig. 6D). Considering this surface pattern, in a small area, on virtually a plane surface, as the side of a compressed fish, we have such a pattern as typified in the above-mentioned figure. Since, however, the total surface of a fish is not a plane but a variously distorted cylinder, double cone, or other solid, it follows that the pattern of squamation must be appropriately modified.

Nor is this all, for by suitable analysis the whole arrangement of the squamation of a fish may be shown to subscribe to certain basic principles. The nature of these is known to fish artists, as they must recognize such matters, even if not consciously. The details of these basic principles, however, have received scant attention from ichthyologists.

THE ARRANGEMENT OF SCALES

If, for example, one takes such a fish as a tarpon and traces one diagonal row of scales, it will be found to wind around the fish in a continuous course from head to tail. Likewise, if one takes an intersecting row of scales, it will be found to wrap around the fish in a reverse direction. This is indicated in figure 29F. Furthermore, it can be easily shown that a thread so wound about a fish substantially falls on the line of scale rows. That is to say, the scale rows on the bodies of a fish, in either direction, are following well-defined mathematical lines, the geodesics of the geometricians. The truth of this postulate will appear as the argument develops. Also, since the underlying myomeres bear definite relations to the arrangements of the scales, it follows that this effect is more than skin deep, and it may not be an exaggeration to say that this geodesic arrangement of the scales has an influence on the whole structure of the creature.

If we examine fishes generally in respect to this feature of squamation, we find that they tend to follow geodesic lines closely. Seeming exceptions in cases where the scales have been reduced to the point of disappearance, or enlarged and modified into individual bucklers, or are otherwise highly specialized will be discussed later. This arrangement, as will be shown, has bearing on the relation of the size of the fish to size of the elements in its exoskeleton. The angles of the intersection of the crossing geodesics and the number of complete revolutions, however, are all characteristic of the form and the group to which a given type of fish belongs. A thorough survey of fishes in this regard is without the province of the present communication, but a brief examination of a variety of fishes is clearly indicative of the evident trends.

Before entering into a discussion of such matters, however, an understanding of the basic nature of the geodesic line is essential. Thompson (1942), after a considerable discussion, defines the geodesic " . . . as a curve drawn upon a surface such that, if we take any two *adjacent* points on the curve, the curve gives the shortest distance between them." Simple examples of this are given in figure 29. In that figure A shows a cylinder with such a line drawn parallel to its axis and another drawn parallel to its base. These are the two extremes possible on such a solid: a straight line and a circle. Any other line will be a helix, an example of which is shown in B. In the case of a sphere, such as in C, the only geodesic is a "great circle," the reasons for which may be found in any elementary treatise on solid geometry. In the case of a cone the straight line and circle are possible, as in the cylinder, and any geodesic not either parallel to the base or in a plane with the axis becomes a spiral helix, as indicated in D. Actually only one-half is shown in the illustration, for after reaching the apex the spiral travels down again oppositely. In either an oblate or prolate ellipsoid the geodesic forms more or less elaborated figures-of-eight as indicated in E.

According to Thompson (1942) this may be expressed mathematically as follows:

$$r \cos \quad a = k$$

where r equals the radius of the circular section, a equals the angle at which the radius is crossed by the geodesic, and k equals a constant which is measured by the smallest circle that the geodesic can reach.

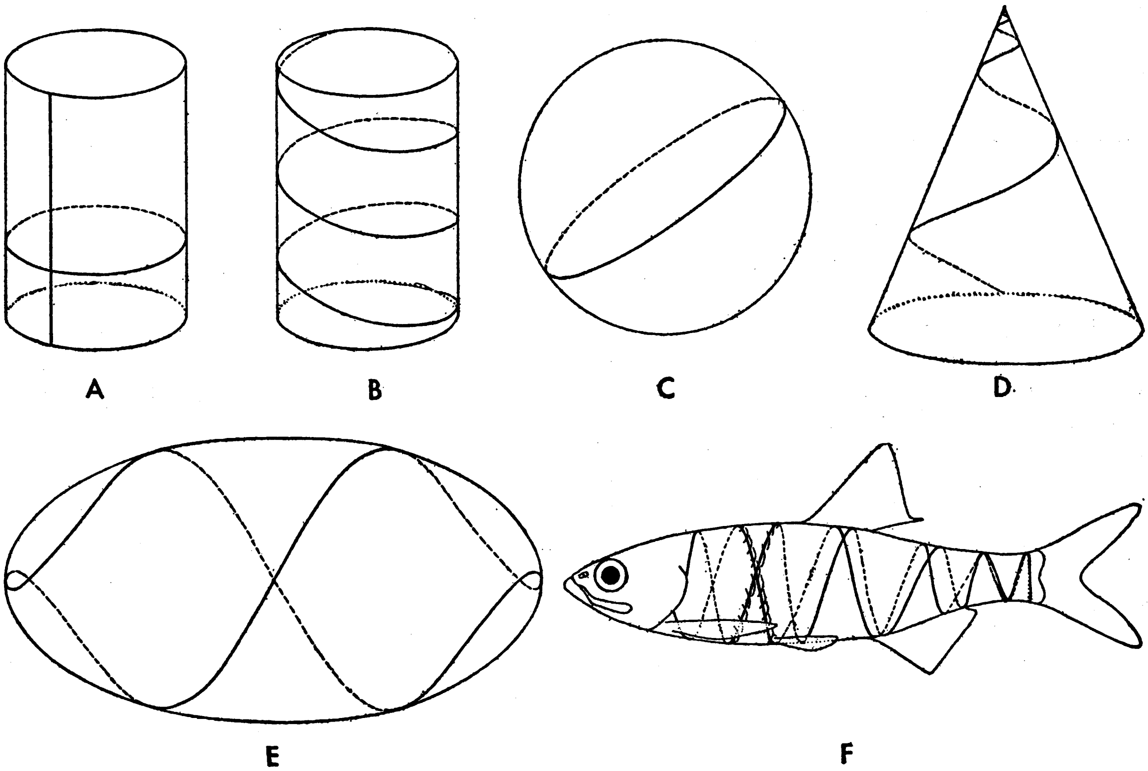


FIG. 29. Geodesics on solids of revolution and on a fish. A. Cylinder with a geodesic parallel to the axis and another at right angles to it and parallel to the base. B. Cylinder with a geodesic not parallel to axis or base. C. Sphere with its geodesic (great circle). D. Cone with a geodesic not in a plane with axis or parallel to base. E. Prolate ellipsoid with a geodesic not in the plane of the minor or major axis. F. A *Tarpon atlanticus* of 15 cm. standard length, showing lines following two scale rows indicating their basic geodesic nature. The actual scales are indicated at one place of intersection of the oppositely winding rows.

As indicated before, this is the line a stretched string will take between two points, that is, the shortest distance between them confined to the curvature of the surface. If we now refer this to a real fish, as is done in figure 29F, in which a tarpon is shown, it appears that the scale rows are actually following a geodesic on the surface of a solid which may be looked upon as a modified (mostly compressed) solid of revolution.

The mathematical treatment of this is rather involved (see, for example, Alexandroff, 1945), but it may be easily demonstrated mechanically on actual specimens by the string method above mentioned. A string started from a pin pushed into the fish at some point, wound so as to follow the scale rows will hug the form tightly. If these rows were not geodesics, such a stretched thread could not follow them for it would automatically snap to its own geodesic. Since it can conform to those lines marked by the scale rows and still wind tightly, it follows that these are geodesics.

As with many such attempts to indicate

the inherent mathematical regularity of organic structure, it is easy to point to various slight departures from it, but, as in most such cases, the remarkable point is not that there are slight irregularities—which in fact may be generally understood when sufficiently analyzed—but that there is so much truly fundamental agreement with the basic formula. This, of course, indicates the nature of the restrictions under which organic growth proceeds and in this specific instance shows that scales are basically arranged in straight lines, on the surface of a solid in an intersecting net which produces a pattern of surface symmetry. Thompson (1942) in discussing entirely other matters writes, "It often happens, in the geodesic systems which we meet with in morphology, that two opposite spirals or rather helices run separate and distinct from one another . . . and it is also common to find the two interfering with one another, and forming a crisscross or reticulated arrangement. This indeed is a common source of reticulated patterns."

Since inherent in this analysis is the nature of the evident tendency of growing forms to continue in a straight line, we can see at once the relationship between surface symmetry and linear symmetry in repeated structures. Considered in other terms, this is the polyisomerism of Gregory (1934) involving two intersecting axial lines.

A perhaps simpler expression of the same principle is to be found in growing plants, which being non-locomotor constructions frequently grow with fewer incidental complicating factors. One of the prettiest of the opposite spiraling of right- and left-handed geodesics may be found on the substantially cylindrical trunk of the common cabbage palm or palmetto (*Sabal palmetto*). As these plants grow in height the lower leaves die and hang down, more or less enveloping the "stalk." On estates and private grounds, in Florida, for example, this is considered unsightly and the gardeners cut off these dead leaves, resulting in a plant as shown in plate 16. This operation exposes the rather pretty growth pattern of the leaf stalk bases. It is evident in the plate that these are following simple geodesic spirals. In the photograph of the entire tree it appears that these files of cut stems wind upward and clockwise. This is only apparent, however, for in the close view of the trunk alone it is evident that there is a similar counterclockwise spiral. Actually these stems fork at their base, and the cut is made in the stem just above where the two prongs join. The more prominent appearance of the prongs "pointing" to the left in the photographs is due to the fact that these are outside of the similar but right-pointing prong of the adjacent leaf stem to the right. Thus, the left-pointing ones are brought into greater optical prominence, as may be clearly seen in the detailed photograph. That this arrangement of reduplicated details on a simple cylinder is basically the same as the squamation on a fish, but interfered with by no eruptive structures or distortions of the surface, should be evident.

The elongate and nearly cylindrical *Calamoichthys calabaricus*, covered with virtually uniform ganoid scales, is shown comparatively in plate 16. This species gives a very pretty example of the basic geodesic nature of such growths as well as indicates some of the variables introduced by various needs in the life or growth of the animal. The photographs 1 and 3 of plate 16 show clearly the regularly spiraling nature of these scale rows. As in the case of the palm, shown on the same plate, one set of spirals predominates. In the case of the fish the second intersecting set actually can be seen clearly only on close inspection. The reason for this, as in the palm, is due to structural details. The edges of the scales which form the conspicuous set of spirals are virtually straight lines, while those forming the inconspicuous set are rounded curves that optically break the continuity. A close inspection of photograph 3 of plate 16 will show these differences in boundaries. Actually the difference can also be felt in handling the specimen, the conspicuous edge being thickened and raised while the other comes to a thin adherent edge. Furthermore, pigmentation is so disposed as to emphasize this, as there is a slightly darker elongate blotch on each scale parallel to the conspicuous edge, and there is a considerable irregularity in the edges forming the inconspicuous spiral in that it is broken to some extent by the edges of adjacent scales not always being exactly flush.

A tracing of the photograph of this fish is shown in plate 16, figure 2, with a single scale row outlined, following it as it winds around the fish. The number of each scale row as it reappears in winding about the fish is indicated above the outline. It is thus apparent that until the body begins to taper towards the tail, the rows of scales between each spiral are regularly 15, as is indicated more fully in the following tabulation:

Scale rows from last	15	15	15	14	12	11	10	6
Distance between in mm.	23.2	24.4	23.9	24.8	20.7	19.8	16.6	9.2
Body depth in mm.	11.0	11.0	11.0	11.0	10.1	8.7	6.9	4.1

If the object under discussion were a machine screw instead of a fish, it would be said to have multiple threads to the number of 15. The all but hidden dropping out of scale rows is difficult to locate but appears to be associated with the modification introduced by the interruptions of the dorsal fin spines and a peculiar interruptive feature along the dorsal profile. *Calamoichthys* is not a perfect cylinder but is very slightly and regularly quadrate in this equally scaled portion of its body. For purposes of this analysis, however, this difference is so slight as to be nearly negligible. The regularity of the number of scale rows, their distance between centers, and the depth of the body are rather striking for such an organic construction and are indicated in the above tabulation.

The second outline in plate 16, figure 2, shows the same fish with its body corrected to lie in a straight line along the back for purposes of analysis. Here the spiral is reduced to a single line, the mid-line of the scales. It is apparent in plate 16, figure 1, that the dotted lines representing the scale rows on the side away from the observer are at a slightly different angle to the horizontal than are the others. To this extent the whole line cannot be considered a simple geodesic. Passing the mid-ventral line, these rows on the opposite side become the indistinct series. Thus, if the fish is viewed from below, the distinct rows are seen to meet at an angle herringbone fashion, and superficially this would seem to do violence to the whole idea of geodesic arrangement. However, if we "unroll" the cylindrical portion of the fish, as is done in the lower diagram of plate 16, figure 2, other features appear which indicate the nature of this peculiarity. In this diagram the central horizontal line represents the mid-ventral line and the upper and lower the mid-dorsal line. The dots represent points of reference picked off the outline of the fish and transferred to the diagram by means of the divisions indicated at the extreme left. The dotted lines connect the adjacent dorsal points and represent a true path of a geodesic on such a slightly modified cylinder. The solid lines connect the dorsal and ventral adjacent points and indicate a geodesic between those points on a true cylinder. From this it is evident that reading from left to right the first complete encirclement is virtually a true geodesic on a cylinder, within observational error. The minor variations are fully explainable but will be taken up later. As one passes on successively, it will be noted that there is a regular retreat from the cylinder's geodesic. This may be best measured by noting the increasing distance between where the dotted line crosses the mid-ventral line and where the scale rows cross that line. This regression is in accordance with what is to be expected on such a gradually tapering form and shows here clearly before the actual taper can be easily measured. Beyond that point it becomes even more marked, as should be evident. No attempt has been made to show this because of the difficulty in the geometry of "unrolling" what is essentially from here on a much flattened cone. Considering the cylinder's geodesics of each side alone, which are indicated by the solid lines, it is likewise evident that the angle between the two sides at the mid-ventral line starting at nearly 180° progressively becomes less—really a measure of the same feature.

Apart from these deviations of the geodesics of a cylinder shown by this fish, there are regularly recurring fine variations in the arrangements of the dots in reference to the solid lines which most closely follow their course. At the upper left there is a tendency for the dots to fall below the solid lines and at the lower right to fall above them, crossing over at some intermediate point. This is owing to nothing more than the fact, as already noted, that the fish is not truly cylindrical but somewhat quadrate. This accounts for this minor variation and indicates that the scale rows are following a geodesic in respect to the actual form of the fish and not an approximated cylinder. The falling away from the dotted lines is a measure of the progressively greater compression of the fish caudad, as well as the change in angles between the two sides. In this connection it is to be recalled that the most anterior complete circling of the body, where the body is most nearly cylindrical, shows the dotted line, the solid line, and the rows of dots to approximate one another most closely, approaching the limits of observational error. Thus it follows that here, in what may at first appear to be a fair departure of the scale rows from a geodesic arrangement, is actually a very close approximation of it when the requirements of the body form of the fish are critically considered.

Another way to examine these constructions is to consider the winding line of a file of scales about a fish, as in plate 16, figure 2, as a projection on a plane, which it actually is as here drawn. Such a line projected from a cylinder is clearly a sine curve which may be stated by the expression

$$y=a \sin bx$$

in which y and x are vertical and horizontal coördinates, respectively, and a and b are constants. Expressions of any of those actually shown by a fish would require a complicated series of modifiers induced by the complications introduced in the fish body primarily by its locomotor requirements. The simple cylinder of the palmetto, on the other hand, is closely met by the introduction of only the constants a and b.

On the sides of many fish, such as the tarpon, such a simple equation applies only to a very limited area, in the region of where the apposed files of scales cross in figure 29F, for, owing to the tapering, both caudal and cephalad, and the flattened profile, the equation calls for much modification.

If various representative fishes of diverse groups be examined in this regard, it is found that they all, no matter what their modification of body form, subscribe to the same basic principles. Figures 30 and 31 show such a series. For purposes of convenience fishes with fairly large scales have been chosen. In the case of *Neoceratodus* the large scales of the body are replaced on the vertical fins by very small scales and these, too, follow the generalization, the geodesics becoming nearly straight lines as the fins become virtually plane surfaces. Little need be added about the simple arrangements of the scales on *Lepisosteus* and *Amia*. In the case of the much-flattened *Osteoglossum* a double intersecting row has been indicated. Here on the nearly knife-edged caudal peduncle the lines again become almost straight. In the case of the more fusiform *Astyanax*, again showing two rows of scales, the approach to the cone and ellipsoid of figure 27 becomes evident. The resemblance to the rather similar *Carassius* is clear. In the nearly cylindrical and only slightly tapering *Synodus* the conic regularity again appears. The rows of *Platypoecilus* and *Xiphophorus* forms, which readily hybridize, clearly differ only in a way closely related to the greater elongation of the one and the slight difference in scale row number, which averages about 25 in the first and 29 in the second. In the case of the ventrally flattened *Cypselurus* the simplest type of winding is retained, the apparent break along the ventral surface anterior to the pelvic fins being due to the fact that the line connecting the right and left side is contained in the profile of the ventral surface which is sharply angulated at its edges.

In *Membras*, showing a double row of scales, there is the feature of these two virtually connecting anteriorly, except as interrupted by the base of the pectoral fin. In the deeper and more compressed acanthopterygians, such as *Eupomotis* and *Tilapia*, the essential features are nevertheless retained. This is also evidently associated with the peculiar squamation in this region of the Labridae as well as the Scaridae. In such advanced and extremely flattened forms as *Angelichthys* similar features appear, including a virtually straight line on the reduced scale rows which run out onto the vertical fins. In the case of the balistids, which have a change in the squamation of the area associated with the expansible ventral area, one

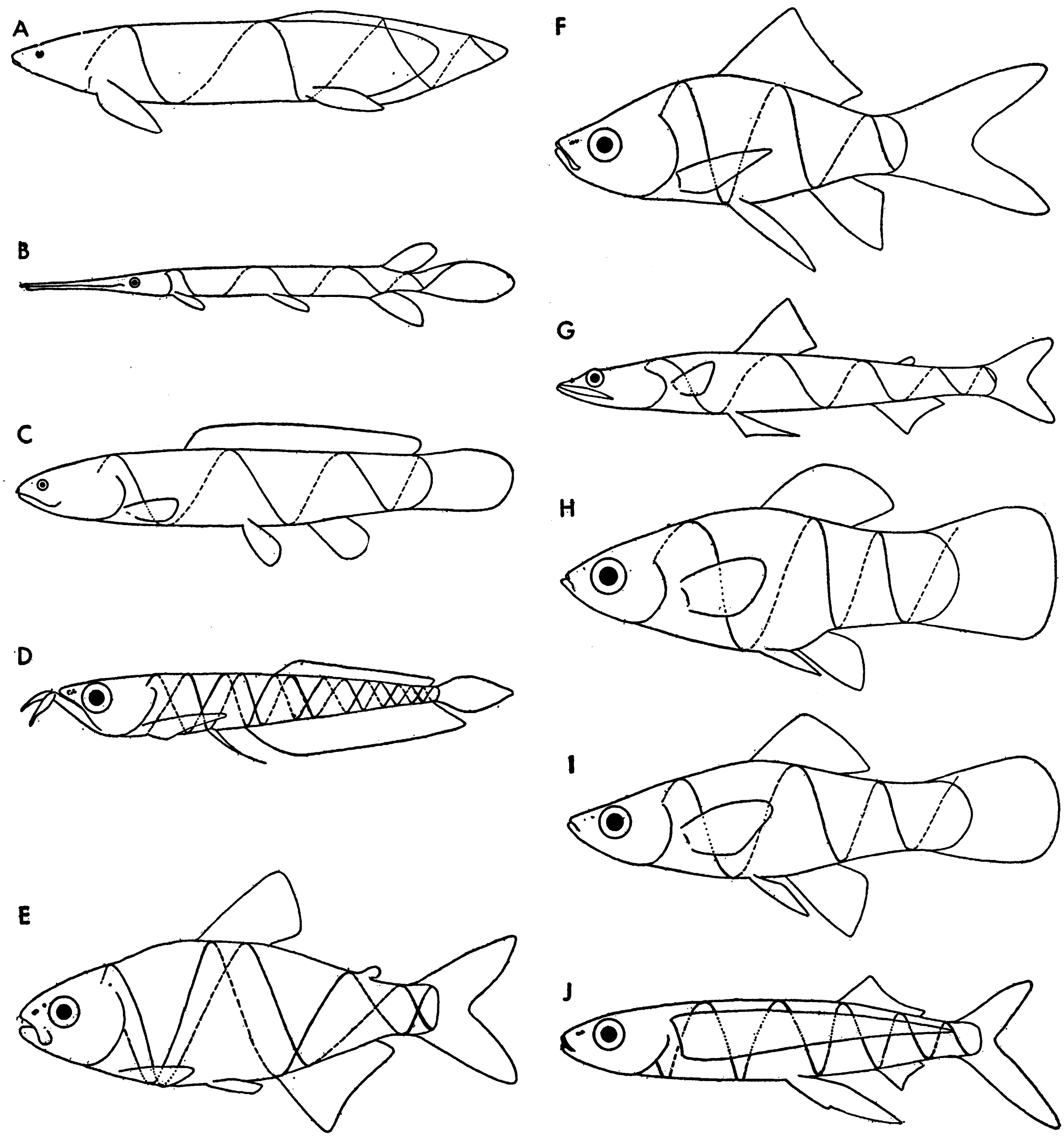


FIG. 30. Geodesics as found on various representative fishes. Dipneusta: A. *Neoceratodus fosteri* (Günther), 394 mm. s. l. Chondrostei: (See pl. 16 for *Calamoichthys calabaricus.*) Protospondyli: B. *Lepisosteus osseus* (Linnaeus), 242 mm. s. l. C. *Amia calva* Linnaeus, 350 mm. s. l. Isospondyli: (See fig. 7 for *Tarpon atlanticus.*) D. *Osteoglossum bicirrhosum* Vandelli, 88 mm. s. l. Heterognathi: E. *Astyanax mexicanus* (Philippi), 70 mm. s. l. Eventognathi: F. *Carassius auratus* (Linnaeus), 56 mm. s. l. Inomi: G. *Synodus foetens* (Linnaeus), 119 mm. s. l. Cyprinodontes: H. *Xiphophorus hellerii* (Heckel), 47.5 mm. s. l. I. *Platypoecilus maculatus* Günther, 36.5 mm. s. l. Synentognathi: J. *Cypselurus heterurus* (Rafinesque), 236 mm. s. l.

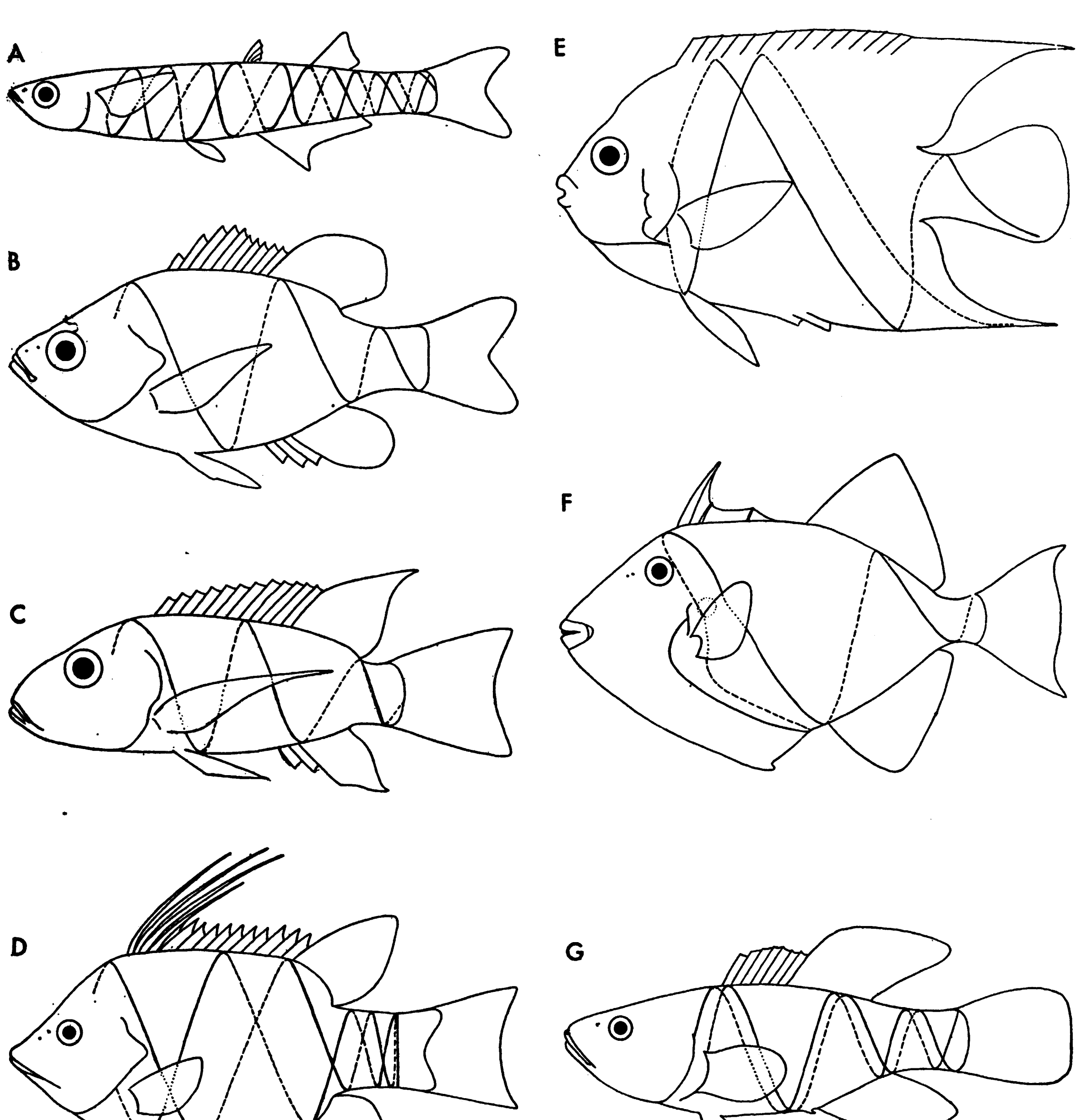


FIG. 31. Geodesics as found on various representative fishes. Percosoces: A. *Membras vagrans vagrans* (Goode and Bean), 99 mm. s. l. Percoidei: B. *Eupomotis gibbosus* (Linnaeus), 123 mm. s. l. C. *Tilapia macrocephala* (Bleeker), 135 mm. s. l. Pharyngognathi: D. *Lachnolaimus maximus* (Walbaum), 160 mm. s. l. Chaetodontoidei: E. *Angelichthys isabelita* Jordan and Ritter, 90 mm. s. l. Balistoidea: F. *Balistes carolinensis* Gmelin, 240 mm. s. l. Gobiodei: G. *Dormitator maculatus* (Bloch), 122 mm. s. l.

finds an associated modification of the squamation. Using the most anterior of the rows that are not directly involved in this feature, starting at a point anterior to the gill cleft (!), the line traces around as shown and finally smooths out in regular fashion after the involvement with the tympanic area above the pectoral fin is passed. In the case of *Dormitator* a simple arrangement is again seen, associated with its simple form. Here two adjacent rows are indicated. Many other cases not here illustrated were found to subscribe to the same principles, each with some slight modification clearly associated with form. In such species, in groups as widely diverse as the Sygnathidae, Callichthyidae and Loricariidae, Hypostomides, all heavily and secondarily armored, these plates all occur as annular bands about the fish. That is, their crossing geodesics are respectively parallel and at right angles to the axis of the fish and are essentially similar to those shown on the

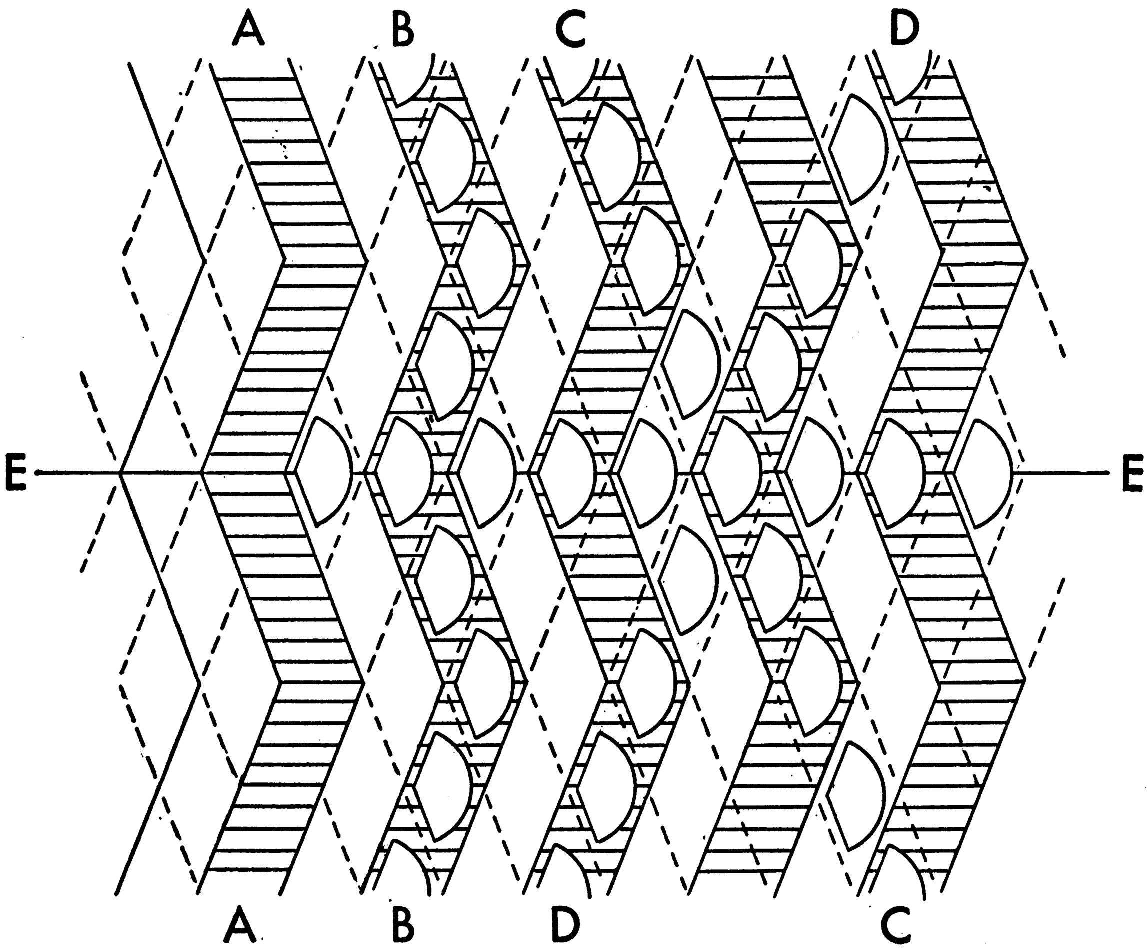


FIG. 32. Diagram of the relationships of scale rows to muscle segments. Based, in part, on Ryder (1891) and Hase (1907). A–A. One myomere as seen with skin stripped off. Alternate myomeres are shaded for purpose of clarity. B–B. One myomere with scales in place, showing how they follow the muscle bands. The scales are shown in reduced size so as to avoid the confusion of their overlapping imbrication. C–C, D–D. Two diagonal rows of scales, showing how they cross each other and pass from one myomere to another and occupy alternately large and small sections of muscle bands, in this case three and one alternately. E–E. The median fascia separating the dorsal from the ventral sections of the myomeres. It is along this or parallel to it that the horizontal rows of scales appear, as indicated. See text for full explanation.

cylinder. These general geodesic principles were likewise found to hold on fine-scaled fishes down to the point where they become very much smaller than the underlying myomeres and almost reach the point of disappearance. Here, as in the case of *Anguilla* and various ophidions, the scales tend to become arranged in small patches and lose their individual geodesic alinement. In the instance of the solidly encased lactophryds the hexagonal plates could be traced in such series, just as they could be in the all-over pattern of six-sided elements shown in figure 7. Associated with the complete ankylosis of the covering and the consequently enforced rigidity, reference to the nature of an all-over pattern of hexagons discussed under "On the nature of surface patterns" (p. 338) should make this clear. It must be borne in mind that the fish scale arrangement has its roots in the necessary flexibility of body found in most fishes.

It has already been indicated that the squamation of fishes is intimately associated with the myomeres which the scales overlie. Ryder (1891, 1892) and Hase (1907) have already discussed the anatomical relationships between the squamation and the muscle bands, but not from the present viewpoint. Figure 32, partly based on the diagrams of these students, indicates the nature of these relationships. Although these scale rows can be traced in their essentially spiral path, as here shown, it is evident from this diagram that they cross over from one muscle band to another as these bands pursue their zigzag course. Since it has been shown by Ryder (1891) that these muscle bands are necessarily arranged in this fashion for purposes of sufficient locomotion—actually nested cones, as shown very elegantly in the diagrams of Greene and Greene (1914)—the scales may be thought of as following them in similar zigzag rows but combining to form the spiral paths already discussed. It is of more than passing interest in this connection that Gabriel (1944) was able to show that *Fundulus* reared at high temperatures sometimes produced helical sutures in the vertebrae and that this resulted from asymmetrical anteroposterior displacement of the myotomes. Foerster and Pritchard (1935) and Neave (1943) discuss the relationships between scales, myomeres, and vertebrae in certain salmonids.

Since these muscles find their attachment on the segmented vertebral column, which is not a spiral structure but one of serial symmetry as here used, the muscles must of necessity express a transition between that of serial symmetry and one of a surface symmetry. How this is accomplished is indicated diagrammatically in figure 33. This figure, compared with the preceding and the explanatory legends of each, shows clearly the essential nature of this transition. The resulting construction is evidently forced upon fishes by the dynamic necessity of the situation. The serially symmetrical vertebral column attached by the complicated muscle mass to the bending surface and its appropriate fragmentation into basically a rhombic pattern of symmetry of surface present a whole that is at once rigid and flexible in a manner that would be hard to conceive of by any other mechanically possible arrangement, providing a beautifully streamlined form which at the same time is the propulsive mechanism.

There are still further complications to be found in the arrangement of the scales in some fishes which call for examination. In a crossing network of lines, from a geometrical standpoint, the intersecting lines may be at any angle to one another and in any relationship to a vertical or horizontal axis of reference. If such a net is constructed with lines crossing at an angle of 45°, with a vertical line bisecting this angle, a net is produced as shown in the upper left index diagram of figure 34. This is a fairly close approximation to the condition found on the central portions of the sides of many fishes, an example of which is shown at A of that figure. Either of the series of lines may be shifted in regard to the angles it intercepts. For purposes of illustration that series of lines which runs upward and right has been swung around clockwise in the second two left-hand index diagrams so that in the lowest one it is horizontal. An example of the first, although in reverse, that is, with the other file of lines departing most from the original symmetrical condition, is indicated in D. A case in which the horizontal has been reached and even slightly exceeded is shown in G. Many other combinations of angular relationship could be found covering virtually the entire gamut of geometrical possibility, but the present one will serve for purposes of illustration.

Still another modification of the simple crossing of lines can be found. Such is the condition in which one series of lines breaks and is displaced some distance where it intersects the other. Such a series of geometrical constructions is shown along the top index row of figure 34. Starting with a simple crossing of lines identical to the top diagram of the left index column, one may shift the one series through two stages, as is done in the other two to the right. A further shift would eventually bring the fragmented line again into coincidence, but with the next upper one so that geometrically we would be back where we started from, a condition which, so far as we know, never actually occurs in fish scales —nor would it seem likely that such a full shift could take place for various complications that the form of a fish imposes on such geometrical shifting. Evidently it is possible for both of the modifications under consider-

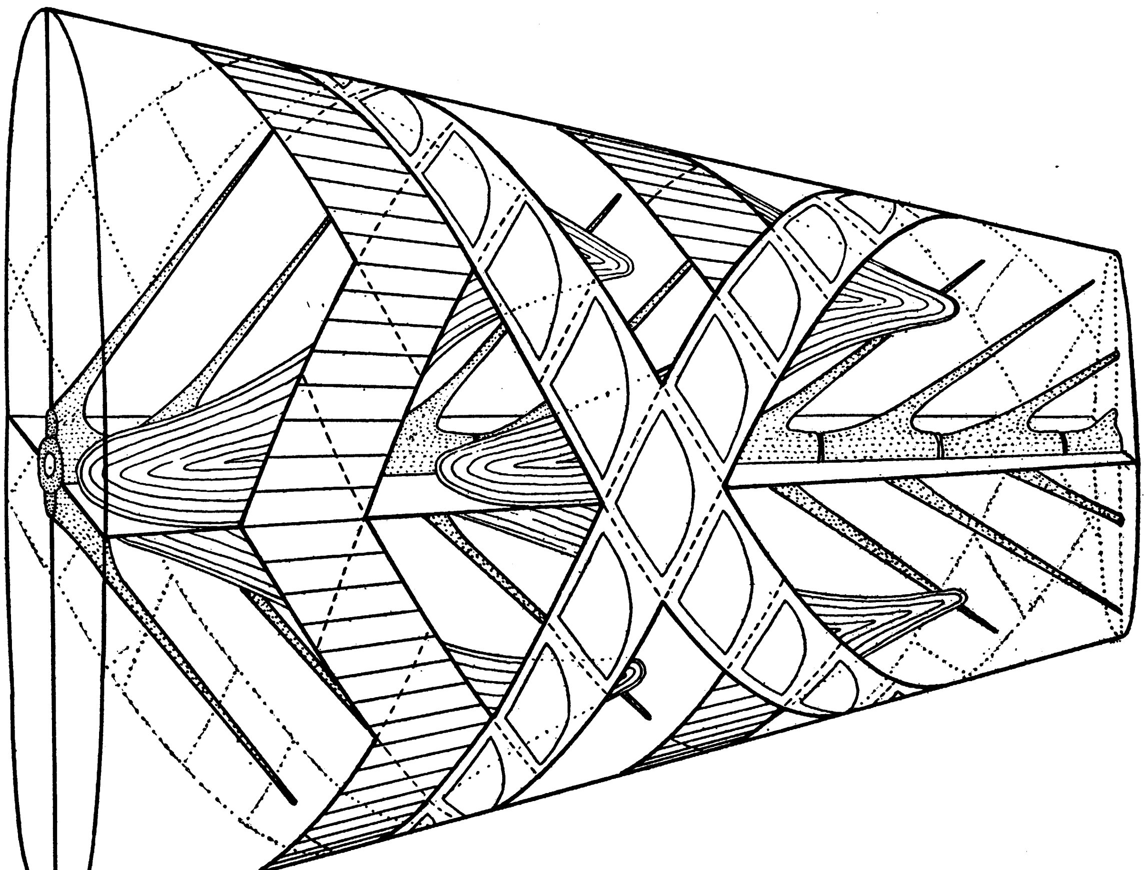


FIG. 33. Diagram of the relationships of scales to myomeres and myomeres to axial skeleton, greatly simplified for purposes of explanation. The section as shown is posterior to the body cavity and in such a peduncular portion as not to include any vertical fin. Two crossing diagonal scale rows are indicated, as in figure 32. One myomere is indicated on the near side completely exposed. A second is shown which runs under the posterior arms of the crossing scale rows. In each the posterior nesting extensions above and below the mid-line are indicated. These point to the attachment at the base of the tail fin. The anterior median extensions of the myomeres attach to the vertebral column as indicated. The spiral wrapping of the scale rows is indicated by dotted lines on the far side. For a full explanation of the relationships of the spiral winding scale rows and the serially segmented central skeleton, see text.

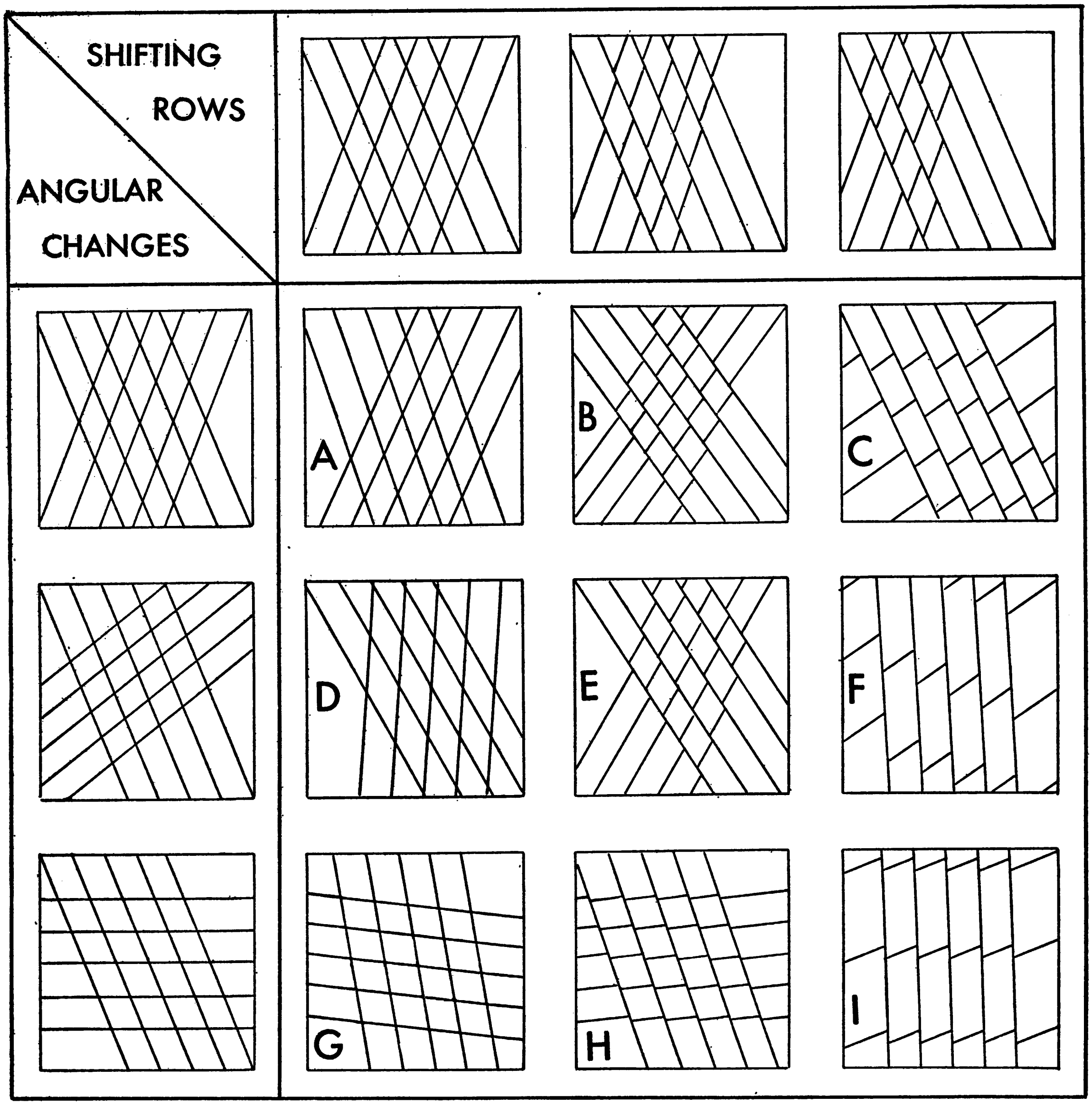


FIG. 34. Diagram of the shifting of scale rows and their angular incidence. The index diagrams at the left vertical column show changes of intersecting lines set at 45° to an extreme where one set reaches the horizontal. The index diagrams at the top horizontal row show shifting of one set of diagonal lines where intersected by the other set, reaching an extreme where the shifting lines nearly reach the next row, at which point they would be indistinguishable. The other diagrams, in the body of the chart, are based on real fishes and show the actual approach to each of the conditions of the top and left index diagrams. A. *Osteoglossum bicirrhosum* Vandelli. B. *Lepisosteus osseus* (Linnaeus). C. *Meidichthys browni* Broom. D. *Sparus aurata* Linnaeus. E. *Polypterus bichir* Geoffroy. F. *Bobasatrania groenlandica* Stensio. G. *Holurus parki* Traquair. H. *Palaeoniscus macropomus* Traquair. I. *Aspidorhynchus acutirostris* (De Blainville). See text for full explanation.

ation to take place simultaneously to a greater or less extent. Actually such conditions are to be found in fishes as is indicated in the rest of the diagrams, B, E, F, H, and I, each arranged under and opposite the two index series which it most closely approaches.

The causes and origins of such modifications are far from clear at this writing, but most probably a thorough study of the myology of the lateralis muscles would help to illuminate the situation. It is notable, however, that such shifting is both largely an expression of fishes covered with ganoid scales and possessing the peg-and-socket interlocking arrangements as discussed by Woodward (1893). Thus it appears that all of the extreme illustrations are drawn from fossil fishes. Thus, whatever the cause of this shifting around of scale rows in these fashions, it is not a marked characteristic of the preponderance of recent fishes, which mostly show rather simple arrangements of their scale rows, as has already been discussed at length. Furthermore, those recent species that do partake of the shifting rows are all survivors of ancient groups now mostly extinct. The angular changes, in simple scales, while present in many recent teleosts, are not, in any cases examined, so extreme as those of the archaic fishes. It is clear from this that only in case of relatively heavily scaled or armored fishes, including the old ganoids and the modern secondarily armored forms, such as *Lactophrys*, the loricariates, etc., is there this kind of freedom from the rather limited arrangements of scales found in the less heavily armored teleosts. Very likely this is a mechanical condition associated with thickness of scale and consequent flexibility of the body. Much more must be learned of the details of the mechanics of this condition before any considerable light can be thrown on these associations of features of structure and evolution.

Fishes of the family Haplolepidae show certain of these modifications in a rather complicated fashion. Westoll (1944) shows several of the species of this family in dorsal, side, and ventral views as reconstructions which greatly help an understanding of the arrangement of the scales of this type of fish. Viewed laterally the scale rows are similar to the condition here shown in plate 16 for *Calamoichthys*, but with a much greater offset of the less conspicuous diagonals, which are arranged in such a fashion as to make following them extremely difficult. Viewed dorsally the "herringbone" effect is very marked. Viewed ventrally a superficial com-

TABLE 6

RELATIONSHIPS BETWEEN DEPTH OF BODY AND ANGLES FORMED BY CROSSING SCALE ROWS
(Arranged according to area ratio)

Species[a]	Angle in Degrees[b]	Area Ratio—D/L[c]
Calamoichthys	83	6
Lepisosteus	68	7
Aspidorhynchus acutirostris[d]	36	12
Synodus	63	14
Osteoglossum	45	16
Membras	42	17
Amia	65	18
Osteolepis macrolepidotus[d]	60	18
Neoceratodus	58	18
Cypselurus	42	18
Dipterus valenciennesi[d]	61	20
Palaeoniscus macropomes[d]	67	22
Tarpon	31	26
Holoptychus flemmingi[d]	68	28
Xiphophorus	36	29
Lepidotus minor[d]	53	31
Dormitator	38	32
Astyanax	56	33
Tilapia	33	34
Platypoecilus	28	36
Carassius	34	37
Eurynotus crenatus[d]	58	43
Eupomotis	40	44
Lachnolaimus	42	46
Balistes	48	57
Angelichthys	46	61
Dapedius politus[d]	41	64
Cheirodus granulosus[d]	16	91
Mean	48.4	

[a] For full specific names, see figures 30 and 31.

[b] The angle in degrees is measured between the crossing scale rows in the widest part of the body as, for example, where the scales are shown on the tarpon of figure 7. All the above have been based on the specimens shown in figures 7, 8, or 9, and plate 16. This is the upper or lower angle of the quadrilateral *b* of table 3.

[c] The ratio of depth to length is given as the depth in per cent of the standard length. That is when *s. l.* = 1, depth = X or D/L.

[d] Fossil forms.

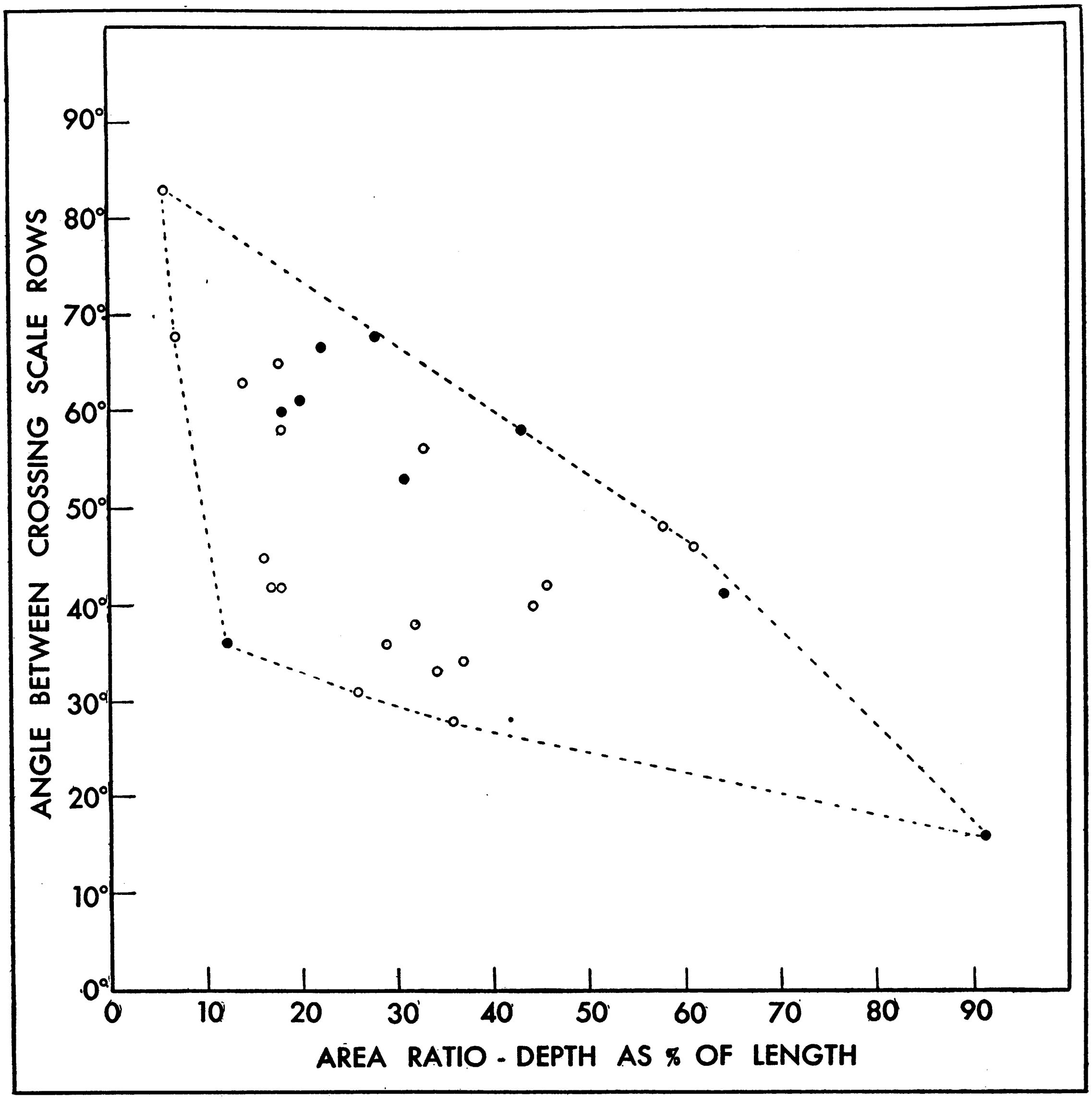


FIG. 35. Graphic presentation of the data of table 6. Open circles: recent fishes. Solid circles: fossil fishes. See text for explanation.

plication arises in that, anterior to the anal fin and between the paired fins, the outline is strongly flattened, making a distinct angle at the ventral profile. Crossing this angle the traceable geodesics make a sharp turn as they would be expected to do, in a manner similar to that found in the modern Exocoetidae, but more emphasized and modified by the condition of having one set of the crossing lines showing a large amount of offset.

The fishes studied are listed in table 6 which gives the angle in degrees between the crossing rows of scales on the side of the fish at its flattest place and an area ratio, which is the depth expressed as percentage of the length. Although the fishes represent widely diverse groups, these data, when s' read out as in figure 35, clearly show a trend which would not be expected to appear if there were not an underlying regularity running through the entire group. It is clearly indicated that as the depth of body increases the angle formed between the crossing scale rows decreases. There is no purely geometrical need for this, as a geodesic may trend in any direction, its only restriction being that it be the shortest possible line between adjacent points. The adjacent points may be adjacent in any direction.

Since it has been shown that the scale rows on these fishes, here used, are following geodesics, it also follows that as fishes have deepened or lengthened, in an evolutionary sense, the angles between these crossing scale rows have closed or opened accordingly, like the members of a pair of lazy tongs. This is exactly what should be expected of a system of geodesics on a distorting area and indeed has a resemblance to the Cartesian transformations of Thompson, only in the present case the "grids" are an integral part of the organism instead of being arbitrarily imposed upon it. It is perhaps not too hopeful to anticipate a practical application of these organic grids and these distortions for a better understanding of the relationships of fishes. Considering the large number of ways in which scales may vary in addition to their orderly arrangement, it seems rather remarkable that the scatter diagram of figure 27 shows so slight a spread.

That the scales of fishes could be treated from the standpoint of the Fibionacci series should be evident, but it is doubtful if such an approach would throw further light on the subject at this time. Thompson (1942) discusses these relationships in other organisms at considerable length, as does Jaeger (1917), who uses a pineapple fruit as an interesting and illuminating example. Those interested in this approach to the subject should consult the above authors which give a lead into the extensive literature which reaches far into antiquity. The study of phyllotaxis has employed this series in an interesting fashion which is clearly related to the present study of fish squamation and which has been set forth by Church (1901a, 1901b, 1902, 1904, 1920), Van Iterson (1907), Snow and Snow (1934), and others.

For some reason that is certainly not clear to the writer, the patterns formed by the scales of fishes have escaped the attention of the many students who have examined symmetry and pattern in nature from various standpoints. (See the long list of these in the bibliography.) The closest approach to the present analysis is that of Cook (1914), who in discussing spiral structures used the teeth of *Cestracion* and *Rhinobatis* as illustrative of structures with intersecting spirals, but made no mention of geodesics or of the shagreen denticles. Since the dermal denticles of sharks fall into similar geodesic lines, as do the scales of teleosts, and the jaw teeth of sharks are part of the same series, it is not surprising that they, too, show the same sort of relationships.

If one refers back to the general discussion on the arrangement of all-over patterns on a surface, certain items concerning the arrangement of fish scales become apparent. The same three types of grids based on 90°, 60°, and 45°, considered in figures 9 and 15, can be still further analyzed as to be the relationships of the loci of the various points. The construction of polygons of various types about these points brings out features that have not so far been considered, as indicated in figure 16. If quadrilaterals are circumscribed that have sides equal to the distances between the intersections, a checkerboard or grid results. If circles of the same diameter, they show mutual contacts in all except the grid of 45°, in which there is overlapping related to the fact that some of the points are closer than the chosen locus, as shown in figure 16. Regular hexagons could be packed only in the 60° grid. The relationship of this packing to circles is clearly indicated in figure 7E. In all cases with the use of figures with dimensions greater than the distances between the points of intersection of the grid the figures must intersect in various ways. If circles are used with a radius equal to the distance between intersections, a series of interlacing figures is produced, the lines of which mark the loci of all the intersections. If a single one of these circles be lifted from each of the grids, with only the lines cutting through and freed from the rest, figures as shown at the top of figure 36 are revealed, which is still another way of expressing the differences inherent in the use of the three angles, 90°, 60°, and 45°. It is evident that these figures present, respectively, a four-fold,

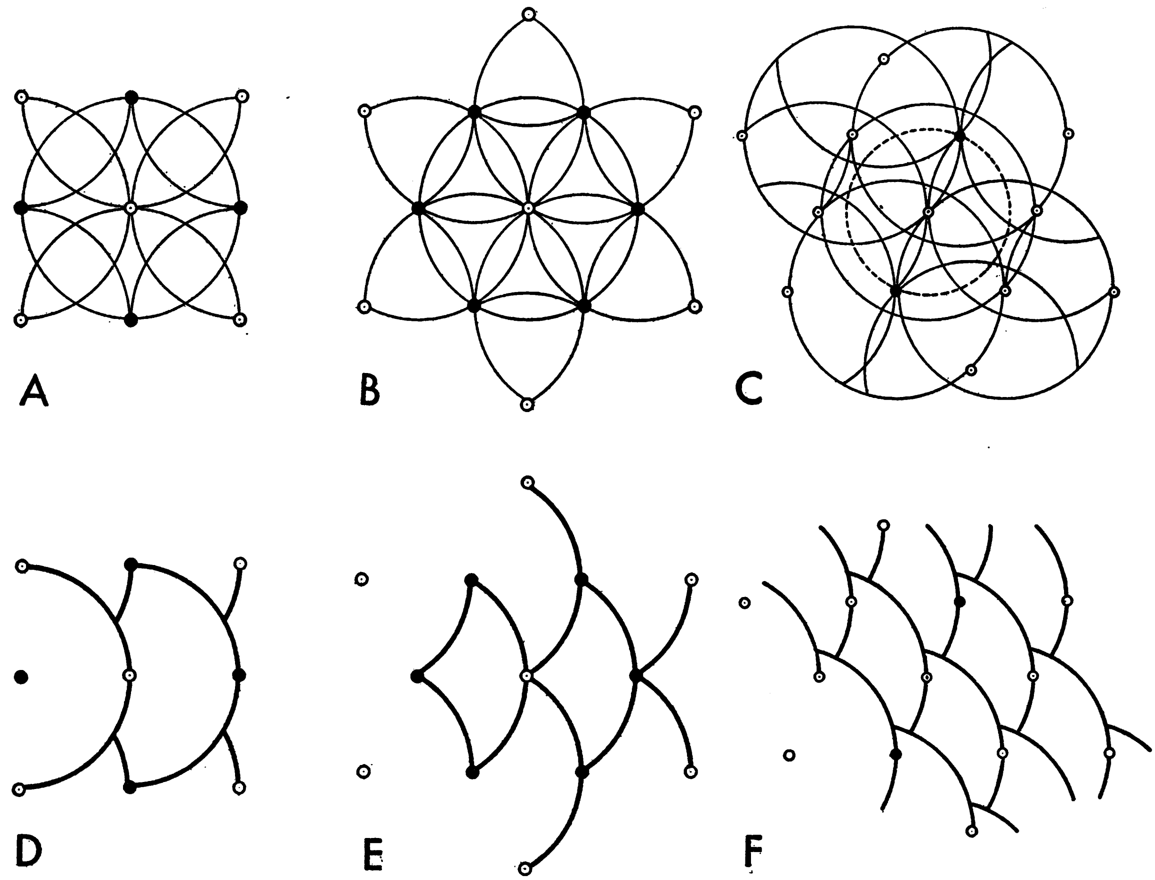


FIG. 36. Top row: Intersections of single grid circle. A. 90°. B. 60°. C. 45°. Bottom row: Shingling based on above three grid circles.

six-fold, and two-fold degree of symmetry, and the following values vary through them in a systematic manner:

CHARACTERISTIC	90°	60°	45°
Degree of symmetry (double bilateral)	4	6	1
Number of grid points exterior to circle	4	6	6
Number of grid points on circle	4	6	4
Number of grid points within circle	1	1	3
Total number of grid points involved	9	13	13

From this it is evident that the 45° figure shows the lowest numerical degree of symmetry and has the highest number of grid points within the circle. The other two have only one each, their center of symmetry. Furthermore, reference to the general discussion of the geometry of symmetry clearly indicates the fact that these two are flower-like and the 45° figure "metemaral" is mòre than a mathematical accident.

Since these figures are all constructions based on a systematic intersection of equal circles regularly placed, as shown in figure 36, it follows that they may be taken to represent solid transparent discs systematically superimposed. If these discs now be thought of as some opaque substance, they may be

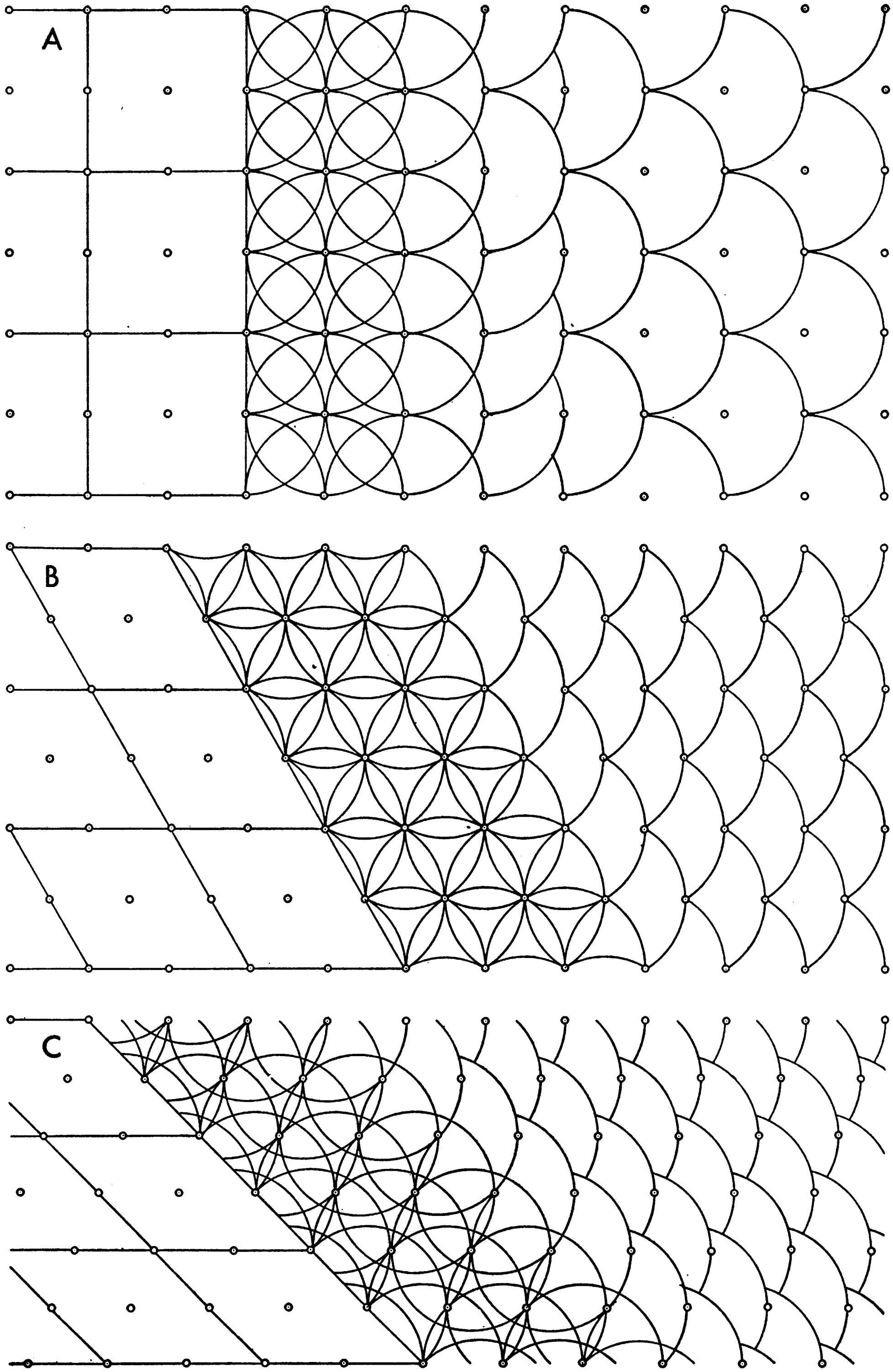


FIG. 37. Shingling based on grids. A. 90° grid. B. 60° grid. C. 45° grid, showing all-over pattern effect.

similarly arranged, but under such conditions most of the lines shown in these geometric designs will not show. Those that do remain to show have a very special significance in present connections. If we dispose such opaque discs, beginning at the right and moving to the left, various overlying patterns appear which are shingle-like in characteristics, and indeed certain of them are used by carpenters for the shingling of roofs. The possible arrangements for the three angular degrees are shown in figure 36 under the primary designs. The exposed edges only are shown. Their identity with the full design is evident. Also it will be noted that four such arrangements are possible for the 90° grid, one for the 60° grid, and two for the 45° grid. No other arrangements of "shingling" are possible for such discs centered according to these grids, except in varying the direction of the shingling, for purely geometrical reasons.

If these constructions are spread over a large but similar surface to that of figure 36, there appear the all-over patterns shown in figure 37. It here becomes obvious that the surface of the 90° and 60° grids are covered with regular and symmetrical areas, while that based on 45° is covered with regular areas of no symmetry. It will be evident that the one based on the 60° grid, with its peculiarities derived from the all-over coverage of regular equilateral triangles or hexagons, resembles to a remarkable extent the squamation pattern of a generalized teleost fish, and the other two do not. When it is considered that this is merely the geometrical deployment of a series of circles whose centers are at the apices of adjacent equilateral triangles the resemblance is truly remarkable. That there are other items that fortify this superficial agreement will be subsequently shown, and this construction may be taken as a first approximation to the conditions to be found on actual fishes. The significance of the other two grids will be taken up in still another connection, but it may be pointed out here that the quadrilaterals at the left side of the 60° grid resemble the placoid scales of more primitive fishes, such as *Lepidosteus*, in a similar manner.

THE FORM OF SCALES

Thus far, the discussion on the nature of geometric grids has concerned itself with the purely mathematical aspects of such grids, with nothing more than a general reference to the manner in which shingles or scales themselves may be arrived at by pure processes of plane geometry. If we now take some measurements of actual fishes and compare them with the foregoing abstractions, certain other and illuminating features appear. For this purpose the tarpon has been selected for the simple reason that it has large, well-defined scales and very flat sides, introducing a minimum of warping of the plane of reference.

Five tarpon of various sizes were measured in the following manner. The central horizontal scale row was taken as a line of reference, and the two files of scales upward from it were measured by a protractor at a point midway between the head and the origin of the dorsal fin. The three values so obtained, beginning with the anterior one, are, respectively, A, B, and C in the following tabulation:

Standard Length in Inches	Angles in Degrees		
	A	*B*	*C*
4	80	31	69
23	64	60	56
37	76	50	54
60	60	55	65
75	74	42	64
Mean	*70.8*	*47.6*	*61.6*

From this tabulation it is evident that there is some amount of variation in this measurement, and while the mean is not far from the 60° of the equilateral triangle, it is clearly not tending to form a mean about that value. If a grid is constructed using the values actually found to be the mean of five specimens, it appears as in figure 38. The angles, as measured, A, B, and C, are indicated in the lower right-hand corner of the grid letter correspondingly. The head of the fish is at the left. On a circle constructed with a radius equal to that between the near points of the grid, which for purely geometrical reasons must be the horizontal ones (see fig. 6), the intersections of the other similar circles appear as indicated, showing only those portions within the original circle. This compares with figures 36 and 37. To indicate more clearly how these discs overlap, a system of cross hatching has been drawn in. Where no other disc overlaps the first the area is indicated in black; where one overlaps horizontal lines are used; where two overlap, vertical lines; and where three are superimposed, diagonal lines. While this diagram is clearly related to those of figures 36 and 37, it clearly has new characteristics not so far discussed. This is based on the fact that the angles *A* and *C* of the figure are not equal, showing a difference of nearly 10°. Except for the asymmetry noted, it is not far from the example of 120° of figure 6, being in this notation actually 132.4°. A larger grid of this sort but otherwise directly comparable to the previous grid constructions is shown in figure 39. The lower left-hand portion of this diagram shows similar complete circles for comparison with figures 36, 37, and 38. Above them some of the solid lines are reduced to dotted lines, and at the top running to the right the hidden portion is dropped out

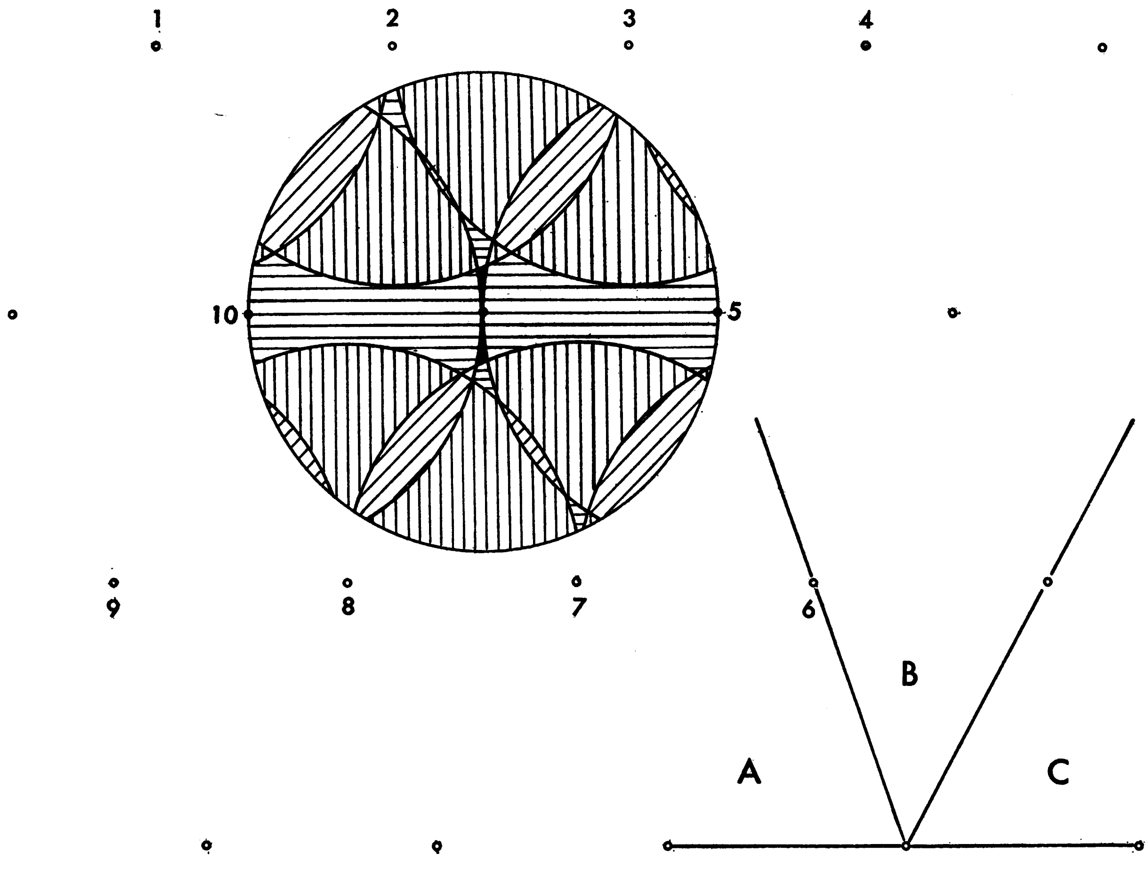


FIG. 38. Overlapping circles based on a grid derived from the angles of tarpon scale rows.

entirely. This effect is actually very close to the squamation of tarpon, based on the geometry of grids into which has been brought only the two angular values from the measurement of tarpon. A typical tarpon scale reduced to the diameter of the circles used has replaced them in the lower right-hand part of this diagram. Nine have been drawn in full showing the hidden portions by dots. These compare with the previous figure, using only circles. In each, eight discs encroach on the central one. In the upper right-hand portion three circles are shown with dotted lines representing the edge of the tarpon scale and indicating the extent to which it departs from a true circular arc. Since the scale selected was taken at random from a collection, with no data other than that it was of moderate size, the fit is remarkably good. Thus by placing such a scale end to end on a grid of the suitable angular values a very close approximation of tarpon scalation is arrived at. This may be taken as a second approximation.

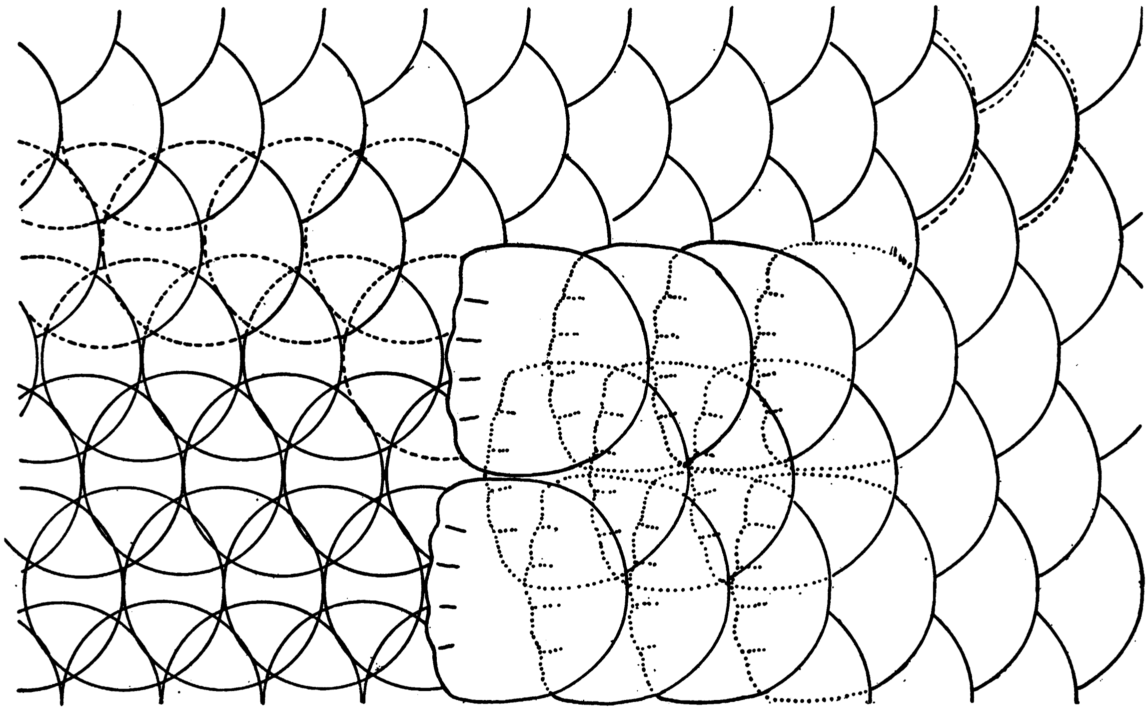


FIG. 39. Circular shingling of scale rows based on the angles of tarpon scale rows.

It is to be noted in this connection that the geometrical constructions of figure 37A and B have the edges of two "scales" meeting at the point of overlap, whereas in C they meet at some point behind it which, considering the circles as "discs," leads to the asymmetry of the area included. In all such arrangements based on less than a 60° angle, the overlapping scale falls short of the juncture of the two underlying ones, as is clearly indicated in figure 7. At 60° they meet in a point. Above 60° it again falls short until 120° is reached where they again meet in a point. Above that value the overlapping scale exceeds and hides the juncture of the other two, and the exposed portion of the scale is a symmetrical four-sided figure instead of a three-sided or asymmetrical four-sided area. Such a case is illustrated by the tarpon, in which this angle equals 132.4°. Consequently, other things being equal, we may state that the addition of such a side to an exposed area indicates that this angle is over 120°.

Now it does not necessarily follow that such scales are arranged in exactly this manner, except that for geometrical necessity they cannot be far from it and at the same time present the external appearance which they do. Actually, a piece from the side of such a fish overlaps its scales, as shown in figure 40, which is based on dissection and has nothing to do with geometrical constructions, nor is it in the least to be considered as diagrammatic, being an uumodified outline of each scale in its place.

If the angles of the scale rows of the garfish, *Atractosteus spatula* (Lacépède), be treated

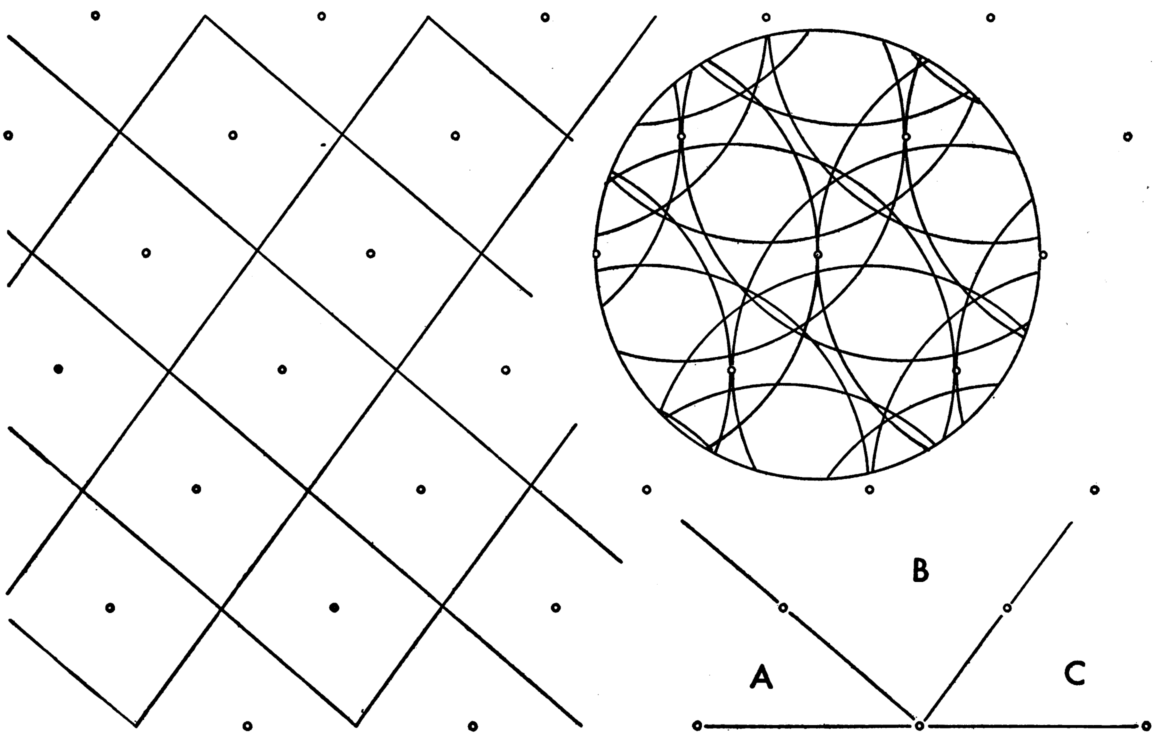


FIG. 41. Overlapping circles based on a grid derived from the angles of gar scale rows.

in a similar fashion, we find the values for angle *A* equal 40°, *B* equal 86°, and *C* equal 54°, which are indicated in the lower right of figure 41. Immediately above it is a diagram

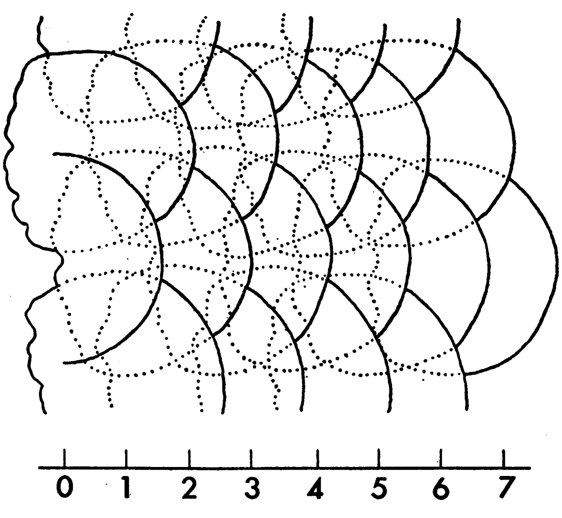


FIG. 40. Actual and non-diagrammatic section of scale arrangement from the mid-side of a tarpon of medium size.

of the overlap of circles of a radius equal to one horizontal unit and is directly comparable with that of figure 38. It is evident that this particular set of angles gives a much more complicated case of such overlap. In the case of the present species the scales are not subcircular as they are in the tarpon, and this diagram has nothing to do with conditions as found in the scales of this fish but is here introduced for later consideration in connection with other matters. Actually the scales of this garfish are sculptured quadrilaterals that are not imbricated but possess a peculiar peg-and-socket articulation with their fellows characteristic of this group of fishes. (See, for example, Woodward, 1893, and Weed, 1923, and fig. 42.) These quadrilaterals are indicated in the left-hand protion of figure 34 as they appear on the middle of the sides midway between the pectoral and pelvic insertions. This fish is subquadrate, in a manner not unlike that described for *Calamoichthys*. Two sections of an unrolled skin of a large specimen are shown in figure 43. Here again is a marked interruption of the regularity of the geodesic lines by the mid-line of the back. A very pretty demonstration of the geodesic nature of these lines may be made by rolling the figure into a cylinder and winding a thread along any of the scale rows. It will be found that they do not follow the rows very well, but if the side and back portions are ever so slightly flattened, i.e., made subquadrate, the fit becomes excellent. When the proper amount of flattening is produced, we find that we have reproduced the shape of the fish in considerable detail. In crossing the back the line passes through two of the enlarged median plates. Thus each of these has two parallel geodesics of the two sets passing through it, suggesting that these represent two fused plates. In fact on other bases there is reason to suppose that such is the case, just as with the elements of the vertical fins, and should be looked upon as nothing more than an interruption of the geodesic, in the same sense that the fins are.

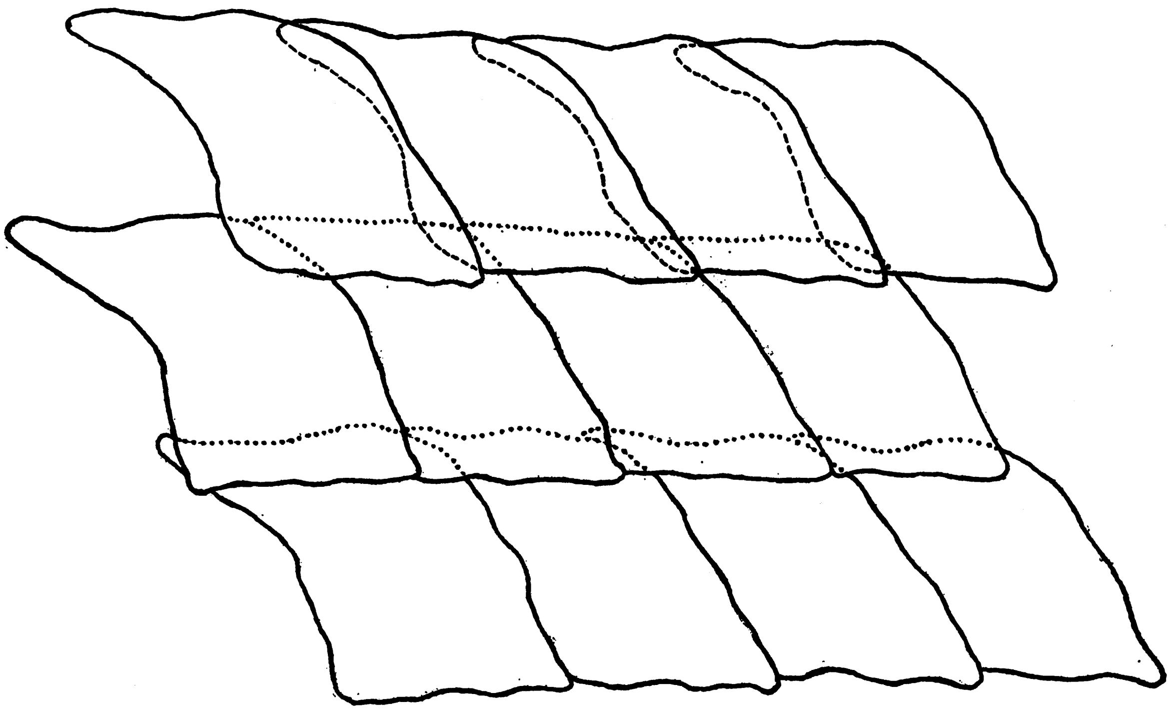


FIG. 42. Alligator gar scales. Based on Weed (1923).

If these two examples of the angular arrangement of two very different fish scales be compared with some of the earlier geometrical considerations indicated by figures 9, 10, and 11, their relationship to these constructions becomes apparent. A simple calculation in trigonometry gives the dimensions of these areas since in any triangle

$$\frac{a}{\sin A} = \frac{b}{\sin B} = \frac{c}{\sin C}$$

Consequently, in reference to figure 12, these values would produce similar triangles in which the ratios would be proportional to as a is to c or 1.000 to 0.933 . . . and 1.000 to 1.258 . . . , respectively. Thus, as has been here done, by equating one side of such a triangle to unity, then the value of c standing alone is all that is necessary to express the arrangement of such scales as they cross the mid-line of the fish body. In practice two values are measured, angle A and angle C. Then by the following formula this index value may be directly obtained:

$$\frac{a \sin C}{\sin A} = c$$

Species	Angles			Sides		
	A	*B*	*C*	*a*	*b*	*c*
Tarpon	70.8	47.6	61.6	1.000	0.794..	0.933..
Atractosteus	40.0	86.0	54.0	1.000	1.552..	1.258..

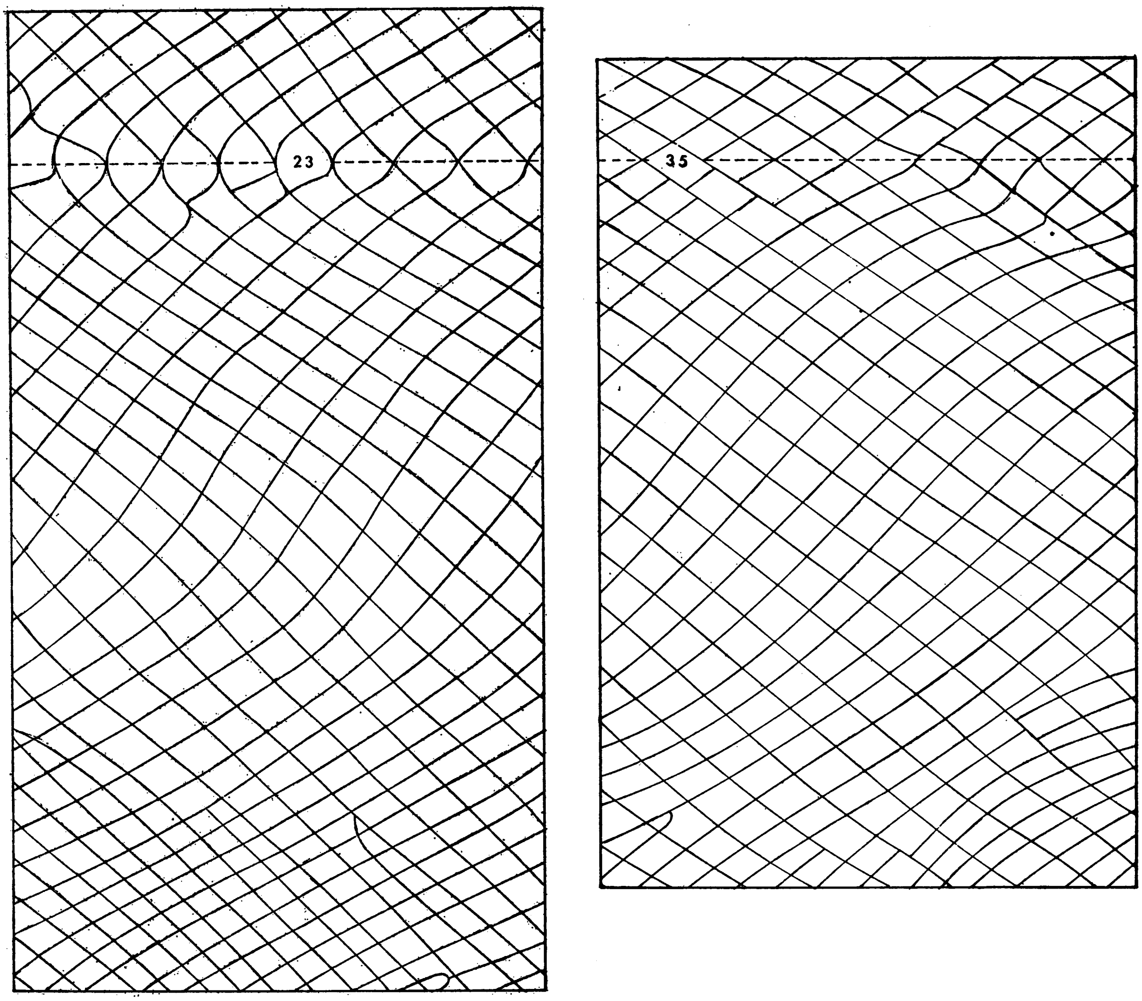


FIG. 43. Unrolled gar skin from an actual specimen. The numbered dorsal scale indicates its position from the first one.

Or, since a equals 1 and c equals the index value,

$$\frac{\sin C}{\sin A} = c$$

Such values may be directly compared with figure 14 in which various ratios are marked off. By simple graphic methods these relationships become quite clear. This is indicated in figure 37A and B. It shows as well one of the prominent differences of these two scale arrangements. While one of the diagonals of both runs in a horizontal direction, the other diagonal in neither case is vertical. It, of course, could be vertical only if angles

A and *C* were equal. In *Tarpon* this diagonal falls ahead of the vertical, and in *Atractosteus* it falls after it. In taxonomic practice it is along this line that the number of horizontal rows are customarily counted, although sometimes they are counted along either of the diagonal rows of scales. It will be noted that either of the diagonal rows of scales yields the same value, but the diagonal of the areas gives half the value. Thus the true value may be obtained by multiplying this count by two or, what is more frequently done, by counting two rows at a time so as to include all the horizontal lines that can be made to intersect the crossing of the diagonals.

If the two sides of such triangles have a factor in common, the greatest common factor determines and names the row which will fall on a vertical. This is shown in figure 11 where in A the factor in common is one, and each point exactly over another has one horizontal row intervening; in B with four and eight sides, two is common and there are two rows intervening between points on a vertical line, and so on. If the numbers, however, are prime to one another, as in the present case, no such mathematical superposition is possible. Figure 37C shows the data of B referred to a vertical instead of a horizontal. This line in a fish wraps itself around the animal at right angles to its long axis, and it should be obvious that this line does not pass through more than one point. This treatment is the same as that given to leaf arrangement about a stem by students of phyllotaxis and is much more useful for their purposes than the present because of the greater regularity of their objects. It is introduced here principally to indicate the basic geometrical similarity between structures in such widely separated forms of life as fish and higher plants. For a useful and clear discussion of the principles of phyllotaxic analysis, see Thompson (1942). As indicated in figure 37, here again any number of diagonals (here spirals) may be found, but for present purposes the corn-field diagram of figure 9 is simpler and adequate. It may be noted again that here is where the Fibionacci series figures prominently, but it is believed this series of diagrams shows why for purely geometric reasons it must be an implicit part of all such surface designs.

SURFACE STRUCTURES IN OTHER ANIMALS

THE TETRAPODS

IF OTHER VERTEBRATES be briefly considered in reference to dermal structures, certain striking differences appear. In the Amphibia, the dermis is naked save only for the minute embedded scales of the Caecilia, the arrangement of which is not clear, as in fishes, with similarly reduced scales. Related to these considerations, moreover, is the discussion of cuticular folds of Amphibia by Rosin (1944).

The prominent squamose condition of the dermal covering of most reptiles, on examination, is found to be exceedingly various and specialized. In the Sauria many forms have the geodesics parallel and at right angles to the longitudinal axis of the animal so that the scale rows may be thought of as paralleling the length of the animal or as in annular bands, such as the arrangement indicated in figure 29. Some, such as *Trachysaurus*, *Scincus*, and *Pygopus*, show the ordinary fish-scale type of squamation. In case it be thought that the great elongation of *Pygopus* may be to some extent associated with this type of arrangement, although *Trachysaurus* is notably short, it may be pointed out that in other elongate forms the annular arrangement obtains. *Amphishaena*, also an elongate form, shows such a scale arrangement.

The squamation of snakes might be expected to show the following of simple, diagonal, geodesic lines very distinctly because of their elongate and nearly cylindrical form. Actually the scales across the back of a number of species examined do just this, but because of the modification of the ventral scales into transverse members of a locomotor function there is a rather striking interruption. The angles of the crossing geodesics on the back, in *Coluber* for example, are equal as related to the axis of the body. By following such a row across the back and under the ventral surface on the transverse locomotor scale and continuing on the returning line crossing the back and down to the appropriate ventral scale, it is found, returns one to the scale row on the back that was the point of departure. Thus in effect each such line forms a figure-of-eight with the central "cross" of the eight on the back, halfway between either "loop" which runs around the snake as a band. This is possible because each transverse ventral scale is joined at its edge by two lines of the regularly arranged scale rows of the back and sides. In a sense the snake type of squamation may be thought of as being arranged ventrally in annular bands and dorsally in crossing diagonals.

Little can be said about the complications introduced in such forms as the Chelonia, but the squamation of the legs indicates definite geodesic trends.

In the crocodilians the annular band type of squamation is predominant. It should be pointed out in this connection that there is in virtually all reptiles a strong dorsoventral differentiation, as already noted for snakes, which is probably an expression of the close affinity to a horizontal surface to which most are forced to adhere.

In birds the squamation of the tarsus and toes is mostly differentiated from front to back in a manner not dissimilar to that of reptiles. The forward surfaces of these members are often relatively large and disposed as annular bands. The after surface may be covered with smaller scales not always arranged in such bands, but sometimes approximating the condition found in the dorsoventral relationship in snakes. In the fine-scaled leg of the Diomedeidae there are some evidences of a tendency towards spiral arrangement. Frequently at the tibial-tarsal joint the skin covering the area shows a very pretty pattern of geodesic lines formed by the relatively regular scale rows.

Pterylosis presents a field of considerable complication in reference to present studies. The tracts bearing feathers and the naked tracts are each so specialized in regard to functional necessity that it is a little difficult to see at first if present considerations have any bearing whatever on the subject. However, if such a bird as *Columba* or even a plucked chicken or other fowl be examined it can be seen that the feather pockets are following crossing diagonal geodesic rows within their tracts on a very complicated surface. Furthermore, when the differentiation of feathers is much reduced, as on the backs of penquins, a distinct fish-scale pattern is evident.

The arrangement of the dermal covering on mammals superficially would not seem to be especially influenced by considerations of geodesics. The hair tracts of mammals seem to be governed more in their arrangement over the essentially complicated form of the mammalian surface by pointing away from the chief direction of motion (see, for example, Boardman, 1943). This is obviously true of scales as well, and it may be only because of the smallness of hairs that they seemingly lose this spiral arrangement, as in fishes with very minute scales. The "scales" of the pangolin (*Manis*) are clearly following geodesics in a rather simple fish-scale fashion. De Meijere (1894), moreover, shows that hairs or hair groups in many mammals line up in crisscross patterns, varying in detail with the species. Undoubtedly they could be compared to the considerations herein discussed in a manner similar to that treatment accorded the fishes. Gregory (1910), in discussing the origin of mammalian hair, indicates the relationship of hairs in primitive mammals to scales.

In the recent armadillos the bands are annular, but in the extinct glyptodonts the arrangement is one of intersecting diagonals.

Thus it is evident that in all the vertebrate groups scale or scale-like dermal structures are constrained to follow geodesic lines, excepting only when some other interfering growth force, such as eruption of a special member, dorsoventral specialization, or similar matter, interferes. Only when the size of the individual items becomes relatively minute does this feature otherwise disappear.

THE INVERTEBRATES AND PLANTS

Invertebrates and plants could be similarly treated whenever there are comparatively large members of similar, small-sized, but not too small, units spread over an organic surface. Such things as the scales on the wings of butterflies, the surface patterns of echinoderms and coelenterates, the webs of spiders, and flowers and their petals, to mention only a few, immediately suggest themselves. These effects are evidently rooted in the nature of lines of strain in materials and may also be shown in inorganic structures. Quraisky (1944) has even shown experimentally that the meandering of streams, originally straight on a bed of completely uniform fine material, by an interaction of forces causes a regular disposal of the sand in piles of what he calls a "fish-scale" arrangement. The "distal" edges of the "scales" are downstream. These become eventually alternately skewed and lead to the observed meandering.

The purpose of this paper, as indicated in the introduction, is to call attention to the fundamental and abstract nature of symmetrical systems and to offer a method for considering their various aspects in one unified concept. This last section of the paper is intended merely in a suggestive way to indicate a few of the various biological matters that may be examined in regard to the present concept of symmetrical organization. Others still doubtlessly occur to the reader. Many of these could be pursued in greater detail with an expectation of reaching a better understanding of the mechanical necessity to which all forms of life must adjust themselves or perish. The section on the squamation of fishes, its mechanical implications, and the complexities involved in any such study indicate sufficiently the nature of the interaction of the forces concerned, which in the final analysis are the causative agencies involved in the various expressions of symmetry as found in both inorganic and organic forms.

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