ON GROWTH AND FORM

BY

D'ARCY WENTWORTH THOMPSON

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EDITED BY
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CHAPTER VI

THE EQUIANGULAR SPIRAL

Spirals in Nature

The very numerous examples of spiral conformation which we meet with in our studies of organic form are peculiarly adapted to mathematical methods of investigation. But ere we begin to study them we must take care to define our terms, and we had better also attempt some rough preliminary classification of the objects with which we shall have to deal.

In general terms, a Spiral is a curve which, starting from a point of origin, continually diminishes in curvature as it recedes from that point; or, in other words, whose *radius of curvature* continually increases. This definition is wide enough to include a number of different curves, but on the other hand it excludes at least one which in popular speech we are apt to confuse with a true spiral. This latter curve is the simple *screw*, or cylindrical *helix*, which curve neither starts from a definite origin nor changes its curvature as it proceeds. The 'spiral' thickening of a woody plant-cell, the 'spiral' thread within an insect's tracheal tube, or the 'spiral' twist and twine of a climbing stem are not, mathematically speaking, *spirals* at all, but *screws* or *helices*. They belong to a distinct, though not very remote, family of curves.

Of true organic spirals we have no lack.[1] We think at once of horns of ruminants, and of still more exquisitely beautiful molluscan shells —in which (as Pliny says) *magna ludentis Naturae varietas*. Closely related spirals may be traced in the florets of a sunflower; a true spiral, though not, by the way, so easy of investigation, is seen in the outline of a cordiform leaf; and yet again, we can recognise typical though transitory spirals in a lock of hair, in a staple of wool,[2] in the coil of an elephant's trunk, in the 'circling spires' of a snake, in the coils of a cuttle-fish's arm, or of a monkey's or a chameleon's tail.

[1] A great number of spiral forms, both organic and artificial, are described and beautifully illustrated in Sir T. A. Cook's *Spirals in Nature and Art* (1903) and *Curves of Life* (1914).

[2] On this interesting case see, for example, J. E. Duerden, in *Science* (25 May 1934).

Among such forms as these, and the many others which we might easily add to them, it is obvious that we have to do with things which, though mathematically similar, are biologically speaking fundamentally different; and not only are they biologically remote, but they are also physically different, in regard to the causes to which they are severally due. For in the first place, the spiral coil of the elephant's trunk or of the chameleon's tail is, as we have said, but a transitory configuration, and is plainly the result of certain muscular forces acting upon a structure of a definite, and normally an essentially different, form. It is rather a position, or an *attitude*, than a *form*, in

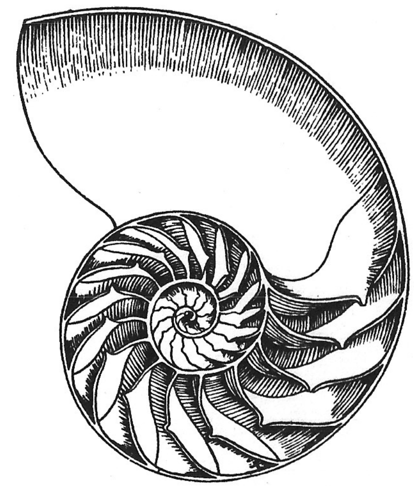


Fig. 70. The shell of *Nautilus pompilius*. From J. C. Chenu.

the sense in which we have been using this latter term; and, unlike most of the forms which we have been studying, it has little or no direct relation to the phenomenon of growth.

Again, there is a difference between such a spiral conformation as is built up by the separate and successive florets in the sunflower, and that which, in the snail or *Nautilus* shell, is apparently a single and indivisible unit. And a similar if not identical difference is apparent between the *Nautilus* shell and the minute shells of the Foraminifera which so closely simulate it: inasmuch as the spiral shells of these latter are composite structures, combined out of successive and separate chambers, while the molluscan shell, though it may (as in *Nautilus*) become secondarily subdivided, has grown as one continuous tube. It follows from all this that there cannot be a physical or dynamical, though there may well be a mathematical *law of growth*, which is common to, and which defines, the spiral form in *Nautilus*, in *Globigerina*, in the ram's horn, and in the inflorescence of the sunflower. Nature at least exhibits in them all '*un reflet des formes rigoureuses qu'étudie la géometrie*'.[1]

Of the spiral forms which we have now mentioned, every one (with the single exception of the cordate outline of the leaf) is an example of the remarkable curve known as the equiangular or logarithmic spiral. But before we enter upon the mathematics of the equiangular spiral, let us carefully observe that the whole of the organic forms in which it is clearly and permanently exhibited, however different they may be from one another in outward appearance, in nature and

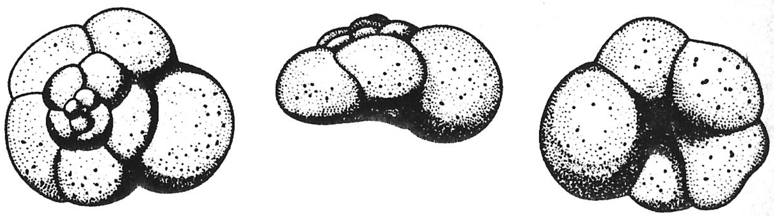


Fig. 71. Three views of a foraminiferal shell (*Trochamma inflata*). After Brady. From P. Grassé, *Traité de Zoologie* (Paris: Masson et Cie).

in origin, nevertheless all belong, in a certain sense, to one particular class of conformations. In the great majority of cases, when we consider an organism in part or whole, when we look (for instance) at our own hand or foot, or contemplate an insect or a worm, we have no reason (or very little) to consider one part of the existing structure as *older* than another; through and through, the newer particles have been merged and commingled among the old; the outline, such as it is, is due to forces which for the most part are still at work to shape it, and which in shaping it have shaped it as a whole. But the horn, or the snail-shell, is curiously different; for in these the presently existing structure is, so to speak, partly old and partly new. It has been conformed by successive and continuous increments; and each successive stage of growth, starting from the origin, remains as an integral and unchanging portion of the growing structure.

We may go further, and see that horn and shell, though they belong to the living, are in no sense alive.[2] They are by-products of the animal; they consist of 'formed material', as it is sometimes called; their growth is not of their own doing, but comes of living cells beneath them or around. The many structures which display the logarithmic spiral increase, or accumulate, rather than grow. The shell of nautilus or snail, the chambered shell of a foraminifer, the elephant's tusk, the beaver's tooth, the cat's claws or the canary-bird's—all these show the same simple and very beautiful spiral curve. And all alike consist of stuff secreted or deposited by living cells; all grow, as an edifice grows, by accretion of accumulated material; and in all alike the parts once formed remain in being, and are thenceforward incapable of change.

In a slightly different, but closely cognate way, the same is true of the spirally arranged florets of the sunflower. For here again we are regarding serially arranged portions of a composite structure, which portions, similar to one another in form, *differ in age*; and differ also in magnitude in the strict ratio of their age. Somehow or other, in the equiangular spiral the *time-element* always enters in; and to this important fact, full of curious biological as well as mathematical significance, we shall afterwards return.

The Spiral of Archimedes

In the elementary mathematics of a spiral, we speak of the point of origin as the pole (O); a straight line having its extremity in the pole, and revolving about it, is called the radius vector; and a point (P), travelling along the radius vector under definite conditions of velocity, will then describe our spiral curve.

Of several mathematical curves whose form and development may be so conceived, the two most important (and the only two with which we need deal) are those which are known as (1) the equable spiral, or spiral of Archimedes, and (2) the equiangular or logarithmic spiral.

The former may be roughly illustrated by the way a sailor coils a rope upon the deck; as the rope is of uniform thickness, so in the whole spiral coil is each whorl of the same breadth as that which precedes and as that which follows it. Using its ancient definition, we may define it by saying, that 'If a straight line revolve uniformly about its extremity, a point which likewise travels uniformly along it will

[1] Haton de la Goupillière, in the introduction to his important study of the *Surfaces Nautiloides, Annaes sci. da Acad. Polytechnica do Porto*, Coimbra, III, 1908.

[2] For Oken and Goodsir the logarithmic spiral had a profound significance, for they saw in it a manifestation of life itself. For a like reason Sir Theodore Cook spoke of the *Curves of Life*; and Alfred Lartigues says (in his *Biodynamique générale*, 1930, p. 60): 'Nous verrons la Conchyliologie apporter une magnifique contribution à la Stéréodynamique du tourbillon vital.' The fact that the spiral is always formed of non-living matter helps to contradict these mystical conceptions.

describe the equable spiral'.[1] Or, putting the same thing into our more modern words, 'If, while the radius vector revolve uniformly about the pole, a point (P) travel with uniform velocity along it, the curve described will be that called the equable spiral, or spiral of Archimedes'. It is plain that the spiral of Archimedes may be compared, but again roughly, to a *cylinder* coiled up. It is plain also that a radius ($r = OP$), made up of the successive and equal whorls, will increase in *arithmetical* progression: and will equal a certain constant quantity (a) multiplied by the whole number of whorls or (more strictly speaking) multiplied by the whole angle (θ) through which it has revolved: so that $r = a\theta$. And it is also plain that the radius meets the curve (or its tangent) at an angle which changes slowly but continuously, and which tends towards a right angle as the whorls increase in number and become more and more nearly circular.

The equiangular Spiral

But, in contrast to this, in the equiangular spiral of the *Nautilus* or the snail-shell or *Globigerina*, the whorls continually increase in breadth, and do so in a steady and unchanging ratio. Our definition is as follows: 'If, instead of travelling with a *uniform* velocity, our point move along the radius vector with a velocity *increasing as its distance from the pole*, then the path described is called an equiangular spiral.' Each whorl which the radius vector intersects will be broader than its predecessor in a definite ratio; the radius vector will increase in length in *geometrical* progression, as it sweeps through successive equal angles; and the equation to the spiral will be $r = a^{\theta}$. As the spiral of Archimedes, in our example of the coiled rope, might be looked upon as a coiled cylinder, so (but equally roughly) may the equiangular spiral, in the case of the shell, be pictured as a *cone* coiled upon itself; and it is the conical shape of the elephant's trunk or the chameleon's tail which makes them coil into a rough simulacrum of an equiangular spiral.

While the one spiral was known in ancient times, and was investigated if not discovered by Archimedes, the other was first recognised by Descartes, and discussed in the year 1638 in his letters to Mersenne.[2] Starting with the conception of a growing curve which should cut each radius vector at a constant angle—just as a circle does—Descartes showed how it would necessarily follow that radii at equal

[1] Leslie's *Geometry of Curved Lines* (1821), p. 417. This is practically identical with Archimedes' own definition (ed. Torelli, p. 219); cf. Cantor, *Geschichte der Mathematik* (1880), I, 262.
[2] *Œuvres*, ed. Adam et Tannery (Paris, 1898), p. 360.

angles to one another at the pole would be in continued proportion; that the same is therefore true of the parts cut off from a common radius vector by successive whorls or convolutions of the spire; and furthermore, that distances measured along the curve from its origin, and intercepted by any radii, as at B, C, are proportional to the lengths

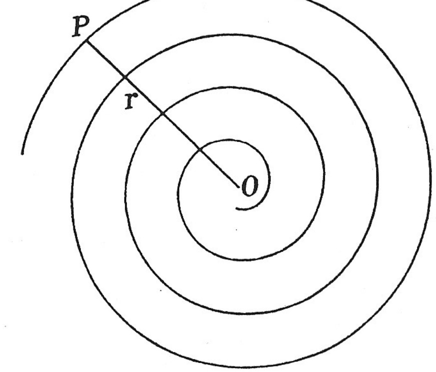


Fig. 72. The spiral of Archimedes.

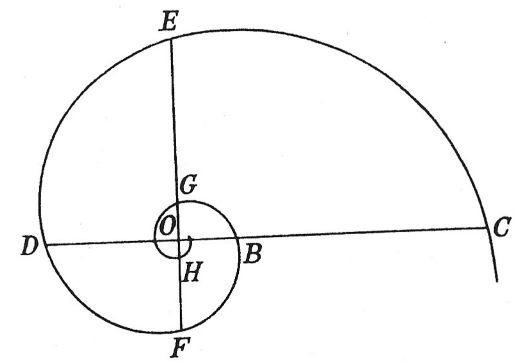


Fig 73. The equiangular spiral.

of these radii, OB, OC. It follows that the sectors cut off by successive radii, at equal vectorial angles, are similar to one another in every respect; and it further follows that the figure may be conceived as growing continuously without ever changing its shape the while.

The many specific properties of the equiangular spiral are so inter-related to one another that we may choose pretty well any one of them as the basis of our definition, and deduce the others from it either by analytical methods or by elementary geometry. In algebra, when $m^x = n$, x is called the logarithm of n to the base m. Hence, in this instance, the equation $r = a$ may be written in the form $\log r = \theta \log a$, or $\theta = \log r / \log a$, or (since a is a constant) $\theta = k \log r$.[1] Which is as much as to say that (as Descartes discovered) the vector angles about the pole are proportional to the logarithms of the successive radii; from which circumstance the alternative name of the 'logarithmic spiral' is derived.

Moreover, for as many properties as the curve exhibits, so many names may it more or less appropriately receive. James Bernoulli called it the logarithmic spiral, as we still often do; P. Nicolas called it the geometrical spiral, because radii at equal polar angles are in geometrical progression; Halley, the proportional spiral, because the parts of a radius cut off by successive whorls are in continued proportion; and lastly, Roger Cotes, going back to Descartes' first description or first definition of all, called it the equiangular spiral.[2] We may also recall Newton's remarkable demonstration that, had the force of gravity varied inversely as the *cube* instead of the *square* of the distance, the planets, instead of being bound to their ellipses, would have been shot off in spiral orbits from the sun, the equiangular spiral being one case thereof.[3]

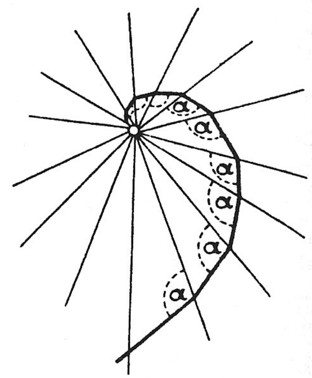


Fig. 74. Spiral path of an insect, as it draws towards a light. From Wigglesworth (after van Buddenbroek).

A singular instance of the same spiral is given by the route which certain insects follow towards a candle. Owing to the structure of their compound eyes, these insects do not look straight ahead but make for a light which they see abeam, at a certain angle. As they continually adjust their path to this constant angle, a spiral pathway brings them to their destination at last.[4]

[1] Instead of $r = a^\theta$, we might write $r = r_0 a^\theta$; in which case r_0 is the value of r for zero value of θ.

[2] James Bernoulli, in *Acta Eruditorum* (1691), p. 282; P. Nicolas, *De novis spiralibus* (Tolosae, 1693), p. 27; E. Halley, *Phil. Trans.* **19** (1696), 58; Roger Cotes, *ibid.* (1714), and *Harmonia Mensurarum* (1722), p. 19. For the further history of the curve see (e.g.) Gomes de Teixeira, *Traité des courbes remarquables* (Coimbra, 1909), pp. 76–86; Gino Loria, *Spezielle algebräische Kurven* (1911), II, 60 seq.; R. C. Archibald (to whom I am much indebted) in *Amer. Math. Mon.* **25** (1918), 189–93, and in Jay Hambidge's *Dynamic Symmetry* (1920), pp. 146–57.

[3] *Principia*, I, 9; II, 15. On these 'Cotes's spirals' see Tait and Steele, p. 147.

[4] Cf. W. Buddenbroek, *Sitzungsber. Heidelb. Akad.* (1917); V. B. Wigglesworth, *The Principles of Insect Physiology* (1939), p. 167.

In mechanical structures, *curvature* is essentially a mechanical phenomenon. It is found in flexible structures as the result of *bending*, or it may be introduced into the construction for the purpose of resisting such a bending-moment. But neither shell nor tooth nor claw are flexible structures; they have not been *bent* into their peculiar curvature, they have *grown* into it.

In the growth of a shell, we can conceive no simpler law than this, namely, that it shall widen and lengthen in the same unvarying proportions: and this simplest of laws is that which Nature tends to follow. The shell, like the creature within it, grows in size *but does not change its shape*; and the existence of this constant relativity of growth, or constant similarity of form, is of the essence, and may be made the basis of a definition, of the equiangular spiral.[1]

Such a definition, though not commonly used by mathematicians, has been occasionally employed; and it is one from which the other properties of the curve can be deduced with great ease and simplicity. In mathematical language it would run as follows: 'Any [plane] curve proceeding from a fixed point (which is called the pole), and such that the arc intercepted between any two radii at a given angle to one another is always similar to itself, is called an equiangular, or logarithmic, spiral.'

In this definition, we have the most fundamental and 'intrinsic' property of the curve, namely the property of continual similarity, and the very property by reason of which it is associated with organic growth in such structures as the horn or the shell. For it is peculiarly characteristic of the spiral shell, for instance, that it does not alter as it grows; each increment is similar to its predecessor, and the whole, after every spurt of growth, is just like what it was before. We feel no surprise when the animal which secretes the shell, or any other animal whatsoever, grows by such symmetrical expansion as to preserve its form unchanged; though even there, as we have already seen, the unchanging form denotes a nice balance between the rates of growth in various directions, which is but seldom accurately maintained for long. But the shell retains its unchanging form in spite of its *asymmetrical* growth; it grows at one end only, and so does the horn. And this remarkable property of increasing by *terminal* growth, but nevertheless retaining unchanged the form of the entire figure, is characteristic of the equiangular spiral, and of no

[1] See an interesting paper by W. A. Whitworth, 'The Equiangular Spiral, its Chief Properties Proved Geometrically', *Messenger of Mathematics* (1), **1** (1862), 5. The celebrated Christian Wiener gave an explanation on these lines of the logarithmic spiral of the shell, in his highly original *Grundzüge der Weltordnung* (1863).

other mathematical curve. It well deserves the name, by which James Bernoulli was wont to call it, of *spira mirabilis*.

We may at once illustrate this curious phenomenon by drawing the outline of a little *Nautilus* shell within a big one. We know, or we may see at once, that they are of precisely the same shape; so that, if we look at the little shell through a magnifying glass, it becomes identical with the big one. But we know, on the other hand, that the little *Nautilus* shell grows into the big one, not by growth or magnification in all parts and directions, as when the boy grows into the man, but by growing *at one end only*.[1]

Though of all plane curves, this property of continued similarity is found only in the equiangular spiral, there are many rectilinear figures in which it may be shown. For instance, it holds good of any cone; for evidently, in Fig. 75, the little inner cone (represented in its triangular section) may become identical with the larger one either by magnification all round (as in *a*), or by an increment at one end (as in *b*); or for that matter on the rest of its surface, represented by the other two sides (as in *c*). All this is associated with the fact, which we have already noted, that the *Nautilus* shell is but a cone rolled up; that, in other words, the cone is but a particular variety, or 'limiting case', of the spiral shell.

[1] If we should want further proof or illustration of the fact that the spiral shell remains of the same shape while increasing in magnitude by its terminal growth, we may find it by help of our ratio $W:L^3$, which remains constant so long as the shape remains unchanged. Here are weights and measurements of a series of small land-shells (*Clausilia*):

W (mg)	L (mm)	$\sqrt[3]{W}/L$
50	14·4	2·56
53	15·1	2·49
56	15·2	2·52
56	15·2	2·52
56	15·4	2·44
58	15·5	2·50
61	16·4	2·40
63	16·0	2·49
67	16·0	2·54
69	16·1	2·56
	Mean	2·50

In 100 specimens of *Clausilia* the mean value of $\sqrt[3]{W}/L$ was found to be 2·517, the coefficient of variation 0·092, and the standard deviation 3·6. That is to say, over 90 per cent grouped themselves about a mean value of 2·5 with a deviation of less than 4 per cent. Cf. C. Petersen, *Das Quotientengesetz* (1921), p. 55.

This singular property of continued similarity, which we see in the cone, and recognise as characteristic of the logarithmic spiral, would seem, under a more general aspect, to have engaged the particular attention of ancient mathematicians even from the days of Pythagoras, and so, with little doubt, from the still more ancient days of that Egyptian school whence he derived the foundations of his learning;[1] and its bearing on our biological problem of the shell, however indirect, is close enough to deserve our very careful consideration.

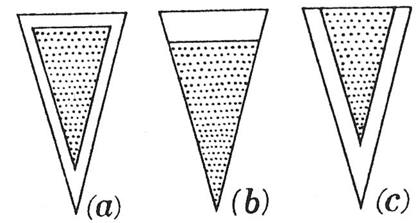


Fig. 75.

There are certain things, says Aristotle, which suffer no alteration (save of magnitude) when they grow.[2] Thus if we add to a square an L-shaped portion, shaped like a carpenter's square, the resulting figure is still a square; and the portion which we have so added, with this singular result, is called in Greek a 'gnomon'.

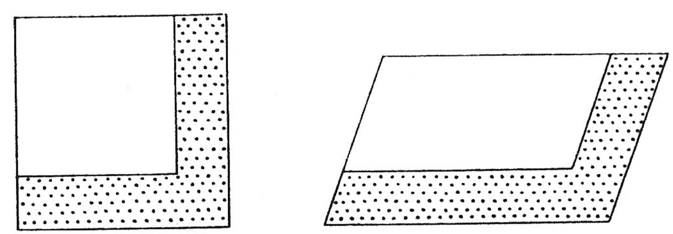


Fig. 76. Gnomonic figures.

Euclid extends the term to include the case of any parallelogram,[3] whether rectangular or not (Fig. 76); and Hero of Alexandria specifically defines a gnomon (as indeed Aristotle had implicitly

[1] I am well aware that the debt of Greek science to Egypt and the east is vigorously denied by many scholars, some of whom go so far as to believe that the Egyptians never had any science, save only some 'rough rules of thumb for measuring fields and pyramids' (Burnet's *Greek Philosophy*, 1914, p. 5).

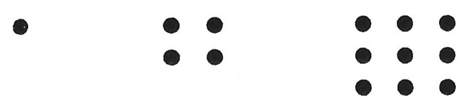
[2] *Categ.* 14, 15*a*, 30: ἔστι τινὰ αὐξανόμενα ἃ οὐκ ἀλλοιοῦται, οἷον τὸ τετράγωνον, γνώμονος περιτεθέντος, ηὔξηται μὲν ἀλλοιότερον δὲ οὐδὲν γεγένηται.

[3] Euclid (II, def. 2).

defined it), as any figure which, being added to any figure whatsoever, leaves the resultant figure similar to the original. Included in this important definition is the case of numbers, considered geometrically; that is to say, the εἰδητικοὶ ἀριθμοί, which can be translated into *form*, by means of rows of dots or other signs (cf. Arist. *Metaph.* 1092 b 12), or in the pattern of a tiled floor: all according to 'the mystical way of Pythagoras, and the secret magick of numbers'. For instance, the triangular numbers, 1, 3, 6, 10, etc., have the natural numbers for their 'differences'; and so the natural numbers may be called their gnomons, because they keep the triangular numbers still triangular. In like manner the square numbers have the successive odd numbers for their gnomons, as follows:

$$0+1 = 1^2$$
$$1^2+3 = 2^2$$
$$2^2+5 = 3^2$$
$$3^2+7 = 4^2 \text{ etc.}$$

And this gnomonic relation we may illustrate graphically (σχηματογραφεῖν) by the dots whose addition keeps the annexed figures perfect squares:[1]



There are other gnomonic figures more curious still. For example, if we make a rectangle (Fig. 77) such that the two sides are in the ratio of $1:\sqrt{2}$, it is obvious that, on doubling it, we obtain a similar figure; for $1:\sqrt{2}::\sqrt{2}:2$; and each half of the figure, accordingly, is now a gnomon to the other. Were we to make our paper of such a shape (say, roughly, 10 in. × 7 in.), we might fold and fold it, and the shape of folio, quarto and octavo pages would be all the same. For another elegant example, let us start with a rectangle (*A*) whose sides are in the proportion of the 'divine' or 'golden section'[2] that is to say as $1:\frac{1}{2}(\sqrt{5}-1)$, or, approximately, as 1:0·618.... The gnomon to this rectangle is the square (*B*) erected on its longer side, and so on successively (Fig. 78).

In any triangle, as Hero of Alexandria tells us, one part is always a gnomon to the other part. For instance, in the triangle *ABC* (Fig. 79), let us draw *BD*, so as to make the angle *CBD* equal to the angle *A*. Then the part *BCD* is a triangle similar to the whole triangle *ABC*, and *ABD* is a gnomon to *BCD*. A very elegant case is when

[1] Cf. Treutlein, *Z. Math. Phys.* **28** (1883), 209.

[2] Euclid, II, 11.

the original triangle *ABC* is an isosceles triangle having one angle of 36°, and the other two angles, therefore, each equal to 72° (Fig. 80). Then, by bisecting one of the angles of the base, we subdivide the large isosceles triangle into two isosceles triangles, of which one is similar to the whole figure and the other is its gnomon.[1] There is good reason to believe that this triangle was especially studied by the

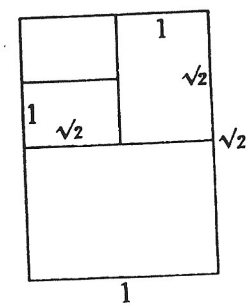


Fig. 77.

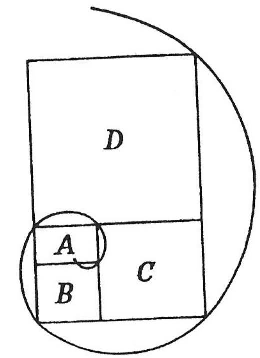


Fig. 78.

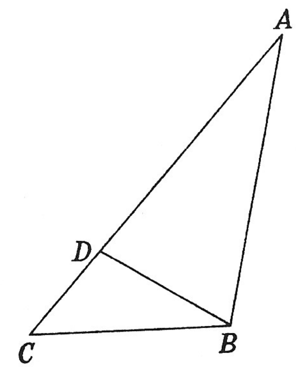


Fig. 79.

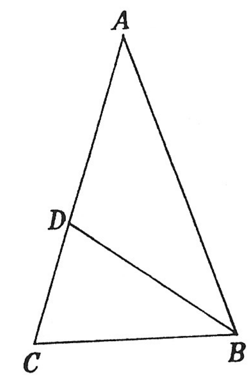


Fig. 80.

Pythagoreans; for it lies at the root of many interesting geometrical constructions, such as the regular pentagon, and its mystical 'pentalpha', and a whole range of other curious figures beloved of the ancient mathematicians:[2] culminating in the regular, or pentagonal,

[1] This is the so-called *Dreifachgleichschenkelige Dreieck*; cf. Naber, *op. cit. infra*. The ratio 1:0·618 is again not hard to find in this construction.

[2] See, on the mathematical history of the gnomon, Heath's *Euclid* (1908), I, *passim*; Zeuthen, *Théorème de Pythagore* (Genève, 1904); also a curious and interesting book, *Das Theorem des Pythagoras*, by Dr H. A. Naber (Haarlem, 1908).

dodecahedron, which symbolised the universe itself, and with which Euclidean geometry ends.

If we take any one of these figures, for instance the isosceles triangle which we have just described, and add to it (or subtract from it) in succession a series of gnomons, so converting it into larger and larger (or smaller and smaller) triangles all similar to the first, we find that the apices (or other corresponding points) of all these triangles have their *locus* upon an equiangular spiral: a result which follows directly from that alternative definition of the equiangular spiral which I have quoted from Whitworth (p. 179).

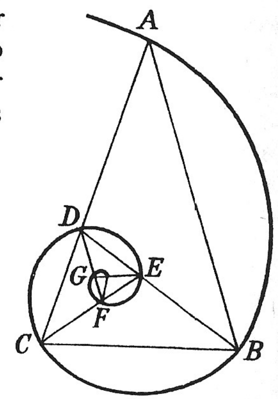


Fig. 81.

If in this, or any other isosceles triangle, we take corresponding median lines of the successive triangles, by joining C to the mid-point (M) of AB, and D to the mid-point (N) of BC, then the pole of the spiral, or centre of similitude of ABC and BCD, is the point of intersection of CM and DN.[1]

Again, we may build up a series of right-angled triangles, each of which is a gnomon to the preceding figure; and here again, an equiangular spiral is the locus of corresponding points in these successive triangles. And lastly, whensoever we fill up space with a collection of equal and similar figures, as in Figs. 82, 83, there we can always discover a series of equiangular spirals in their successive multiples.

Once more, then, we may modify our definition, and say that: 'Any plane curve proceeding from a fixed point (or pole), and such that the vectorial area of any sector is always a gnomon to the whole preceding figure, is called an equiangular, or logarithmic, spiral.' And we may now introduce this new concept and nomenclature into our description of the *Nautilus* shell and other related organic forms, by saying that: (1) if a growing structure be built up of successive parts, similar in form, magnified in geometrical progression, and similarly situated with respect to a centre of similitude, we can always trace through corresponding points a series of equiangular spirals; and (2) it is characteristic of the growth of the horn, of the shell, and of all other organic forms in which an equiangular spiral can be

[1] I owe this simple but novel construction, like so much else, to Dr G. T. Bennett.

recognised, that *each successive increment of growth is similar, and similarly magnified, and similarly situated to its predecessor, and is in consequence a gnomon to the entire pre-existing structure.* Conversely

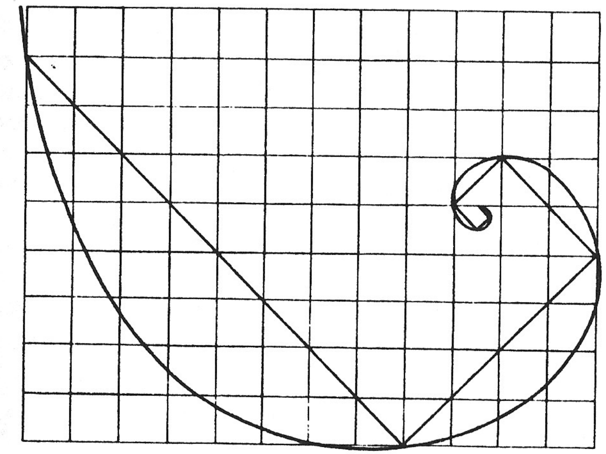


Fig. 82. Logarithmic spiral derived from corresponding points in a system of squares.

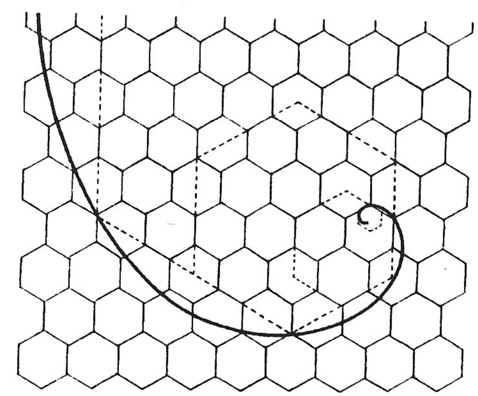


Fig. 83. The same in a system of hexagons. From Naber.

(3) it follows that in the spiral outline of the 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.[1] But

[1] For many beautiful geometrical constructions based on the molluscan shell, see S. Colman and C. A. Coan, *Nature's Harmonic Unity*, ch. IX, Conchology (New York, 1912).

observe that the gnomons to a square may form increments of any size, and the same is true of the gnomons to a *Haliotis*-shell; but in the higher symmetry of a chambered *Nautilus*, or of the successive triangles in Fig. 81, growth goes on by a progressive series of gnomons, each one of which is the gnomon to another.

Of these three propositions, the second is of great use and advantage for our easy understanding and simple description of the molluscan shell, and of a great variety of other structures whose mode of growth is analogous, and whose mathematical properties are therefore identical. We see that the successive chambers of a spiral *Nautilus* or of a straight *Orthoceras*, each whorl or part of a whorl of a periwinkle or other gastropod, each new increment of the operculum

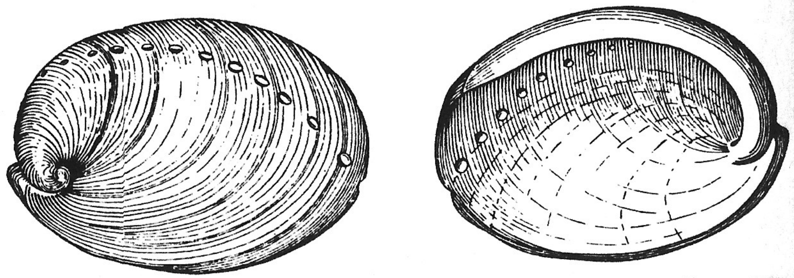


Fig. 84. A shell of *Haliotis*, showing the many lines of growth, or generating curves: the areas bounded by these lines of growth being in all cases gnomons to the pre-existing shell. From J. C. Chenu.

of a gastropod, each additional increment of an elephant's tusk, or each new chamber of a spiral foraminifer, has its leading characteristic at once described and its form so far explained by the simple statement that it constitutes a *gnomon* to the whole previously existing structure. And herein lies the explanation of that 'time-element' in the development of organic spirals of which we have spoken already; for it follows as a simple corollary to this theory of gnomons that we must never expect to find the logarithmic spiral manifested in a structure whose parts are simultaneously produced, as for instance in the margin of a leaf, or among the many curves that make the contour of a fish. But we must look for it wherever the organism retains, and still presents at a single view, the successive phases of preceding growth: the successive magnitudes attained, the successive outlines occupied, as growth pursued the even tenor of its way. And it follows from this that it is in the hard parts of organisms, and not the soft, fleshy, actively growing parts, that this spiral is commonly and characteristically found: not in the fresh mobile tissue

whose form is constrained merely by the active forces of the moment; but in things like shell and tusk, and horn and claw, visibly composed of parts successively and permanently laid down. The shell-less molluscs are never spiral; the snail is spiral but not the slug.[1] In short, it is the shell which curves the snail, and not the snail which curves the shell. The logarithmic spiral is characteristic, not of the living tissues, but of the dead. And for the same reason it will always or nearly always be accompanied, and adorned, by a pattern formed of 'lines of growth', the lasting record of successive stages of form and magnitude.

Spirals in Plants

The cymose inflorescences of the botanists are analogous in a curious and instructive way to the equiangular spiral. In Fig. 85 (*b*) (which represents the *Cicinnus* of Schimper, or *cyme unipare scorpioide* of Bravais, as seen in the Borage), we begin with a primary shoot from which is given off, at a certain definite angle, a secondary shoot: and from that in turn, on the same side and at the same angle, another shoot, and so on. The deflection, or curvature, is continuous and progressive, for it is caused by no external force but only by causes intrinsic in the system. And the whole system is symmetrical: the angles at which the successive shoots are given off being all equal, and the lengths of the shoots diminishing *in constant ratio*. The result is that the successive shoots, or successive increments of growth, are tangents to a curve, and this curve is a true logarithmic spiral. Or in other words, we may regard each successive shoot as forming, or defining, a gnomon to the preceding structure. While in this simple case the successive shoots are depicted as lying in *a plane*, it may also happen that, in addition to their successive angular divergence from one another within that plane, they also tend to diverge by successive equal angles *from* that plane of reference; and by this means, there will be superposed upon the equiangular spiral a twist or screw. And, in the particular case where this latter angle of divergence is just equal to 180°, or two right angles, the successive shoots will once

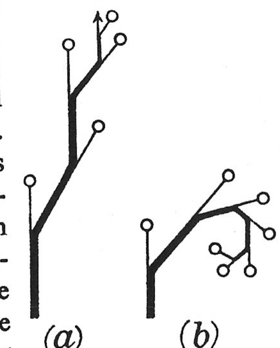


Fig. 85. (*a*) a scorpoid; (*b*) a helicoid cyme.

[1] Note also that *Chiton*, where the pieces of the shell are disconnected, shows no sign of spirality.

more come to lie in a plane, but they will appear to come off from one another on *alternate* sides, as in Fig. 85, *a*. This is the *Schraube* or *Bostryx* of Schimper, the *cyme unipare hélicoide* of Bravais. The equiangular spiral is still latent in it, as in the other; but is concealed from view by the deformation resulting from the helicoid. Many botanists did not recognise (as the brothers Bravais did) the mathematical significance of the latter case, but were led by the snail-like spiral of the scorpoid cyme to transfer the name 'helicoid' to it.[1]

The Molluscan Shell

The paper in which, more than a hundred years ago, Canon Moseley[2] gave a simple mathematical account of the spiral forms of univalve shells, is one of the classics of Natural History. But other students before, and sometimes long before, him had begun to recognise the same simplicity of form and structure. About the year 1818 Reinecke had declared *Nautilus* to be a well-defined geometrical figure, whose chambers followed one another in a constant ratio or continued proportion; and Leopold von Buch and others accepted and even developed the idea.

Long before, Swammerdam[3] had grasped with a deeper insight the root of the whole matter; for, taking a few diverse examples, such as *Helix* and *Spirula*, he showed that they and all other spiral shells whatsoever were referable to one common type, namely to that of a simple tube, variously curved according to definite mathematical laws; that all manner of ornamentation, in the way of spines, tuberosities, colour-bands and so forth, might be superposed upon them, but the type was one throughout and specific differences were of a geometrical kind.

Nay more, we may go back yet another hundred years and find Sir Christopher Wren contemplating the architecture of a snail-shell, and finding in it the logarithmic spiral. For Wallis,[4] after defining and describing this curve with great care and simplicity, tells us that Wren not only conceived the spiral shell to be a sort of cone

[1] The names of these structures have been often confused and misunderstood; cf. S. H. Vines, 'The History of the Scorpoid Cyme', *J. Bot.* (n.s.), **10** (1881), 3–9.

[2] The Rev. Henry Moseley (1801–72), of St John's College, Cambridge, Canon of Bristol, Professor of Natural Philosophy in King's College, London, was a man of great and versatile ability. He was father of H. N. Moseley, naturalist on board the *Challenger* and Professor of Zoology in Oxford; and he was grandfather of H. G. J. Moseley (1887–1915)—Moseley of the Moseley numbers—whose death at Gallipoli, long ere his prime, was one of the major tragedies of the Four Years War.

[3] *Biblia Naturae sive Historia Insectorum* (Leyden, 1737), p. 152.

[4] Joh. Wallis, *Tractatus duo, de Cycloide*, etc. (Oxon., 1659), pp. 107, 108.

or pyramid coiled round a vertical axis, but also saw that on the magnitude of *the angle of the spire* depended the specific form of the shell.

The surface of any shell, whether discoid or turbinate, may be imagined to be generated by the revolution about a fixed axis of a closed curve, which, remaining always geometrically similar to itself, increases its dimensions continually: and, since the scale of the figure increases in geometrical progression while the angle of rotation increases in arithmetical, and the centre of similitude remains fixed, the curve traced in space by corresponding points in the generating curve is, in all such cases, an equiangular spiral. In discoid shells, the generating figure revolves in a plane perpendicular to the axis, as in the Nautilus, the Argonaut and the Ammonite. In turbinate shells, it follows a skew path with respect to the axis of revolution, and the curve in space generated by any given point makes a constant angle to the axis of the enveloping cone, and partakes, therefore, of the character of a helix, as well as of a logarithmic spiral; it may be strictly entitled a helico-spiral. Such turbinate or helico-spiral shells include the snail, the periwinkle and all the common typical gastropods.

Fig. 86. Section of a spiral univalve, *Triton corrugatus* Lam. From Woodward.

The generating figure may be taken as any section of the shell, whether parallel, normal, or otherwise inclined to the axis. It is very commonly assumed to be identical with the mouth of the shell; in which case it is sometimes a plane curve of simple form; in other and more numerous cases, it becomes complicated in form and its boundaries do not lie in one plane: but in such cases as these we may replace it by its 'trace', on a plane at some definite angle to the direction of growth, for instance by its form as it appears in a section through the axis of the helicoid shell. The generating curve is of very various shapes. It is circular in *Scalaria* or *Cyclostoma*, and in *Spirula*; it may be considered as a segment of a circle in *Natica* or in *Planorbis*. It is triangular in *Conus* or *Thatcheria*, and rhomboidal in *Solarium* or *Potamides*. It is very commonly more or less elliptical: the long axis of the ellipse being parallel to the axis of the shell in *Oliva* and *Cypraea*;

all but perpendicular to it in many Trochi; and oblique to it in many well-marked cases, such as *Stomatella, Lamellaria, Sigaretus haliotoides* (Fig. 87) and *Haliotis*. In *Nautilus pompilius* it is approximately a semi-ellipse, and in *N. umbilicatus* rather more than a semi-ellipse, the long axis lying in both cases perpendicular to the axis of the shell.[1] Its form is seldom open to easy mathematical expression, save when it is an actual circle or ellipse; but an exception to this rule may be found in certain Ammonites, forming the group 'Cordati', where (as Blake points out) the curve is very nearly represented by a cardioid, whose equation is $r = a(1+\cos\theta)$.

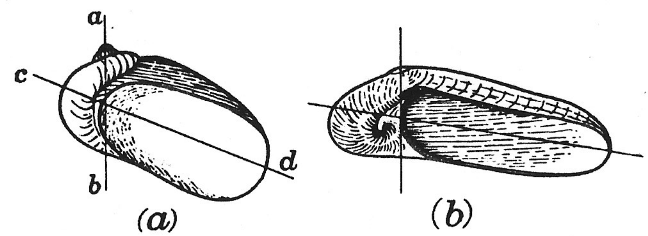


Fig. 87. (*a*) *Lamellaria perspicua*; (*b*) *Sigaretus haliotoides*. After Woodward.

When the generating curves of successive whorls cut one another, the line of intersection forms the conspicuous helico-spiral or loxodromic curve called the *suture* by conchologists.

The generating curve may grow slowly or quickly; its growth-factor is very slow in *Dentalium* or *Turritella*, very rapid in *Nerita*, or *Pileopsis*, or *Haliotis* or the Limpet. It may contain the axis in its plane, as in *Nautilus*; it may be parallel to the axis, as in the majority of gastropods; or it may be inclined to the axis, as it is in a very marked degree in *Haliotis*. In fact, in *Haliotis* the generating curve is so oblique to the axis of the shell that the latter appears to grow by additions to one margin only (cf. Fig. 84).

The general appearance of the entire shell is determined (apart from the form of its generating curve) by the magnitude of three angles; and these in turn are determined by the ratios of certain velocities of growth. These angles are (1) the constant angle of the

[1] In *Nautilus*, the 'hood' has somewhat different dimensions in the two sexes, and these differences are impressed upon the shell, that is to say upon its 'generating curve'. The latter constitutes a somewhat broader ellipse in the male than in the female. But this difference is not to be detected in the young; in other words, the form of the generating curve perceptibly alters with advancing age. Somewhat similar differences in the shells of Ammonites were long ago suspected, by d'Orbigny, to be due to sexual differences. (Cf. Willey, *Natural Science*, 1895, VI, 411; *Zoological Results*, 1902, p. 742.)

equiangular spiral (α); (2) in turbinate shells, the enveloping angle of the cone, or (taking half that angle) the angle (β) which a tangent to the whorls makes with the axis of the shell; and (3) an angle called the 'angle of retardation' (γ), which expresses the retardation in growth of the inner as compared with the outer part of each whorl, and therefore measures the extent to which the one whorl overlaps, or the extent to which it is separated from, another.

The spiral angle (α) is very small in a limpet, where it is usually taken as $=0°$; but it is evidently of a significant amount, though obscured by the shortness of the tubular shell. In *Dentalium* it is still small, but sufficient to give the appearance of a regular curve; it amounts here probably to about 30° to 40°. In *Haliotis* it is from about 70° to 75°; in *Nautilus* about 80°; and it lies between 80° and 85° or even more, in the majority of gastropods.[1]

The case of *Fissurella* is curious. Here we have, apparently, a conical shell with no trace of spiral curvature, or (in other words) with a spiral angle which approximates to 0°; but in the minute embryonic shell (as in that of the limpet) a spiral convolution is distinctly to be seen. It would seem, then, that what we have to do with here is an unusually large growth-factor in the generating curve, causing the shell to dilate into a cone of very wide angle, the apical portion of which has become lost or absorbed, and the remaining part of which is too short to show clearly its intrinsic curvature. In the closely allied *Emarginula*, there is likewise a well-marked spiral in the embryo, which however is still manifested in the curvature of the adult, nearly conical, shell. In both cases we have to do with a very wide-angled cone, and with a high retardation-factor for its inner, or posterior, border. The series is continued, from the apparently simple cone to the complete spiral, through such forms as *Calyptraea*.

The angle α is not always, nor rigorously, a constant angle. In some Ammonites it may increase with age, the whorls becoming closer and closer; in others it may decrease rapidly and even fall to zero, the coiled shell then straightening out, as in *Lituites* and similar forms. It diminishes somewhat, also, in many Orthocerata, which are slightly curved in youth but straight in age. It tends to increase notably in some common land-shells, the *Pupae* and *Bulimi*; and it decreases in *Succinea*.

A variation with advancing age of β is common, but (as Blake

[1] What is sometimes called, as by Leslie, the *angle of deflection* is the complement of what we have called the *spiral angle* (α), or obliquity of the spiral. When the angle of deflection is 6° 17′ 41″, or the spiral angle 83° 42′ 19″, the radiants, or breadths of successive whorls, are doubled at each entire circuit.

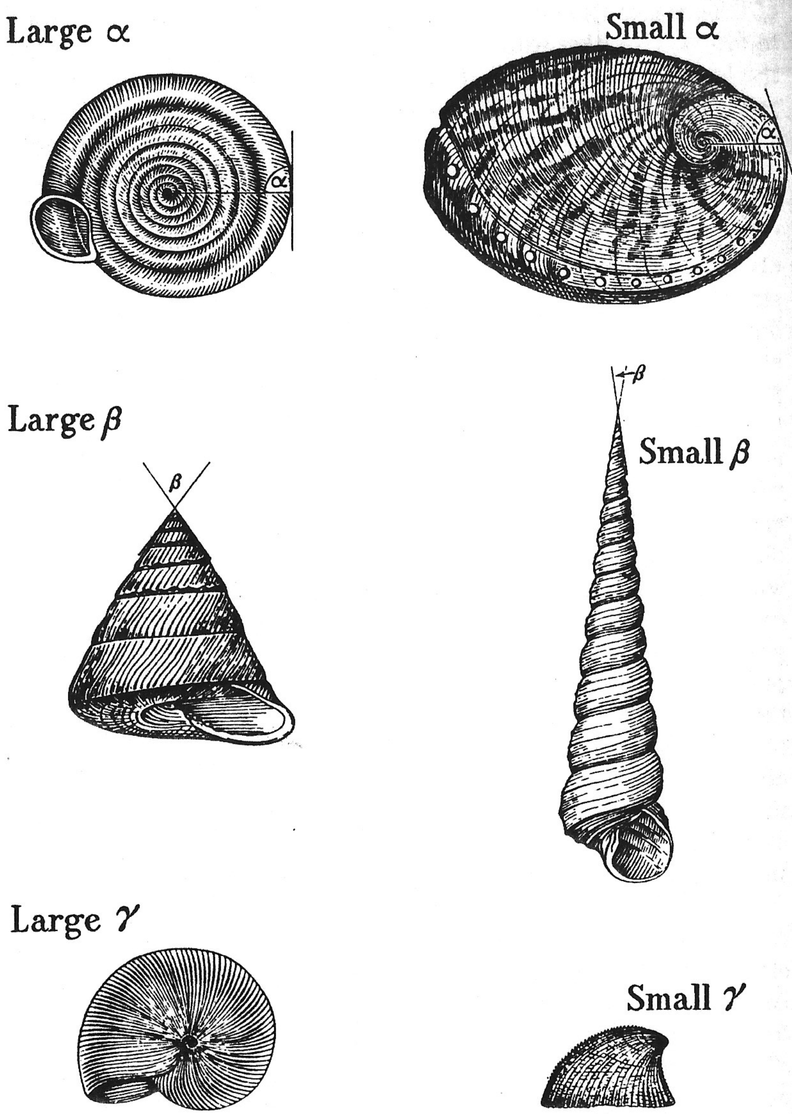


Fig. 88. Various gastropods showing the effect of the alteration of different angles. In the top row the shells have large and small spiral angles (α); in the middle row they have large and small enveloping angles of the conical ends (β); in the bottom row there are large and small angles of retardation (γ) which govern the extent to which the whorls overlap. From J. C. Chenu.

points out) it is often not to be distinguished or disentangled from an alteration of α. Whether alone, or combined with a change in α, we find it in all those many gastropods whose whorls cannot all be touched by the same enveloping cone, and whose spire is accordingly described as *concave* or *convex*. The former condition, as we have it in *Cerithium*, and in the cusp-like spire of *Cassis*, *Dolium* and some Cones, is much the commoner of the two.

The angle of retardation (γ) is very small in *Dentalium* and *Patella*; it is very large in *Haliotis*; it becomes infinite in *Argonauta* and in *Cypraea*. Connected with the angle of retardation are the various possibilities of contact or separation, in various degrees, between adjacent whorls in the discoid shell, and between both adjacent and opposite whorls in the turbinate.

Foraminiferan Spirals

It is characteristic and even diagnostic of the Foraminifera (1) that development proceeds by a well-marked alternation of rest and of activity—of activity during which the protoplasm increases, and of rest during which the shell is formed; (2) that the shell is formed at the outer surface of the protoplasmic organism, and tends to constitute a continuous or all but continuous covering; and it follows (3) from these two factors taken together that each successive increment is added on outside of and distinct from its predecessors, that the successive parts or chambers of the shell are of different and successive ages, so that one part of the shell is always relatively new, and the rest old in various grades of seniority.

That the shell in the Foraminifera should tend towards a spiral form need not surprise us; for we have learned that one of the fundamental conditions of the production of a concrete spiral is just precisely what we have here, namely the development of a structure by means of successive graded increments superadded to its exterior, which then form part, successively, of a permanent and rigid structure. This condition is obviously forthcoming in the foraminiferal, but not at all in the radiolarian, shell. Our second fundamental condition of the production of a logarithmic spiral is that each successive increment shall be so posited and so conformed that its addition to the system leaves the form of the whole system unchanged. We have now to enquire into this latter condition; and to determine whether the successive increments, or successive chambers, of the foraminiferal shell actually constitute *gnomons* to the entire structure.

This may be best examined by investigating the various configurations to be found among the Foraminifera.

Firstly we have the typically spiral shells, which occur in great variety, and which (for our present purpose) we need hardly describe further. We may merely notice how in certain cases, for instance *Globigerina*, the individual chambers are little removed from spheres;

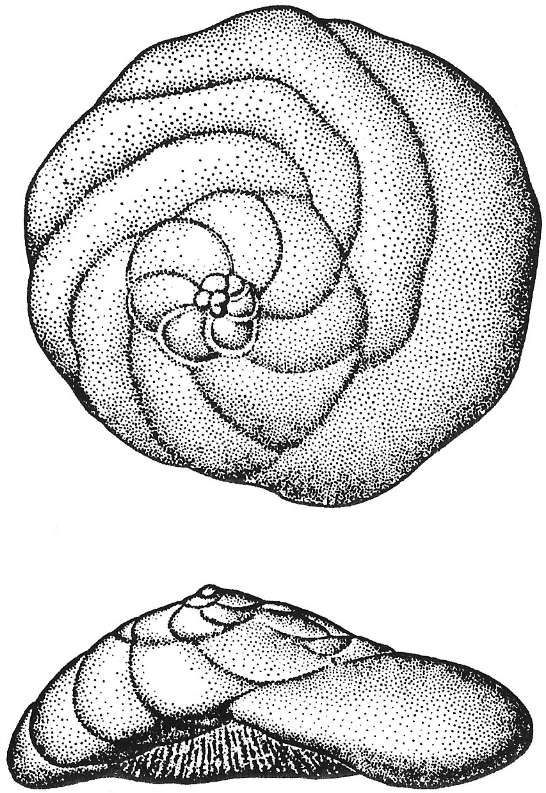


Fig. 89. *Discorbis.* After Le Calvez from K. G. Grell, *Protozoologie* (Berlin: Springer-Verlag).

in other words, the area of contact between the adjacent chambers is small. In such forms as *Cyclammina* and *Pulvinulina*, on the other hand, each chamber is greatly overlapped by its successor, and the spherical form of each is lost in a marked asymmetry. Furthermore, in *Globigerina* and some others we have a tendency to the development of a gauche spiral in space, as in so many of our univalve molluscan shells. The mathematical problem of how a shell should grow, under the assumptions which we have made, would probably

find its most general statement in such a case as that of *Globigerina*, where the whole organism lives and grows freely poised in a medium whose density is little different from its own.

The majority of spiral forms, on the other hand, are plane or discoid spirals, and we may take it that in these cases some force has exercised a controlling influence, so as to keep all the chambers in a plane. This is especially the case in forms like *Rotalia* or *Discorbis* (Fig. 89), where the organism lives attached to a rock or a frond of sea-weed; for here (just as in the case of the coiled tubes which little worms such as *Serpula* and *Spirorbis* make, under similar conditions) the spiral disc is itself asymmetrical, its whorls being markedly flattened on their attached surfaces.

We may also conceive, among other conditions, the very curious case in which the protoplasm may entirely overspread the surface of the shell without reaching a position of equilibrium; in which case a new shell will be formed *enclosing* the old one, whether the old one be in the form of a single, solitary chamber, or have already attained to the form of a chambered or spiral shell. This is precisely what often happens in the case of *Orbulina*, when within the spherical shell we find a small, but perfectly formed, spiral '*Globigerina*'.[1]

The various Miliolidae only differ from the typical spiral, or rotaline forms, in the large angle subtended by each chamber, and the consequent abruptness of their inclination to each other. In these cases the *outward* appearance of a spiral tends to be lost; and it behoves us to recollect, all the more, that our spiral curve is not necessarily identical with the *outline* of the shell, but is always a line drawn through corresponding *points* in the successive chambers of the latter.

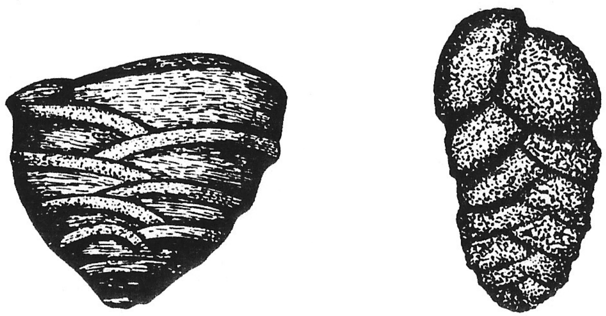
We reach a limiting case of the logarithmic spiral when the chambers are arranged in a straight line; and the eye will tend to associate with this limiting case the much more numerous forms in which the spiral angle is small, and the shell only exhibits a gentle curve with no succession of enveloping whorls. This constitutes the Nodosarian type (Fig. 23); and here again, we must postulate some force which has tended to keep the chambers in a rectilinear series: such for instance as gravity, acting on a system of 'hanging drops'.

In *Textularia* and its allies (Fig. 90) we have a precise parallel to the helicoid cyme of the botanists (cf. p. 187): that is to say we have a screw translation, perpendicular to the plane of the underlying

[1] Cf. G. Schacko, 'Ueber *Globigerina*-Einschluss bei *Orbulina*', *Wiegmann's Archiv*, **49** (1883), 428; Brady, *Chall. Rep.* (1884), p. 607.

logarithmic spiral. In other words, in tracing a genetic spiral through the whole succession of chambers, we do so by a continuous vector rotation through successive angles of 180° (or 120° in some cases), while the pole moves along an axis perpendicular to the original plane of the spiral.

Another type is furnished by the 'cyclic' shells of the Orbitolitidae, where small and numerous chambers tend to be added on round and round the system, so building up a circular flattened disc. This again we perceive to be, mathematically, a limiting case of the logarithmic spiral; the spiral has become wellnigh a circle and the constant angle is wellnigh 90°.



(a) (b)

Fig. 90. (*a*) *Textularia trochus* d'Orb. (*b*) *T. concava* Karrer.

Variation among Foraminifera

Lastly there are a certain number of Foraminifera in which, without more ado, we may simply say that the arrangement of the chambers is irregular, neither the law of constant ratio of magnitude nor that of constant form being obeyed. The chambers are heaped pell-mell upon one another, and such forms are known to naturalists as the Acervularidae.

While in these last we have an extreme lack of regularity, we must not exaggerate the regularity or constancy which the more ordinary forms display. We may think it hard to believe that the simple causes, or simple laws, which we have described should operate, and operate again and again, in millions of individuals to produce the same delicate and complex conformations. But we are taking a good deal for granted if we assert that they do so, and in particular we are assuming, with very little proof, the 'constancy of species' in this group of animals. Just as Verworn has shown that the

typical *Amoeba proteus*, when a trace of alkali is added to the water in which it lives, tends, by alteration of surface-tensions, to protrude the more delicate pseudopodia characteristic of *A. radiosa*—and again when the water is rendered a little more alkaline, to turn apparently into the so-called *A. limax*—so it is evident that a very slight modification in the surface-energies concerned might tend to turn one so-called species into another among the Foraminifera. To what extent this process actually occurs, we do not know.

But that this, or something of the kind, does actually occur we can scarcely doubt. For example, in the genus *Peneroplis*, the first portion of the shell consists of a series of chambers arranged in a spiral or nautiloid series; but as age advances the spiral is apt to be modified in various ways.[1] Sometimes the successive chambers grow rapidly broader, the whole shell becoming fan-shaped. Sometimes the chambers become narrower, till they no longer enfold the earlier chambers but only come in contact each with its immediate predecessor: the result being that the shell straightens out, and (taking into account the earlier spiral portion) may be described as crozier-shaped. Between these extremes of shape, and in regard to other variations of thickness or thinness, roughness or smoothness, and so on, there are innumerable gradations passing one into another and intermixed without regard to geographical distribution: 'wherever Peneroplides abound this wide variation exists, and nothing can be more easy than to pick out a number of striking specimens and give to each a distinctive name, but *in no other way can they be divided into "species"*'.[2] Some writers have wondered at the peculiar variability of this particular shell;[3] but for all we know of the life-history of the Foraminifera, it may well be that a great number of the other forms which we distinguish as separate species and even genera are no more than temporary manifestations of the same variability.

If we can comprehend and interpret on some such lines as these the form and mode of growth of the foraminiferal shell we may also begin to understand two striking features of the group, on the one hand the large number of diverse types or families which exist and

[1] Cf. H. B. Brady, *Chall. Rep., Foraminifera* (1884), p. 203, pl. XIII.

[2] Brady, *op. cit.* p. 206; Batsch, one of the earliest writers on Foraminifera, had already noticed that this whole series of ear-shaped and crozier-shaped shells was filled in by gradational forms; *Conchylien des Seesandes* (1791), p. 4, pl. VI, fig. 15*a–f*. See also, in particular, Dreyer, *Peneroplis; eine Studie zur biologischen Morphologie und zur Speciesfrage* (Leipzig, 1898); also Eimer und Fickert, 'Artbildung und Verwandschaft bei den Foraminiferen', *Tübing. zool. Arbeiten*, 3 (1899), 35.

[3] Doflein, *Protozoenkunde* (1911), p. 263: 'Was diese Art veranlässt in dieser Weise gelegentlich zu variiren, ist vorläufig noch ganz räthselhaft.'

the large number of species and varieties within each, and on the other the persistence of forms which in many cases seem to have undergone little change or none at all from the Cretaceous or even from earlier periods to the present day. In few other groups, perhaps only among the Radiolaria, do we seem to possess so nearly complete a picture of all possible transitions between form and form, and of the whole branching system of the evolutionary tree: as though little or nothing of it had ever perished, and the whole web of life, past and present, were as complete as ever. It leads one to imagine that these shells have grown according to laws so simple, so much in harmony with their material, with their environment, and with all the forces internal and external to which they are exposed, that none is better than another and none fitter or less fit to survive. It invites one also to contemplate the possibility of the lines of possible variation being here so narrow and determinate that identical forms may have come independently into being again and again.

While we can trace in the most complete and beautiful manner the passage of one form into another among these little shells, and ascribe them all at last (if we please) to a series which starts with the simple sphere of *Orbulina* or with the amoeboid body of *Astrorhiza*, the question stares us in the face whether this be an 'evolution' which we have any right to correlate with historic *time*. The mathematician can trace one conic section into another, and 'evolve' for example, through innumerable graded ellipses, the circle from the straight line: which tracing of continuous steps is a true 'evolution', though time has no part therein. It was after this fashion that Hegel, and for that matter Aristotle himself, was an evolutionist—to whom evolution was a mental concept, involving order and continuity in thought but not an actual sequence of events in time. Such a conception of evolution is not easy for the modern biologist to grasp, and is harder still to appreciate. And so it is that even those who, like Dreyer[1] and like Rhumbler, study the foraminiferal shell as a physical system, who recognise that its whole plan and mode of growth is closely akin to the phenomena exhibited by fluid drops under particular conditions, and who explain the conformation of the shell by help of the same physical principles and mathematical laws—yet all the while abate no jot or tittle of the ordinary postulates of modern biology, nor doubt the validity and universal applicability of the concepts of Darwinian evolution. For these writers the *biogenetisches*

[1] F. Dreyer, 'Prinzipien der Gerüstbildung bei Rhizopoden, etc.', *Jena Z. Naturw.* 26 (1892), 204–468.

Grundgesetz remains impregnable. The Foraminifera remain for them a great family tree, whose actual pedigree is traceable to the remotest ages; in which historical evolution has coincided with progressive change; and in which structural fitness for a particular function (or functions) has exercised its selective action and ensured 'the survival of the fittest.' By successive stages of historic evolution we are supposed to pass from the irregular *Astrorhiza* to a *Rhabdammina* with its more concentrated disc; to the forms of the same genus which consist of but a single tube with central chamber; to those where this chamber is more and more distinctly segmented; so to the typical many-chambered Nodosariae; and from these, by another definite advance and later evolution, to the spiral Trochamminae. After this fashion, throughout the whole varied series of the Foraminifera, Dreyer and Rhumbler (following Neumayr) recognise so many successions of related forms, one passing into another and standing towards it in a definite relationship of ancestry or descent. Each evolution of form, from simpler to more complex, is deemed to have been attended by an advantage to the organism, an enhancement of its chances of survival or perpetuation; hence the historically older forms are on the whole structurally the simpler; or conversely, the simpler forms, such as the simple sphere, were the first to come into being in primeval seas; and finally, the gradual development and increasing complication of the individual within its own lifetime is held to be at least a partial recapitulation of the unknown history of its race and dynasty.[1]

We encounter many difficulties when we try to extend such concepts as these to the Foraminifera. We are led for instance to assert, as Rhumbler does, that the increasing complexity of the shell, and of the manner in which one chamber is fitted on another, makes for advantage; and the particular advantage on which Rhumbler rests his argument is *strength*. Increase of strength, *die Festigkeitssteigerung*, is according to him the guiding principle in foraminiferal evolution, and marks the historic stages of their development in geologic time. But in days gone by I used to see the beach of a little Connemara bay bestrewn with millions upon millions of foraminiferal shells, simple Lagenae, less simple Nodosariae, more complex Rotaliae: all drifted by wave and gentle current from their sea-cradle to their sandy grave: all lying bleached and dead: one more delicate

[1] A difficulty arises in the case of forms (like *Peneroplis*) where the young shell appears to be more complex than the old, the first-formed portion being closely coiled while the later additions become straight and simple: 'die biformen Arten verhalten sich, kurz gesagt, gerade umgekehrt als man nach dem biogenetischen Grundgesetz erwarten sollte', Rhumbler, *Foraminiferen der Plankton-Expedition*, 1911, p. 33, etc.

than another, but all (or vast multitudes of them) perfect and unbroken. And so I am not inclined to believe that niceties of form affect the case very much: nor in general that foraminiferal life involves a struggle for existence wherein breakage is a danger to be averted, and strength an advantage to be ensured.

In the course of the same argument Rhumbler remarks that Foraminifera are absent from the coarse sands and gravels, as Williamson indeed had observed many years ago: so averting, or at least escaping, the dangers of concussion. But this is after all a very simple matter of mechanical analysis. The coarseness or fineness of the sediment on the sea-bottom is a measure of the current: where the current is strong the larger stones are washed clean, where there is perfect stillness the finest mud settles down; and the light, fragile shells of the Foraminifera find their appropriate place, like every other graded sediment in this spontaneous order of levigation.

The theorem of Organic Evolution is one thing; the problem of deciphering the lines of evolution, the order of phylogeny, the degrees of relationship and consanguinity, is quite another. Among the higher organisms we arrive at conclusions regarding these things by weighing much circumstantial evidence, by dealing with the resultant of many variations, and by considering the probability or improbability of many coincidences of cause and effect; but even then our conclusions are at best uncertain, our judgments are continually open to revision and subject to appeal, and all the proof and confirmation we can ever have is that which comes from the direct, but fragmentary evidence of palaeontology.

But in so far as forms can be shown to depend on the play of physical forces, and the variations of form to be directly due to simple quantitative variations in these, just so far are we thrown back on our guard before the biological conception of consanguinity, and compelled to revise the vague canons which connect classification with phylogeny.

The physicist explains in terms of the properties of matter, and classifies according to a mathematical analysis, all the drops and forms of drops and associations of drops, all the kinds of froth and foam, which he may discover among inanimate things; and his task ends there. But when such forms, such conformations and configurations, occur among *living* things, then at once the biologist introduces his concepts of heredity, of historical evolution, of succession in time, of recapitulation of remote ancestry in individual growth, of common origin (unless contradicted by direct evidence) of similar forms

remotely separated by geographic space or geologic time, of fitness for a function, of adaptation to an environment, of higher and lower, of 'better' and 'worse'. This is the fundamental difference between the 'explanations' of the physicist and those of the biologist.

In the order of physical and mathematical complexity there is no question of the sequence of historic time. The forces that bring about the sphere, the cylinder or the ellipsoid are the same yesterday and to-morrow. A snow-crystal is the same to-day as when the first snows fell. The physical forces which mould the forms of *Orbulina*, of *Astrorhiza*, of *Lagena* or of *Nodosaria* to-day were still the same, and for aught we have reason to believe the physical conditions under which they worked were not appreciably different, in that yesterday which we call the Cretaceous epoch; or, for aught we know, throughout all that duration of time which is marked, but not measured, by the geological record.

In a word, the minuteness of our organism brings its conformation as a whole within the range of the molecular forces; the laws of its growth and form appear to lie on simple lines; what Bergson calls[1] the 'ideal kinship' is plain and certain, but the 'material affiliation' is problematic and obscure; and, in the end and upshot, it seems to me by no means certain that the biologist's usual mode of reasoning is appropriate to the case, or that the concept of continuous historical evolution must necessarily, or may safely and legitimately, be employed.

That things not only alter but improve is an article of faith, and the boldest of evolutionary conceptions. How far it be true were very hard to say; but I for one imagine that a pterodactyl flew no less well than does an albatross, and that Old Red Sandstone fishes swam as well and easily as the fishes of our own seas.

[1] The evolutionist theory, as Bergson puts it, 'consists above all in establishing relations of ideal kinship, and in maintaining that wherever there is this relation of, so to speak, *logical* affiliation between forms, *there is also a relation of chronological succession between the species in which these forms are materialised*' (*Creative Evolution*, 1911, p. 26).