CHAPTER XI

THE EQUIANGULAR SPIRAL

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*. 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†, in the coil of an elephant's trunk, in the "circling spires"

* 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.

† On this interesting case see, e.g. J. E. Duerden, in *Science*, May 25, 1934.

of a snake, in the coils of a cuttle-fish's arm, or of a monkey's or a chameleon's tail.

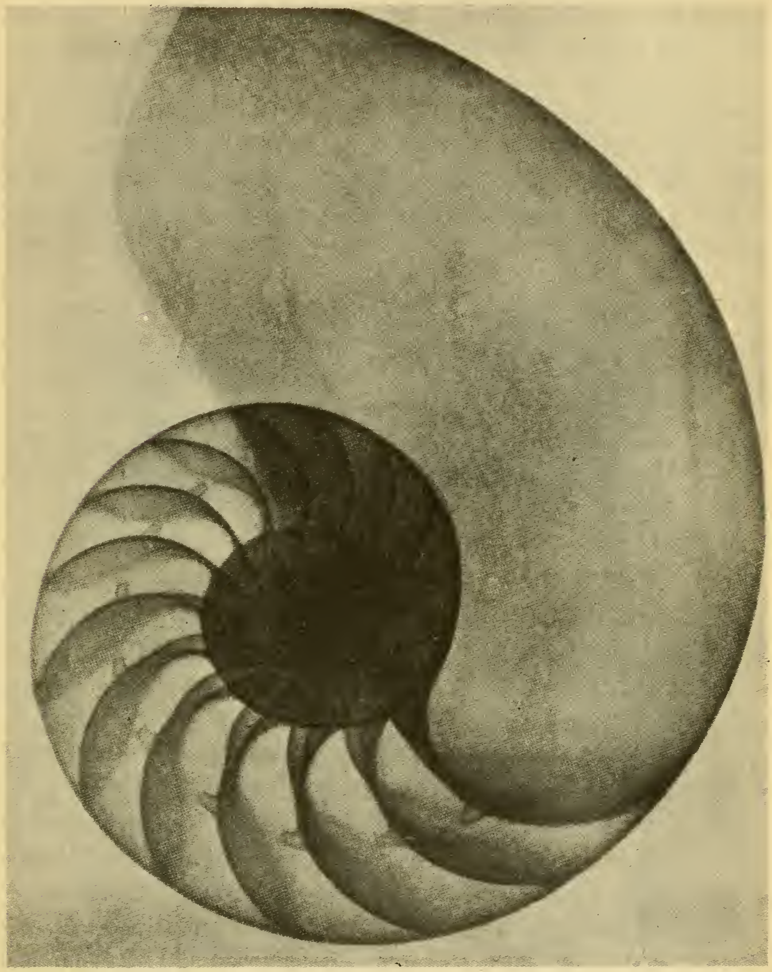


Fig. 347. The shell of *Nautilus pompilius*, from a radiograph: to shew the equiangular spiral of the shell, together with the arrangement of the internal septa. From Green and Gardiner, in *Proc. Malacol. Soc.* II, 1897.

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 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.

Fig. 348. A foraminiferal shell (*Pulvinulina*).

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 géométrie**."

* 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.

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 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*. 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 shew 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

* 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.

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.

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 describe the equable spiral*." 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

* 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*, I, p. 262, 1880.

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.

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

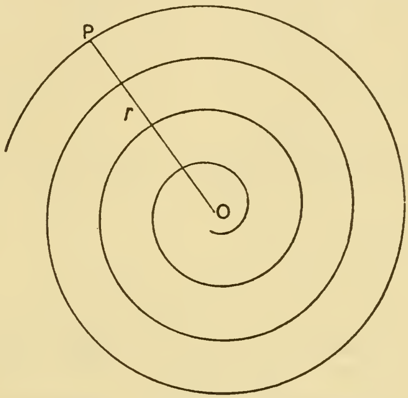


Fig. 349. The spiral of Archimedes.

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*. Starting with the conception of a growing curve which should cut each radius vector at a constant angle—just as a circle does—Descartes shewed how it would necessarily follow that radii at equal 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 of these radii, OB, OC. It follows that

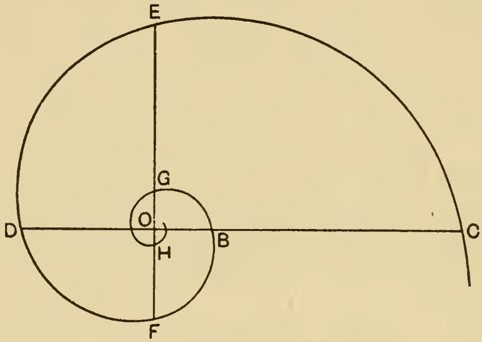


Fig. 350. The equiangular spiral.

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.

If the whorls increase very slowly, the equiangular spiral will come to look like a spiral of Archimedes. The Nummulite is a case in point. Here we have a large number of whorls, very narrow, very close together, and apparently of equal breadth, which give rise to an appearance similar to that of our coiled rope. And, in a case of this kind, we might actually find that the whorls *were* of equal breadth, being produced (as is apparently the case in the Nummulite) not by any very slow and gradual growth in thickness of a continuous tube, but by a succession of similar cells or chambers laid on, round and round, determined as to their size by constant surface-tension conditions and therefore of unvarying dimensions. The Nummulite must always have a central core, or initial cell, around which the coil is not only wrapped, but out of which it springs; and this initial chamber corresponds to our a' in the expression $r = a' + a\theta \cot \alpha$.

* *Œuvres*, ed. Adam et Tannery, Paris, 1898, p. 360.

The many specific properties of the equiangular spiral are so interrelated 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 $r = a^\theta$ may be written in the form $\log r = \theta \log a$, or $\theta = \log r/\log a$, or (since a is a constant) $\theta = k \log r$*. 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‡. 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

* 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.

† Of the two names for this spiral, equiangular and logarithmic, I used the latter in my first edition, but equiangular spiral seems to be the better name; for the constant angle is its most distinguishing characteristic, and that which leads to its remarkable property of continuous self-similarity. Equiangular spiral is its name in geometry; it is the analyst who derives from its geometrical properties its relation to the logarithm. The mechanical as well as the mathematical properties of this curve are very numerous. A Swedish admiral, in the eighteenth century, shewed an equiangular spiral (of a certain angle) to be the best form for an anchor-fluke (*Sv. Vet. Akad. Hdl.* xv, pp. 1–24, 1796), and in a parrot's beak it has the same efficiency. Macquorn Rankine shewed its advantages in the pitch of a cam or non-circular wheel (*Manual of Mechanics*, 1859, pp. 99–102; cf. R. C. Archibald, *Scripta Mathem.* III (4), p. 366, 1935).

‡ James Bernoulli, in *Acta Eruditorum*, 1691, p. 282; P. Nicolas, *De novis spiralibus*, Tolosae, 1693, p. 27; E. Halley, *Phil. Trans.* XIX, p. 58, 1696; 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*, Coimbre, 1909, pp. 76–86; Gino Loria, *Spezielle algebräische Kurven*, II, p. 60 *seq.*, 1911; R. C. Archibald (to whom I am much indebted) in *Amer. Mathem. Monthly*, XXV, pp. 189–193, 1918, and in Jay Hambidge's *Dynamic Symmetry*, 1920, pp. 146–157.

ellipses, would have been shot off in spiral orbits from the sun, the equiangular spiral being one case thereof.*

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†.

In mechanical structures, *curvature* is essentially a mechanical phenomenon. It is found in flexible structures as the result of

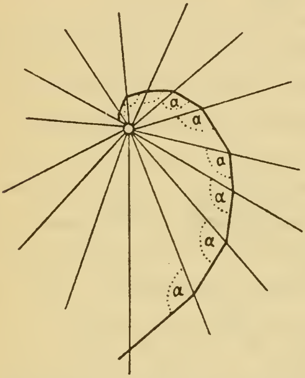


Fig. 351. Spiral path of an insect, as it draws towards a light. From Wigglesworth (after van Buddenbroek).

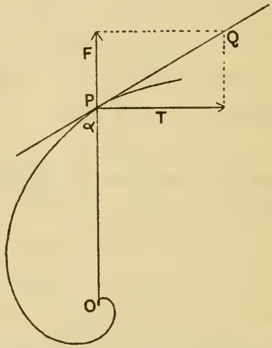


Fig. 352. Dynamical aspect of the equiangular spiral.

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.

We may for a moment, however, regard the equiangular or logarithmic spiral of our shell from the dynamical point of view, by looking on *growth* itself as the force concerned. In the growing structure, let growth at any point P be resolved into a force F acting along the line joining P to a pole O, and a force T acting in a direction perpendicular to OP; and let the magnitude of these forces (or of these rates of growth) remain constant. It follows that

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

† Cf. W. Buddenbroek, *Sitzungsber. Heidelb. Akad.*, 1917; V. H. Wigglesworth, *Insect Physiology*, 1839, p. 167.

the resultant of the forces F and T (as PQ) makes a constant angle with the radius vector. But a constant angle between tangent and radius vector is a fundamental property of the "equiangular" spiral: the very property with which Descartes started his investigation, and that which gives its alternative name to the curve.

In such a spiral, radial growth and growth in the direction of the curve bear a constant ratio to one another. For, if we consider a consecutive radius vector, OP', whose increment as compared with OP is dr, while ds is the small arc PP', then $dr/ds = \cos\alpha = \text{constant}$.

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*.

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

* See an interesting paper by W. A. Whitworth, The equiangular spiral, its chief properties proved geometrically, *Messenger of Mathematics* (1), I, p. 5, 1862. 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.

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 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*.

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 (mgm.)	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

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 shewn. For instance, it holds good of

* 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.

any cone; for evidently, in Fig. 353, 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.

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

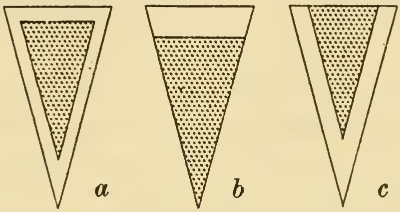


Fig. 353.

his learning*; and its bearing on our biological problem of the shell, however indirect, is close enough to deserve our very careful consideration.

There are certain things, says Aristotle, which suffer no alteration (save of magnitude) when they grow†. 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."

Euclid extends the term to include the case of any parallelogram‡, whether rectangular or not (Fig. 354); and Hero of Alexandria

* 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).

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

‡ Euclid (II, def. 2).

specifically defines a gnomon (as indeed Aristotle had implicitly 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

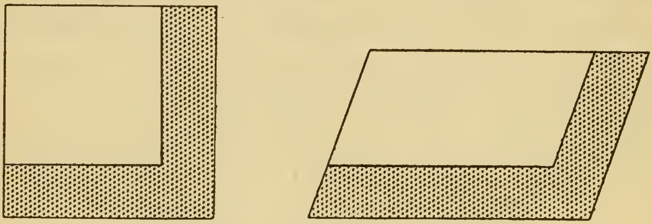


Fig. 354. Gnomonic figures.

magick ot 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:

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

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

There are other gnomonic figures more curious still. For example, if we make a rectangle (Fig. 355) such that the two sides are in the

* Cf. Treutlein, *Ztschr. f. Math. u. Phys.* (*Hist. litt. Abth.*), XXVIII, p. 209, 1883.

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*" that is to say as $1:\frac{1}{2}(\sqrt{5}-1)$, or, approximately, as $1:0{\cdot}618\ldots$. The gnomon to this rectangle is the square (B) erected on its longer side, and so on successively (Fig. 356).

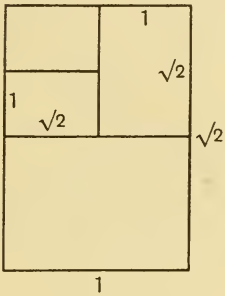


Fig. 355.

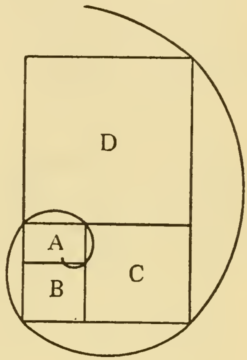


Fig. 356.

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. 357), 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 the original triangle ABC is an isosceles triangle having one angle of 36°, and the other two angles, therefore, each equal to 72° (Fig. 358). 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†. There is good reason to believe that this triangle was especially studied by the Pythagoreans; for it lies at the root of

* Euclid, II, 11.

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

many interesting geometrical constructions, such as the regular pentagon, and its mystical "pentalpha," and a whole range of other curious figures belovèd of the ancient mathematicians*: culminating

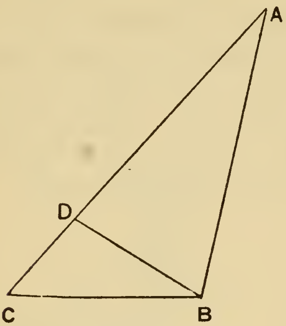


Fig. 357.

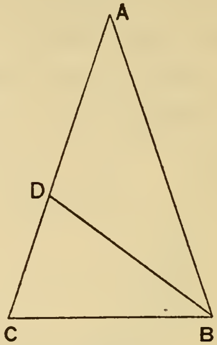


Fig. 358.

in the regular, or pentagonal, 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

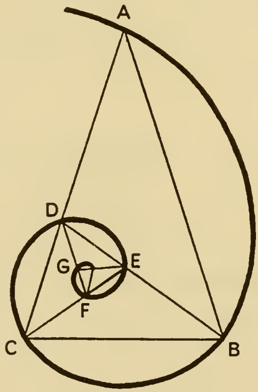


Fig. 359.

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

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

triangles have their *locus* upon a equiangular spiral: a result which follows directly from that alternative definition of the equiangular spiral which I have quoted from Whitworth (p. 757).

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*.

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. 360, 361, 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

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

† In each and all of these gnomonic figures we may now recognise a never-ending polygon, with equal angles at its corners, and with its successive sides in geometrical progression; and such a polygon we may look upon as the natural precursor of the equiangular spiral. If we call the exterior or "bending" angle of the polygon β, and the ratio of its sides λ, then the vertices lie on an equiangular spiral of angle α, given by $\log_e \lambda = \beta \cot \alpha$. In the spiral of Fig. 359 the constant angle is thus found to be about 75° 40′, in that of Fig. 355, 77° 40′, and in that of Fig. 356, 72° 50′.

The calculation is as follows. Taking, for example, the successive triangles of Fig. 359, the ratio (λ) of the sides, as $BC : AC$, is that of the golden section, 1 : 1·618. The external angle (β), as ADB, is 108°, or in radians 1·885. Then

$$\log 1{\cdot}618 = 0{\cdot}209, \text{ from which } \log_e 1{\cdot}618 = 0{\cdot}481$$

and
$$\cot \alpha = \frac{\log_e \lambda}{\beta} = \frac{0{\cdot}481}{1{\cdot}885} = 0{\cdot}255 = \cot 75^\circ\, 45'.$$

growth of the horn, of the shell, and of all other organic forms in which an equiangular spiral can be recognised, that *each successive increment of growth is similar, and similarly magnified, and similarly*

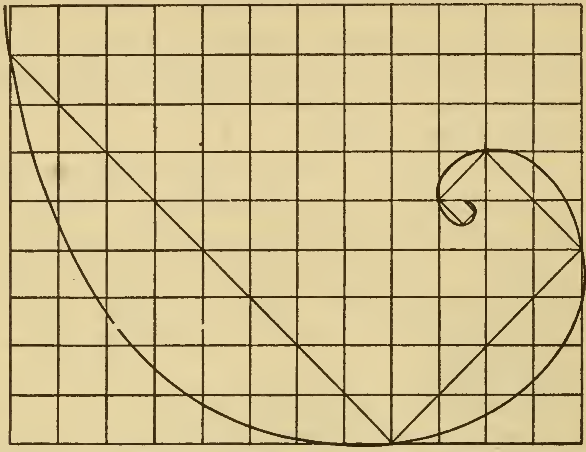


Fig. 360*. Logarithmic spiral derived from corresponding points in a system of squares.

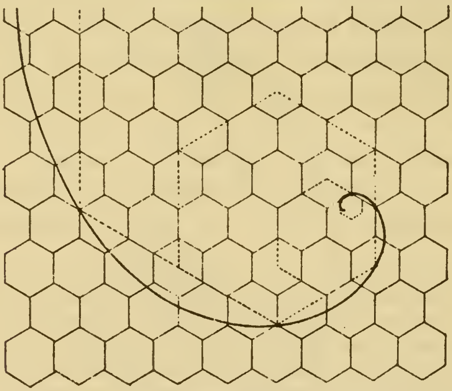


Fig. 361. The same in a system of hexagons. From Naber.

situated to its predecessor, and is in consequence a gnomon to the entire pre-existing structure. Conversely (3) it follows that in the spiral

* This diagram was at fault in my first edition (p. 512), as Dr G. T. Bennett shews me. The curve met its chords at equal angles at either end: whereas it ought to meet the further end at a lesser angle than the other, and ought in consequence to intersect the lines of the coordinate framework. The constant angle of this spiral is about 66° 11′ ($\tan \alpha = \pi/2 \log_e 2$).

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*. But 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. 359, growth goes on by a progressive series of gnomons, each one of which is the gnomon to another.

Fig. 362. A shell of *Haliotis*, with two of the many lines of growth, or generating curves, marked out in black: the areas bounded by these lines of growth being in all cases gnomons to the pre-existing shell.

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 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

* 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.

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

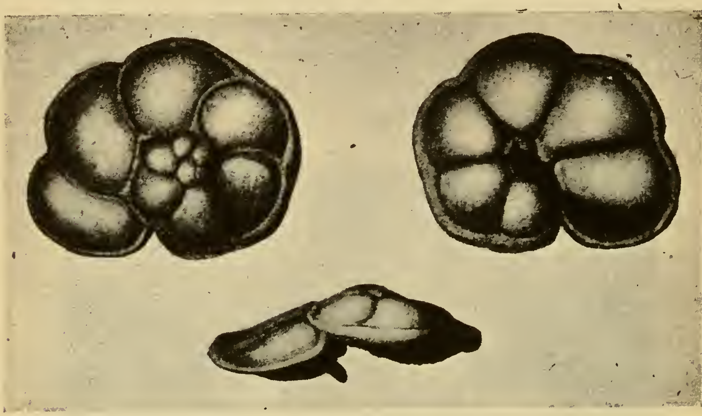


Fig. 363. A spiral foraminifer (*Pulvinulina*), to shew how each successive chamber continues the symmetry of, or constitutes a *gnomon* to, the rest of the structure.

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 most 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 tisssue 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

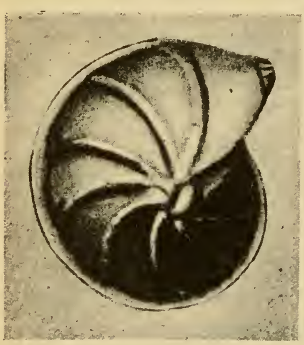


Fig. 364. Another spiral foraminifer, *Cristellaria*.

of parts successively and permanently laid down. The shell-less molluscs are never spiral; the snail is spiral but not the slug*. 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†.

The cymose inflorescences of the botanists are analogous in a curious and instructive way to the equiangular spiral.

In Fig. 365 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

Fig. 365. A, a helicoid; B, a scorpioid cyme.

* Note also that *Chiton*, where the pieces of the shell are disconnected, shews no sign of spirality.

† That the invert to an equiangular spiral is identical with the original curve does not concern us in our study of organic form, but it is one of the most beautiful and most singular properties of the curve. It was this which led James Bernoulli, in imitation of Archimedes, to have the logarithmic spiral inscribed upon his tomb; and on John Goodsir's grave near Edinburgh the same symbol is reinscribed. Bernoulli's account of the matter is interesting and remarkable: "Cum autem ob proprietatem tam singularem tamque admirabilem mire mihi placeat spira haec mirabilis, sic ut ejus contemplatione satiari vix nequeam: cogitavi illam ad varias res symbolice repraesentandas non inconcinne adhiberi posse. Quoniam enim semper sibi et eandem spiram gignit, utcunque volvatur, evolvatur, radiet, hinc poterit esse vel sobolis parentibus per omnia similis Emblema: *Simillima Filia Matri*; vel (si rem aeternae veritatis Fidei mysteriis accommodare non est

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 more come to lie in a plane, but they will appear to come off from one another on *alternate* sides, as in Fig. 365 A. This is the *Schraubel* 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*.

The spiral curve of the shell is, in a sense, a vector diagram of its own growth; for it shews at each instant of time the direction, radial and tangential, of growth, and the unchanging ratio of velocities in these directions. Regarding the *actual* velocity of growth in the shell, we know very little by way of experimental measurement; but if we make a certain simple assumption, then we may go a good deal further in our description of the equiangular spiral as it appears in this concrete case.

Let us make the assumption that *similar* increments are added to the shell in *equal* times; that is to say, that the amount of growth in unit time is measured by the areas subtended by equal angles. Thus, in the outer whorl of a spiral shell a definite area marked out by ridges, tubercles, etc., has very different linear dimensions to the corresponding areas of an inner whorl, but the symmetry of the figure implies that it subtends an equal angle with these; and it is reasonable to suppose that the successive regions, marked out in this way by successive natural boundaries or patterns, are produced in equal intervals of time.

prohibitum) ipsius aeternae generationis Filii, qui Patris veluti Imago, et ab illo ut Lumen a Lumine emanans, eidem ὁμοιούσιος existit, qualiscunque adumbratio. Aut, si mavis, quia Curva nostra mirabilis in ipsa mutatione semper sibi constantissime manet similis at numero eadem, poterit esse vel fortitudinis et constantiae in adversitatibus, vel etiam Carnis nostrae post varias alterationes et tandem ipsam quoque mortem, ejusdem numero resurrecturae symbolum: adeo quidem, ut si Archimedem imitandi hodiernum consuetudo obtineret, libenter Spiram hanc tumulo meo juberem incidi, cum Epigraphe, *Eadem numero mutata resurget*"; *Acta Eruditorum*, M. Maii, 1692, p. 213. Cf. L. Isely, Épigraphes tumulaires de mathématiciens, *Bull. Soc. Sci. nat. Neuchâtel.* XXVII, p. 171, 1899.

* The names of these structures have been often confused and misunderstood; cf. S. H. Vines, The history of the scorpioid cyme, *Journ. Bot.* (n.s.), X, pp. 3–9, 1881.

If this be so, the radii measured from the pole to the boundary of the shell will in each case be proportional to the velocity of growth at this point upon the circumference, and at the time when it corresponded with the outer lip, or region of active growth; and while the direction of the radius vector corresponds with the direction of growth in thickness of the animal, so does the tangent to the curve correspond with the direction, for the time being, of the animal's growth in length. The successive radii are a measure of the acceleration of growth, and the spiral curve of the shell itself, if the radius rotate uniformly, is no other than the *hodograph* of the growth of the contained organism*.

So far as we have now gone, we have studied the elementary properties of the equiangular spiral, including its fundamental property of *continued similarity*; and we have accordingly learned that the shell or the horn tends *necessarily* to assume the form of this mathematical figure, because in these structures growth proceeds by successive increments which are always similar in form, similarly situated, and of constant relative magnitude one to another. Our chief objects in enquiring further into the mathematical properties of the equiangular spiral will be: (1) to find means of confirming and verifying the fact that the shell (or other organic curve) is actually an equiangular spiral; (2) to learn how, by the properties of the curve, we may further extend our knowledge or simplify our descriptions of the shell; and (3) to understand the factors by which the characteristic form of any particular equiangular spiral is determined, and so to comprehend the nature of the specific or generic differences between one spiral shell and another.

Of the elementary properties of the equiangular spiral the following are those which we may most easily investigate in the concrete case of the molluscan shell: (1) that the polar radii whose vectorial angles are in arithmetical progression are themselves in geometrical progression; hence (2) that the vectorial angles are proportional to the *logarithms* of the corresponding radii; and (3) that the tangent at any point of an equiangular spiral makes a constant angle (called the *angle of the spiral*) with the polar radius vector.

* The hodograph of a logarithmic spiral (i.e. of a point which lies on a uniformly revolving radius and describes a logarithmic spiral) is likewise a logarithmic spiral: W. Walton, *Collection of Problems in Theoretical Mechanics* (3rd ed.), 1876, p. 296.

The first of these propositions may be written in a simpler form, as follows: radii which form equal angles about the pole of the equiangular spiral are themselves continued proportionals. That is to say, in Fig. 366, when the angle ROQ is equal to the angle QOP, then $OP : OQ :: OQ : OR$.

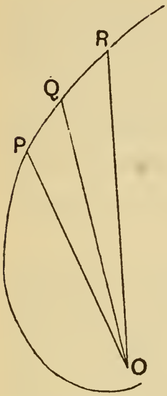


Fig. 366.

A particular case of this proposition is when the equal angles are each angles of 360°: that is to say when in each case the radius vector makes a complete revolution, and when, therefore, P, Q and R all lie upon the same radius.

It was by observing with the help of very careful measurement this continued proportionality, that Moseley was enabled to verify his first assumption, based on the general appearance of the shell, that the shell of *Nautilus* was actually an equiangular spiral, and this demonstration he was soon afterwards in a position to generalise by extending it to all spiral Ammonitoid and Gastropod mollusca*. For, taking a median transverse section of a *Nautilus pompilius*, and carefully measuring the successive breadths of the whorls (from the dark line which marks what was originally the outer surface, before it was covered up by fresh deposits on the part of the growing and advancing shell), Moseley found that "the distance of any two of its whorls measured upon a radius vector is one-third that of the two next whorls measured upon the same radius vector†. Thus (in

* The Rev. H. Moseley, On the geometrical forms of turbinated and discoid shells, *Phil. Trans.* 1838, Pt. I, pp. 351–370. Réaumur, in describing the snail-shell (*Mém. Acad. des Sci.* 1709, p. 378), had a glimpse of the same geometrical law: "Le diamètre de chaque tour de spirale, ou sa plus grande longueur, est à peu près double de celui qui la précède et la moitié de celui qui la suit." Leslie (in his *Geometry of Curved Lines*, 1822, p. 438) compared the "general form and the elegant *septa* of the *Nautilus*" to an equiangular spiral and a series of its involutes.

† It will be observed that here Moseley, speaking as a mathematician and considering the *linear* spiral, speaks of *whorls* when he means the linear boundaries, or lines traced by the revolving radius vector; while the conchologist usually applies the term *whorl* to the whole space between the two boundaries. As conchologists, therefore, we call the *breadth of a whorl* what Moseley looked upon as the *distance between two consecutive whorls.* But this latter nomenclature Moseley himself often uses. Observe also that Moseley gets a very good approximate result by his measurements "upon a radius vector," although he has to be content with a very rough determination of the pole.

Fig. 367), *ab* is one-third of *bc*, *de* of *ef*, *gh* of *hi*, and *kl* of *lm*. The curve is therefore an equiangular spiral."

The numerical ratio in the case of the *Nautilus* happens to be one of unusual simplicity. Let us take, with Moseley, a somewhat more complicated example.

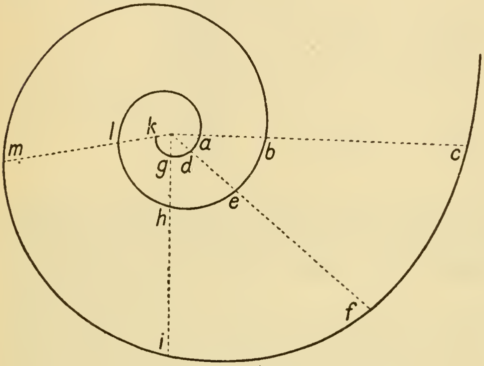


Fig. 367. Spiral of the *Nautilus*.

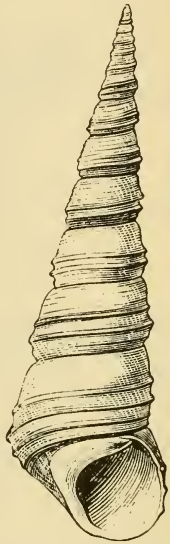


Fig. 368. *Turritella duplicata* (L.), Moseley's *Turbo duplicatus*. From Chenu. $\times \frac{1}{2}$.

From the apex of a large *Turritella* (*Turbo*) *duplicata** a line was drawn across its whorls, and their widths were measured upon it in succession, beginning with the last but one. The measure-

* In the case of "*Turbo*", and all other turbinate shells, we are dealing not with a plane logarithmic spiral, as in *Nautilus*, but with a "gauche" spiral, such that the radius vector no longer revolves in a plane perpendicular to the axis of the system, but is inclined to that axis at some constant angle (β). The figure still preserves its continued similarity, and may be called a logarithmic spiral in space; indeed it is commonly spoken of as a logarithmic spiral *wrapped upon a cone*, its pole coinciding with the apex of the cone. It follows that the distances of successive whorls of the spiral measured on the same straight line passing through the apex of the cone are in geometrical progression, and conversely; just as in the former case. But the ratio between any two consecutive interspaces (i.e. $R_3 - R_2 / R_2 - R_1$) is now equal to $\epsilon^{2\pi \sin\beta \cot\alpha}$, β being the semi-angle of the enveloping cone. (Cf. Moseley, *Phil. Mag.* xxi, p. 300, 1842.)

ments were, as before, made with a fine pair of compasses and a diagonal scale. The sight was assisted by a magnifying glass. In a parallel column to the following admeasurements are the terms of a geometric progression, whose first term is the width of the widest whorl measured, and whose common ratio is 1·1804.

Turritella duplicata

Widths of successive whorls, measured in inches and parts of an inch	Terms of a geometrical progression, whose first term is the width of the widest whorl, and whose common ratio is 1·1804
1·31	1·310
1·12	1·110
0·94	0·940
0·80	0·797
0·67	0·675
0·57	0·572
0·48	0·484
0·41	0·410

The close coincidence between the observed and the calculated figures is very remarkable, and is amply sufficient to justify the conclusion that we are here dealing with a true logarithmic spiral*.

Nevertheless, in order to verify his conclusion still further, and to get partially rid of the inaccuracies due to successive small measurements, Moseley proceeded to investigate the same shell, measuring not single whorls but groups of whorls taken several at a time: making use of the following property of a geometrical progression, that "if μ represent the ratio of the sum of every even number (m) of its terms to the sum of half that number of terms, then the common ratio (r) of the series is represented by the formula

$$r = (\mu - 1)^{\frac{2}{m}}."$$

* Moseley, writing a hundred years ago, uses an obsolete nomenclature which is apt to be very misleading. His *Turbo duplicatus*, of Linnaeus, is now *Turritella duplicata*, the common large Indian *Turritella*, a slender, tapering shell with a very beautiful spiral, about six or seven inches long. But the operculum which he describes as that of *Turbo* does indeed belong to that genus, *sensu stricto*; it is the well-known calcareous operculum or "eyestone" of some such common species as *Turbo petholatus*. *Turritella* has a very different kind of operculum, a thin chitinous disc in the form of a close spiral coil, not nearly filling up the aperture of the shell. Moseley's *Turbo phasianus* is again no true *Turbo*, but is (to judge from his figure) *Phasianella bulimoides* Lam. = *P. australis* (Gmelin); and his *Buccinum subulatum* is *Terebra subulata* (L.).

Accordingly, Moseley made the following measurements, beginning from the second and third whorls respectively:

Width of		Ratio μ
Six whorls	Three whorls	
5·37	2·03	2·645
4·55	1·72	2·645
Four whorls	Two whorls	
4·15	1·74	2·385
3·52	1·47	2·394

"By the ratios of the two first admeasurements, the formula gives

$$r = (1{\cdot}645)^{\frac{1}{3}} = 1{\cdot}1804.$$

By the mean of the ratios deduced from the second two admeasurements, it gives

$$r = (1{\cdot}389)^{\frac{1}{2}} = 1{\cdot}1806.$$

"It is scarcely possible to imagine a more accurate verification than is deduced from these larger admeasurements, and we may with safety annex to the species *Turbo duplicatus* the characteristic number 1·18."

By similar and equally concordant observations, Moseley found for *Turbo phasianus* the characteristic ratio, 1·75; and for *Buccinum subulatum* that of 1·13.

From the measurements of *Turritella duplicata* (on p. 772), it is perhaps worth while to illustrate the logarithmic statement of the same thing: that is to say, the elementary fact, or corollary, that if the successive radii be in geometric progression, their logarithms will differ from one another by a constant amount.

Turritella duplicata

Widths of successive whorls	Logarithms of do.	Differences of logarithms	Ratios of successive widths
131	2·11727	—	—
112	2·04922	0·06805	1·170
94	1·97313	0·07609	1·191
80	1·90309	0·07004	1·175
67	1·82607	0·07702	1·194
57	1·75587	0·07020	1·175
48	1·68124	0·07463	1·188
41	1·61278	0·06846	1·171
	Mean	0·07207	1·1806

And 0·07207 is the logarithm of 1·1805.

Lastly, we may if we please, in this simple case, reduce the whole matter to arithmetic, and, dividing the width of each whorl by that of the next, see that these quotients are nearly identical, and that their mean value, or common ratio, is precisely that which we have already found.

We may shew, in the same simple fashion, by measurements of *Terebra* (Fig. 397), how the relative widths of successive whorls fall into a geometric progression, the criterion of a logarithmic spiral.

Measurements of a large specimen (15·5 *cm.*) *of* Terebra maculata, *along three several tangents* (*a*, *b*, *c*) *to the whorls.* (*After Chr. Peterson*, 1921.)

a		*b*		*c*	
Width (mm.)	Ratio	Width	Ratio	Width	Ratio
25		24·5		23	
	1·25		1·32		1·31
20		18·5		17·5	
	1·33		1·32		1·31
15		14		13·3	
	1·25		1·30		1·36
12		10·75		9·75	
	1·33		1·34		1·34
9		8		7·25	
Mean	1·29		1·32		1·33

Mean ratio, 1·31

The logarithmic spiral is not only very beautifully manifested in the molluscan shell*, but also, in certain cases, in the little lid or "operculum" by which the entrance to the tubular shell is closed after the animal has withdrawn itself within†. In the spiral shell of *Turbo*, for instance, the operculum is a thick calcareous structure, with a beautifully curved outline, which grows by successive increments applied to one portion of its edge, and shews, accordingly, a spiral line of growth upon its surface. The successive increments leave their traces on the surface of the operculum (Fig. 370), which traces have the form of curved lines in *Turbo*, and of straight lines

* It has even been proposed to use a logarithmic spiral in place of a table of logarithms. Cf. Ant. Favaro, *Statique graphique*, Paris, 1885; Hele-Shaw, in *Brit. Ass. Rep.* 1892, p. 403.

† Cf. Fred. Haussay, *Recherches sur l'opercule*, Diss., Paris, 1884.

in (e.g.) *Nerita* (Fig. 371); that is to say, apart from the side constituting the outer edge of the operculum (which side is always and of necessity curved) the successive increments constitute curvilinear

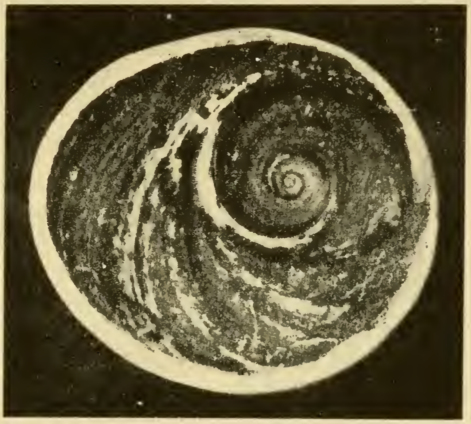


Fig. 369. Operculum of *Turbo*.

triangles in the one case, and rectilinear triangles in the other. The sides of these triangles are tangents to the spiral line of the

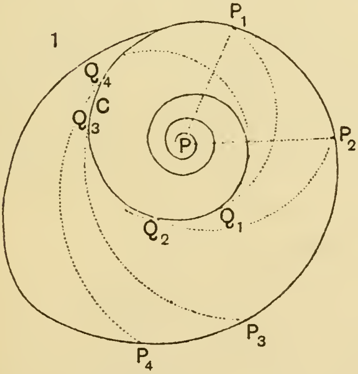


Fig. 370.

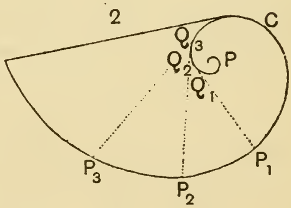


Fig. 371.

Figs. 370, 371. Opercula of *Turbo* and *Nerita*. After Moseley.

operculum, and may be supposed to generate it by their consecutive intersections.

In a number of such opercula, Moseley measured the breadths of the successive whorls along a radius vector*, just in the same way as he did with the entire shell in the foregoing cases; and here is one example of his results.

Operculum of Turbo *sp.; breadth (in inches) of successive whorls, measured from the pole*

Distance	Ratio	Distance	Ratio	Distance	Ratio	Distance	Ratio
0·24		0·16		0·2		0·18	
	2·28		2·31		2·30		2·30
0·55		0·37		0·6		0·42	
	2·32		2·30		2·30		2·24
1·28		0·85		1·38		0·94	

The ratio is approximately constant, and this spiral also is, therefore, a logarithmic spiral.

But here comes in a very beautiful illustration of that property of the logarithmic spiral which causes its whole shape to remain unchanged, in spite of its apparently unsymmetrical, or unilateral, mode of growth. For the mouth of the tubular shell, into which the operculum has to fit, is growing or widening on all sides: while the operculum is increasing, not by additions made at the same time all round its margin, but by additions made only on one side of it at each successive stage. One edge of the operculum thus remains unaltered as it advances into its new position, and comes to occupy a new-formed section of the tube, similar to but greater than the last. Nevertheless, the two apposed structures, the chamber and its plug, at all times fit one another to perfection. The mechanical problem (by no means an easy one) is thus solved: "How to shape a tube of a variable section, so that a piston driven along it shall, by one side of its margin, coincide continually with its surface as it advances, provided only that the piston be made at the same time continually to revolve in its own plane."

As Moseley puts it: "That the same edge which fitted a portion of the first less section should be capable of adjustment, so as to fit a portion of the next similar but greater section, supposes a geometrical provision in the curved form of the chamber of great

* As the successive increments evidently constitute similar figures, similarly related to the pole (P), it follows that their linear dimensions are to one another as the radii vectores drawn to similar points in them: for instance as PP_1, PP_2, which (in Fig. 370) are radii vectores drawn to the points where they meet the common boundary.

apparent complication and difficulty. But God hath bestowed upon this humble architect the practical skill of a learned geometrician, and he makes this provision with admirable precision in that curvature of the logarithmic spiral which he gives to the section of the shell. This curvature obtaining, he has only to turn his operculum slightly round in its own plane as he advances it into each newly formed portion of his chamber, to adapt one margin of it to a new and larger surface and a different curvature, leaving the space to be filled up by increasing the operculum wholly on the other margin." The fact is that self-similar or gnomonic growth is taking place both in the shell and its operculum; in both of them growth is in reference to a fixed centre, and to a fixed axis through that centre; and in both of them growth proceeds in geometric progression from the centre while rotation takes place in arithmetic progression about the axis. The same architecture which builds the house constructs the door. Moreover, not only are house and door governed by the same law of growth, but, growing together, door and doorway adapt themselves to one another.

The operculum of the gastropods varies from a more or less close-wound spiral, as in *Turritella*, *Trochus* or *Pleurotomaria*, to cases in which accretion takes place, by concentric (or more or less excentric) rings, all round. But these latter cases, so Mr Winckworth tells me, are not very common. *Paludina* and *Ampullaria* come near to having a concentric operculum, and so do some of the Murices, such as *M. tribulus*, and a few Turrids, and the genus *Helicina*; but even these opercula probably begin as spirals, adding on their gnomonic increments at one end or side, and only growing on all sides later on. There would seem to be a truly concentric operculum in the *Siphonium* group of *Vermetus*, where the spiral of the shell itself is lost, or nearly so; but it is usually overgrown with Melobesia, and hard to see.

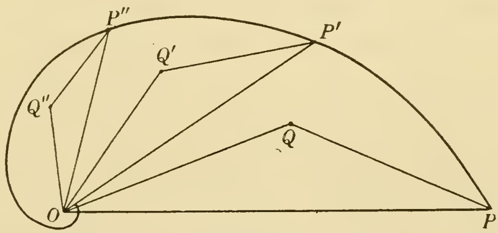


Fig. 372.

One more proposition, an all but self-evident one, we may make passing mention of here: If upon any polar radius vector OP, a triangle OPQ be drawn similar to a given triangle, the locus of the vertex Q will be a spiral similar to the original spiral. We may extend this proposition (as given by Whitworth) from the simple case of the triangle to any similar figures whatsoever; and see from it how every spot or ridge or tubercle repeated symmetrically from one radius vector (or one generating curve) to another becomes part of a spiral pattern on the shell.

Viewed in regard to its own fundamental properties and to those of its limiting cases, the equiangular spiral is one of the simplest of all known curves; and the rigid uniformity of the simple laws by which it is developed sufficiently account for its frequent manifestation in the structures built up by the slow and steady growth of organisms.

In order to translate into precise terms the whole form and growth of a spiral shell, we should have to employ a mathematical notation considerably more complicated than any that I have attempted to make use of in this book. But we may at least try to describe in elementary language the general method, and some of the variations, of the mathematical development of the shell. But here it is high time to observe that, while we have been speaking of the *shell* (which is a *surface*) as a logarithmic spiral (which is a *line*), we have been simplifying the case, in a provisional or preparatory way. The logarithmic spiral is but one factor in the case, albeit the chief or dominating one. The problem is one not of plane but of solid geometry, and the solid in question is described by the movement in space of a certain area, or closed curve*.

Let us imagine a closed curve in space, whether circular or elliptical or of some other and more complex specific form, not necessarily in a plane: such a curve as we see before us when we consider the mouth, or terminal orifice, of our tubular shell. Let

* For a more advanced study of the family of surfaces of which the *Nautilus* is a simple case, see M. Haton de la Goupillière (*op. cit.*). The turbinate shells represent a sub-family, which may be called that of the "surfaces cérithioides"; and "surfaces à front générateur" is a short title of the whole family. The form of the generating curve, its rate of expansion, the direction of its advance, and the angle which the generating front makes with the directrix, define, and give a wide extension to, the family. These parameters are all severally to be recognised in the growth of the living object; and they make of a collection of shells an unusually beautiful materialisation of the rigorous definitions of geometry.

us call this closed curve the "generating curve"; the surface which it bounds we may call (if need arise) the "generating front," and let us imagine some one characteristic point within this closed curve, such as its centre of gravity. Then, starting from a fixed origin, let this characteristic point describe an equiangular spiral

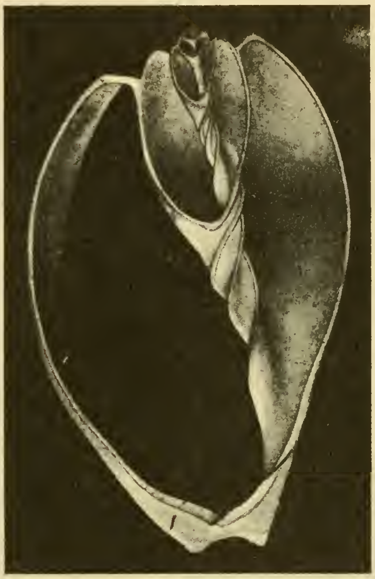


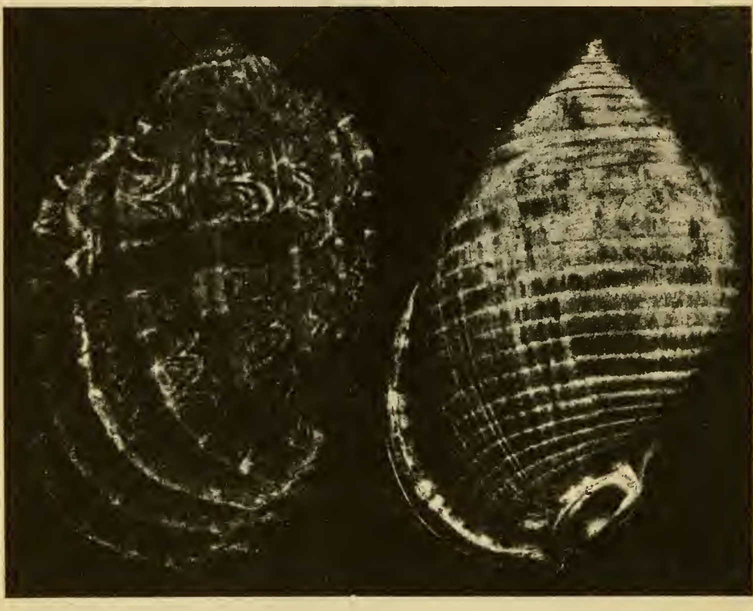
Fig. 373. *Melo ethiopicus* L.

in space about a fixed axis or "conductrix" (namely the axis of the shell), while at the same time the generating curve grows with each increment of rotation in such a way as to preserve the symmetry of the entire figure, with or without a simultaneous movement of translation along the axis.

The resulting shell may now be looked upon in either of two ways. It is, on the one hand, an *ensemble of similar closed curves*, spirally arranged in space, and gradually increasing in dimensions in proportion to the increase of their vector-angle from the pole*. In

* The plumber, the copper-smith and the glass-blower are at pains to conserve in every part of their tubular constructions, however these branch or bend, the constant form which their cross-sections ought to have. Throughout the spiral twisting of the shell, throughout the windings and branchings of the blood-vessels, the same uniformity is maintained.

other words, we can imagine our shell cut up into a system of rings, following one another in continuous spiral succession, from that terminal and largest one which constitutes the lip of the orifice of the shell. Or on the other hand, we may figure to ourselves the whole shell as made up of an *ensemble of spiral lines* in space, each spiral having been traced out by the gradual growth and revolution of a radius vector from the pole to a given point on the boundary of the generating curve.



1 2

Fig. 374. 1, *Harpa*; 2, *Dolium*. The ridges on the shell correspond in (1) to generating curves, in (2) to generating spirals.

Both systems of lines, the *generating spirals* (as these latter may be called), and the closed *generating curves* corresponding to successive margins or lips of the shell, may be easily traced in a great variety of cases. Thus, for example, in *Dolium*, *Eburna*, and a host of others, the generating spirals are beautifully marked out by ridges, tubercles or bands of colour. In *Trophon*, *Scalaria*, and (among countless others) in the Ammonites, it is the successive generating curves which more conspicuously leave their impress on the shell. And in not a few cases, as in *Harpa*, *Dolium perdix*, etc., both alike are conspicuous, ridges and colour-bands intersecting one another in a beautiful isogonal system.

In ordinary gastropods the shell is formed at or near the mantle-edge. Here, near the mantle-border, is a groove lined with a secretory epithelium which produces the horny cuticle or periostracum of the shell*. A narrow zone of the mantle just behind this secretes lime abundantly, depositing it in a layer below the periostracum; and for some little way back more lime may be secreted, and pigment superadded from appropriate glands. Growth and secretion are periodic rather than continuous. Even in a snail-shell it is easy to see how the shell is built up of narrow annular increments; and many other shells record, in conspicuous colour-patterns, the alternate periods of rest and of activity which their pigment-glands have undergone.

The periodic accelerations and retardations in the growth of a shell are marked in various ways. Often we have nothing more than an increased activity from time to time at or near the mantle-edge—enough to give rise to slight successive ridges, each corresponding to a "generating curve" in the conformation of the shell. But in many other cases, as in *Murex*, *Ranella* and the like, the mantle-edge has its alternate phases of rest and of turgescence, its outline being plain and even in the one and folded and contorted in the other; and these recurring folds or pleatings of the edge leave their impress in the form of various ridges, ruffles or comb-like rows of spines upon the shell†.

In not a few cases the colour-pattern shews, or seems to shew, how some play of forces has fashioned and transformed the first elementary pattern of pigmentary drops or jets. As the book-binder drops or dusts a little colour on a viscous fluid, and then produces the beautiful streamlines of his marbled papers by stirring

* That the shell grows by accretion at the mantle-edge was one of Réaumur's countless discoveries (*Mém. Acad. Roy. des Sc.* 1709, p. 364 *seq.*). It follows that the mathematical "generating curves," as Moseley chose them, correspond to the material increments of the shell.

† The periodic appearance of a ridge, or row of tubercles, or other ornament on the growing shell is illustrated or even exaggerated in the delicate "combs" of *Murex aculeatus*. Here normal growth is interrupted for the time being, the mantle-edge is temporarily folded and reflexed, and shell-substance is poured out into the folds.

and combing the colloid mass, so we may see, in the harp-shells or the volutes, how a few simple spots or lines have been drawn out into analogous wavy patterns by streaming movements during the formation of the shell.

In the complete mathematical formula for any given turbinate shell, we may include, with Moseley, factors for the following elements: (1) for the specific form of a section of the tube, or (as we have called it) the generating curve; (2) for the specific rate of growth of this generating curve; (3) for its inclination to the directrix, or to the axis; (4) for its specific rate of angular rotation about the pole, in a projection perpendicular to the axis; and (5) in turbinate (as opposed to nautiloid) shells, for its rate of screw-translation, parallel to the axis, as measured by the angle between a tangent to the whorls and the axis of the shell*. It seems a complicated affair; but it is only a pathway winding at a steady slope up a conical hill. This uniform gradient is traced by any given point on the generating curve while the vector angle increases in arithmetical progression, and the scale changes in geometrical progression; and a certain *ensemble*, or bunch, of these spiral curves in space constitutes the self-similar surface of the shell.

But after all this is not the only way, neither is it the easiest way, to approach our problem of the turbinate shell. The conchologist turned mathematician is apt to think of the generating curve by which the spiral surface is described as necessarily identical, or coincident, with the mouth or lip of the shell; for this is where growth actually goes on, and where the successive increments of shell-growth are visibly accumulated. But it does not follow that this particular generating curve is chosen for the best from the mathematical point of view; and the mathematician, unconcerned with the physiological side of the case and regardless of the succession of the parts in time, is free to choose any other generating curve which the geometry of the figure may suggest to him. We are following Moseley's example (as is usually done) when we think of no other generating curve but that which takes the form of a

* Note that this tangent touches the curve at a series of points, whorl by whorl, instead of at one only. Observe also that we may have various tangent-cones, all centred on the apex of the shell. In an open spiral, like a ram's horn, or a half-open spiral like the shell *Solarium*, we have two cones, one touching the outside, the other the inside of the shell.

frontal plane, outlined by the lip, and *sliding along* the axis while revolving round it; but the geometer takes a better and a simpler way. For, when of two similar figures in space one is derived from the other by a screw-displacement accompanied by change of scale—as in the case of a big whelk and a little whelk—there is a unique (apical) point which suffers no displacement; and if we choose for our generating curve a sectional figure centred on the apical point and passing through the axis of rotation, the whole development of the surface may be simply described as due to a rotation of this generating figure about the axis (z), together with a change of scale with the point 0 as centre of similitude. We need not, and now must not, think of a *slide* or *shear* as part of the operation; the translation along the axis is merely part and parcel of the *magnification* of the new generating curve. It follows that angular rotation in arithmetical progression, combined with change of scale (from 0) in geometrical progression, causes any arbitrary point on the generating curve to trace a path of uniform gradient round a circular cone, or in other words to describe a helico-spiral or gauche equiangular spiral in space. The spiral curve cuts all the straight-line generators of the cone at the same angle; and it further follows that the successive increments are, and the whole figure constantly remains, "self-similar"*.

Apart from the specific form of the generating curve, it is the ratios which happen to exist between the various factors, the ratio for instance between the growth-factor and the rate of angular revolution, which give the endless possibilities of permutation of form. For example, a certain rate of growth in the generating curve, together with a certain rate of vectorial rotation, will give us a spiral shell of which each successive whorl will just touch its predecessor and no more; with a slower growth-factor the whorls will stand asunder, as in a ram's horn; with a quicker growth-factor

* The equation to the surface of a turbinate shell is discussed by Moseley both in terms of polar and of rectangular coordinates, and the method of polar coordinates is used also by Haton de la Goupillière; but both accounts are subject to mathematical objection. Dr G. T. Bennett, choosing his generating curve (as described above) in the axial plane from which the vertical angles are measured (the plane $\theta = 0$), would state his equation in cylindrical coordinates, $f(za^\theta, ra^\theta) = 0$: that is to say in terms of z, conjointly with ordinary plane cylindrical coordinates.

each will cut or intersect its predecessor, as in an Ammonite or the majority of gastropods, and so on.

A similar relation of velocities suffices to determine the apical angle of the resulting cone, and give us the difference, for example, between the sharp, pointed cone of *Turritella*, the less acute one of *Fusus* or *Buccinum*, and the obtuse one of *Harpa* or of *Dolium*. In short it is obvious that *all* the differences of form which we observe between one shell and another are referable to matters of *degree*, depending, one and all, upon the relative magnitudes of the various factors in the complex equation to the curve. This is an immensely important thing. To learn that all the multitudinous shapes of shells, in their all but infinite variety, may be reduced to the variant properties of a single simple curve, is a great achievement. It exemplifies very beautifully what Bacon meant in saying that the forms or differences of things are simple and few, and the degrees and coordinations of these make all their variety*. And after such a fashion as this John Goodsir imagined that the naturalist of the future would determine and classify his shells, so that conchology should presently become, like mineralogy, a mathematical science†.

The paper in which, more than a hundred years ago, Canon Moseley‡ gave a simple mathematical account, on lines like these, 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

* For a discussion of this idea, and of the views of Bacon and of J. S. Mill, see J. M. Keynes, *op. cit.* p. 271.

† On the employment of mathematical modes of investigation in the determination of organic forms; in *Anatomical Memoirs*, II, p. 205, 1868 (posthumous publication).

‡ The Rev. Henry Moseley (1801–1872), 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.

one another in a constant ratio or continued proportion*; and Leopold von Buch and others accepted and even developed the idea.

Long before, Swammerdam had grasped with a deeper insight the root of the whole matter; for, taking a few diverse examples, such as *Helix* and *Spirula*, he shewed 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. "Omnis enim quae inter eas animadvertitur differentia ex sola nascitur diversitate gyrationum: quibus si insuper externa quaedam adjunguntur ornamenta pinnarum, sinuum, anfractuum, planitierum, eminentiarum, profunditatum, extensionum, impressionum, circumvolutionum, colorumque: ...tunc deinceps facile est, quarumcumque Cochlearum figuras geometricas, curvosque, obliquos atque rectos angulos, ad unicam omnes speciem redigere: ad oblongum videlicet tubulum, qui vario modo curvatus, crispatus, extrorsum et introrsum flexus, ita concrevit†."

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‡, 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 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: "Hanc ipsam curvam...contemplatus est Wrennius noster. Nec tantum curvae longitudinem, partiumque ipsius, et

* J. C. M. Reinecke, *Maris protogaei Nautilos*, etc., Coburg, 1818, p. 17: "In eius forma, quae canalis spiram convoluti formam et proportiones simul subministrat, totius testae forma quoddammodo data est. Restaret solum scire, quota cujusque anfractus pars sequenti inclusa sit, ut testam geometrice construere possimus." Cf. Leopold von Buch, Ueber die Ammoniten in den älteren Gebirgsschichten, *Abh. Berlin. Akad.*, *Phys. Kl.* 1830, pp. 135–158; *Ann. Sc. Nat.* XXVIII, pp. 5–43, 1833; cf. Elie de Beaumont, Sur l'enroulement des Ammonites, *Soc. Philom.*, *Pr. verb.* 1841, pp. 45–48.

† *Biblia Naturae sive Historia Insectorum*, Leydae, 1737, p. 152.

‡ Joh. Wallis, *Tractatus duo, de Cycloide*, etc., Oxon., 1659, pp. 107, 108.

magnitudinem adjacentis plani; sed et, ipsius ope, Limacum et Conchiliorum domunculos metitur. Existimat utique, magna verisimilitudine, domunculos hosce non alios esse quam Pyramides convolutas: quarum Axis sit, istiusmodo Spiralis: non quidem in plano jacens, sed sensim in convolutione (circa erectum axim) assurgens: pro variis autem curvae, sive ad rectam circumductam sive ad subjacens planum, angulis, variae Conchiliorum formae enascantur. Atque hac hypothesi, mensurata Pyramide, metitur etiam ea conchiliorum spatia."

For some years after the appearance of Moseley's paper, a number of writers followed in his footsteps, and attempted in various ways to put his conclusions to practical use. For instance, d'Orbigny

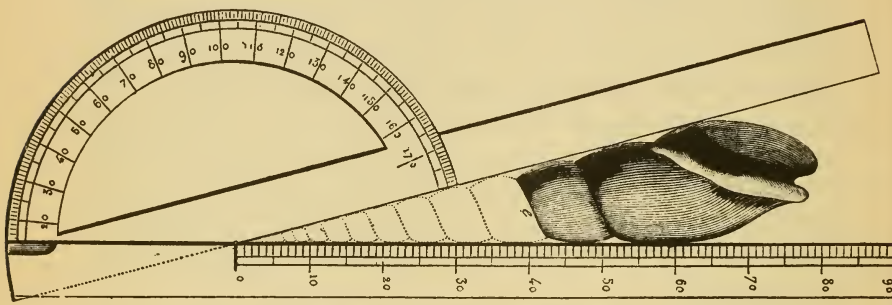


Fig. 375. d'Orbigny's helicometer.

devised a very simple protractor, which he called a Helicometer*, and which is represented in Fig. 375. By means of this little instrument the apical angle of the turbinate shell was immediately read off, and could then be used as a specific and diagnostic character. By keeping one limb of the protractor parallel to the side of the cone while the other was brought into line with the suture between two adjacent whorls, another specific angle, the "sutural angle," could in like manner be recorded. And, by the linear scale upon the instrument, the relative breadths of the consecutive whorls, and that of the terminal chamber to the rest of the shell, might

* Alcide d'Orbigny, *Bull. de la soc. géol. Fr.* XIII, p. 200, 1842; *Cours élém. de Paléontologie*, II, p. 5, 1851. A somewhat similar instrument was described by Boubée, in *Bull. soc. géol.* I, p. 232, 1831. Naumann's conchyliometer (*Poggend, Ann.* LIV, p. 544, 1845) was an application of the screw-micrometer; it was provided also with a rotating stage for angular measurement. It was adapted for the study of a discoid or ammonitoid shell, while d'Orbigny's instrument was meant for the study of a turbinate shell.

also, though somewhat roughly, be determined. For instance, in *Terebra dimidiata* the apical angle was found to be 13°, the sutural angle 109°, and so forth.

It was at once obvious that, in such a shell as is represented in Figs. 369 and 375 the entire outline (always excepting that of the immediate neighbourhood of the mouth) could be restored from a broken fragment. For if we draw our tangents to the cone, it follows from the symmetry of the figure that we can continue the projection of the sutural line, and so mark off the successive whorls, by simply drawing a series of consecutive parallels, and by then filling into the quadrilaterals so marked off a series of curves similar to one another, and to the whorls which are still intact in the broken shell. But the use of the helicometer soon shewed that it was by no means universally the case that one and the same cone was tangent to all the turbinate whorls; in other words, there was not always one specific apical angle which held good for the entire system. In the great majority of cases, it is true, the same tangent touches all the whorls, and is a straight line. But in others, as in the large *Cerithium nodosum*, such a line is slightly concave to the axis of the shell; and in the short spire of *Dolium*, for instance, the concavity is marked, and the apex of the spire is a distinct cusp. On the other hand, in *Pupa* and *Clausilia* the common tangent is convex to the axis of the shell.

So also is it, as we shall presently see, among the Ammonites: where there are some species in which the ratio of whorl to whorl remains, to all appearance, perfectly constant; others in which it gradually though only slightly increases; and others again in which it slightly and gradually falls away. It is obvious that, among the manifold possibilities of growth, such conditions as these are very easily conceivable. It is much more remarkable that, among these shells, the relative velocities of growth in various dimensions should be as constant as they are than that there should be an occasional departure from perfect regularity. In these latter cases the logarithmic law of growth is only approximately true. The shell is no longer to be represented simply as a cone which has been rolled up, but as a cone which (while rolling up) had grown trumpet-shaped, or conversely whose mouth had narrowed in, and which in longitudinal section is a curvilinear instead of a rectilinear triangle. But all that has happened is that a new factor, usually of small or all but imperceptible magnitude, has been introduced into the case; so that the ratio, $\log r = \theta \log \alpha$, is no longer constant but varies slightly, and in accordance with some simple law.

Some writers, such as Naumann* and Grabau, maintained that the molluscan spiral was no true logarithmic spiral, but differed from it specifically, and they gave it the name of *Conchospiral*. They said that the logarithmic spiral originates in a mathematical point, while the molluscan shell starts with a little embryonic shell, or central chamber (the "protoconch" of the conchologists), around which the spiral is subsequently wrapped. But this need not affect the logarithmic law of the shell as a whole; indeed we have already allowed for it by writing our equation in the form $r = ma^\theta$. And Grabau†, while he clung to Naumann's conchospiral against Moseley's logarithmic spiral, confessed that they were so much alike that ordinary measurements would seldom shew a difference between them.

There would seem, by the way, to be considerable confusion in the books with regard to the so-called "protoconch." In many cases it is a definite structure, of simple form, representing the more or less globular embryonic shell before it began to elongate into its conical or spiral form. But in many cases what is described as the "protoconch" is merely an empty space in the middle of the spiral coil, resulting from the fact that the actual spiral shell must have some magnitude to begin with, and that we cannot follow it down to its vanishing point in infinity. For instance, in the accompanying figure, the large space *a* is styled the protoconch, but it is the little bulbous or hemispherical chamber within it, at the end of the spire, which is the real beginning of the tubular shell. The form and magnitude of the space *a* are determined by the "angle of retardation," or ratio of rate of growth between the inner and outer curves of the spiral shell. They

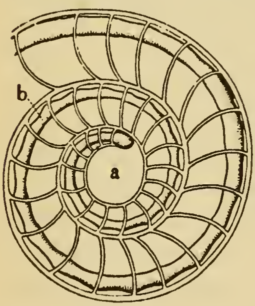


Fig. 376.

* C. F. Naumann, Beitrag zur Konchyliometrie, *Poggend. Ann.* L, p. 223, 1840; Ueber die Spiralen der Ammoniten, *ibid.* LI, p. 245, 1840; *ibid.* LIV, p. 541, 1845; etc. (See also p. 755.) Cf. also Lehmann, *Die von Seyfriedsche Konchyliensammlung und das Windungsgesetz von einigen Planorben*, Constanz, 1855.

† A. H. Grabau, Ueber die Naumannsche Conchospirale, und ihre Bedeutung für die Conchyliometrie, *Inauguraldiss.*, Leipzig, 1872; Ueber die Spiralen der Conchylien, etc., *Leipzig Progr.* No. 502, 1880; cf. *Sb. naturf. Gesellsch.* Leipzig, 1881, pp. 23–32.

are independent of the shape and size of the embryo, and depend only (as we shall see better presently) on the direction and relative rate of growth of the double contour of the shell*.

Now that we have dealt, in a general way, with some of the more obvious properties of the equiangular or logarithmic spiral, let us consider certain of them a little more particularly, keeping in view as our chief object of study the range of variation of the molluscan shell.

There is yet another equation to the logarithmic spiral, very commonly employed, and without the help of which we cannot get far. It is as follows: $r = e^{\theta \cot \alpha}$.

This follows directly from the fact that the angle α (the angle between the radius vector and the tangent to the curve) is constant.

For then,

$$\tan \alpha \; (= \tan \phi) = r\, d\theta / dr;$$

therefore $$dr/r = d\theta \cot \alpha,$$

and, integrating, $$\log r = \theta \cot \alpha,$$

or $$r = e^{\theta \cot \alpha}.$$

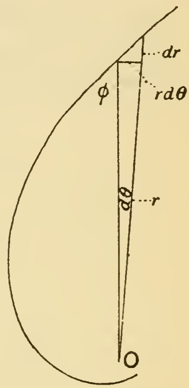


Fig. 377.

It is easy to see (we might indeed have noted it before) that the logarithmic spiral is but a plotting in polar coördinates of *increase by compound interest*. For if A be the "amount" of £1 in one year ($A = 1 + a$, where a is the rate of interest), and PA the amount of P in one year, then the whole amount, M, in t years is $M = PA^t$: this, provided that interest is payable once a year. But, as we are taught by algebra, and as we have seen in our study of growth, this formula becomes Pe^{at} when the intervals of time between the payments of interest decrease without limit, that is to say, when we may consider growth to be continuous. And this formula Pe^{at} is precisely that of our logarithmic spiral, when we represent the time

* J. F. Blake (cf. *infra*, p. 793) says of Naumann's formula: "By such a modification he hoped to bring the measurements of actual shells more into harmony with calculation. The errors of observation, however, are always greater than this change would correct—if founded on fact, which is doubtful; and all practical advantage is lost by the complication of the equations."

by a vector angle θ, and when for a, the particular rate of interest in the case, we write cot α, the constant measure of growth of the particular spiral.

As we have seen throughout our preliminary discussion, the two most important constants (or "specific characters," as the naturalist would say) in an equiangular or logarithmic spiral are (1) the magnitude of the angle of the spiral, or "constant angle" α, and (2) the rate of increase of the radius vector for any given angle of revolution, θ. But our two magnitudes, that of the constant angle and that of the ratio of the radii or breadths of whorl, are directly related to one another, so that we may determine either of them by measurement and calculate the other.

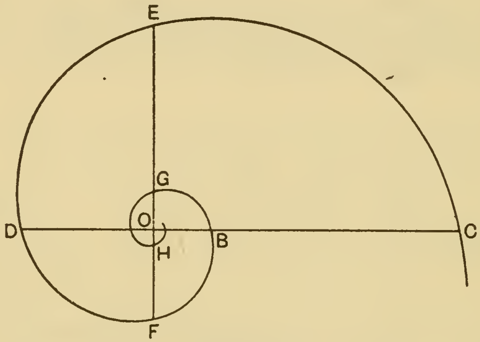


Fig. 378.

In any complete spiral, such as that of *Nautilus*, it is (as we have seen) easy to measure any two radii (r), or the breadths in a radial direction of any two whorls (W). We have then merely to apply the formula

$$\frac{r_{n+1}}{r_n} = e^{\theta \cot \alpha}, \text{ or } \frac{W_{n+1}}{W_n} = e^{\theta \cot \alpha},$$

which we may simply write $r = e^{\theta \cot \alpha}$, etc., when one radius or whorl is regarded, for the purpose of comparison, as equal to unity.

Thus, in Fig. 378, OC/OE, or EF/BD, or DC/EF, being in each case radii, or diameters, at right angles to one another, are all equal to $e^{\frac{\pi}{2} \cot \alpha}$. While in like manner, EO/OF, EG/FH, or GO/HO, all equal $e^{\pi \cot \alpha}$; and BC/BA, or $CO/OB = e^{2\pi \cot \alpha}$.

As soon, then, as we have prepared tables for these values, the determination of the constant angle α in a particular shell becomes a very simple matter.

A complete table would be cumbrous, and it will be sufficient to deal with the simple case of the ratio between the breadths of adjacent, or immediately succeeding, whorls.

Here we have $r = e^{2\pi \cot \alpha}$, or $\log r = \log e \times 2\pi \times \cot \alpha$, from which we obtain the following figures*:

The shape of a nautiloid spiral

Ratio of breadth of each whorl to the next preceding $r/1$	Constant angle α
1·1	89° 8′
1·25	87 58
1·5	86 18
2·0	83 42
2·5	81 42
3·0	80 5
3·5	78 43
4·0	77 34
4·5	76 32
5·0	75 38
10·0	69 53
20·0	64 31
50·0	58 5
100·0	53 46
1000·0	42 17
10,000	34 19
100,000	28 37
1,000,000	24 28
10,000,000	21 18
100,000,000	18 50
1,000,000,000	16 52

We learn several interesting things from this short table. We see, in the first place, that where each whorl is about three times the breadth of its neighbour and predecessor, as is the case in *Nautilus*, the constant angle is in the neighbourhood of 80°; and hence also that, in all the ordinary ammonitoid shells, and in all the typically spiral shells of the gastropods†, the constant angle is also a large one, being very seldom less than 80°, and usually between 80° and 85°. In the next place, we see that with smaller

* It is obvious that the ratios of opposite whorls, or of radii 180° apart, are represented by the square roots of these values; and the ratios of whorls or radii 90° apart, by the square roots of these again.

† For the correction to be applied in the case of the helicoid, or "turbinate" shells, see p. 816.

angles the apparent form of the spiral is greatly altered, and the very fact of its being a spiral soon ceases to be apparent (Figs. 379, 380). Suppose one whorl to be an inch in breadth, then, if the angle of the spiral were 80°, the next whorl would (as we have just seen) be about three inches broad; if it were 70°, the next whorl would be nearly ten inches, and if it were 60°, the next whorl would be nearly four feet broad. If the angle were 28°, the next whorl would be a mile and a half in breadth; and if it were 17°, the next would be some 15,000 miles broad.

In other words, the spiral shells of gentle curvature, or of small constant angle, such as *Dentalium* or *Cristellaria*, are true equiangular spirals, just as are those of *Nautilus* or *Rotalia*: from

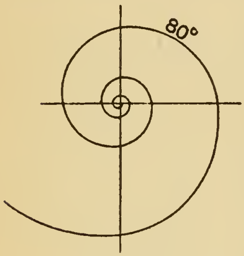


Fig. 379.

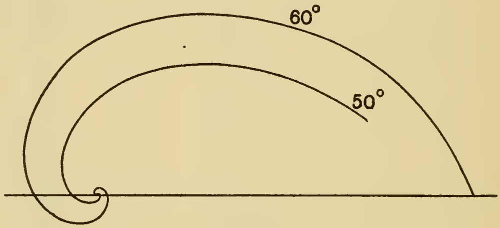


Fig. 380.

which they differ only in degree, in the magnitude of an angular constant. But this diminished magnitude of the angle causes the spiral to dilate with such immense rapidity that, so to speak, it never comes round; and so, in such a shell as *Dentalium*, we never see but a small portion of a single whorl.

We might perhaps be inclined to suppose that, in such a shell as *Dentalium*, the lack of a visible spiral convolution was only due to our seeing but a small portion of the curve, at a distance from the pole, and when, therefore, its curvature had already greatly diminished. That is to say we might suppose that, however small the angle α, and however rapidly the whorls accordingly increased, there would nevertheless be a manifest spiral convolution in the immediate neighbourhood of the pole, as the starting point of the curve. But it is easy to see that it is not so. It is not that there cease to be convolutions of the spiral round the pole when α is a small angle; on the contrary, there are infinitely many, mathematically speaking. But as α diminishes, and $\cot \alpha$ increases towards infinity, the ratio between the breadth of one whorl and the next increases very rapidly. Our table shews us that even when α is no less than 40°, and our shell still looks strongly curved, one whorl is a thousandth part of the breadth of the next. and a thousandfold that of the one before; we cannot expect to see either of them under the materialised conditions of the actual shell. Our shells of small constant angle and gentle curvature, such as *Dentalium*, are accordingly as much as we can ever expect to see of their respective spirals.

The spiral whose constant angle is 45° is both a simple case and a mathematical curiosity; for, since the tangent of 45° is unity, we need merely write $r = e^{\theta}$; which is as much as to say that the natural logarithms of the radii give us, without more ado, the vector angles. In this spiral the ratio between the breadths of two consecutive whorls becomes $r = e^{2\pi} = e^{2\times 3\cdot 1416}$. Reducing this from Naperian to common logs, we have $\log r = 2\cdot 729$; which tells us (by our tables) that the radius vector is multiplied about $535\frac{1}{2}$ times after a whole polar revolution; it is doubled after turning through a polar angle of less than 40°. Spirals of so low an angle as 45° are common enough in tooth and claw, but rare among molluscan shells; but one or two of the more strongly curved Dentaliums, like *D. elephantinum*, come near the mark. It is not easy to determine the pole, nor to measure the constant angle, in forms like these.

Let us return to the problem of how to ascertain, by direct measurement, the spiral angle of any particular shell. The method already employed is only applicable to complete spirals, that is to say to those in which the angle of the spiral is large, and furthermore it is inapplicable to portions, or broken fragments, of a shell. In the case of the broken fragment, it is plain that the determination of the angle is not merely of theoretic interest, but may be of great practical use to the conchologist as the one and only way by which he may restore the outline of the missing portions. We have a considerable choice of methods, which have been summarised by, and are partly due to, a very careful student of the Cephalopoda, the late Rev. J. F. Blake*.

(1) When an equiangular spiral rolls on a straight line, the pole traces another straight line at an angle to the first equal to the complement of the constant angle of the spiral; for the contact point is the instantaneous centre of the rotational movement, and the line joining it to the pole of the spiral is normal to the roulette path of that point. But the difficulty of determining the pole

* On the measurement of the curves formed by Cephalopods and other Mollusks, *Phil. Mag.* (5), vi, pp. 241–263, 1878.

(which is indeed asymptotic) makes this of little use as a method of determining the constant angle. It is, however, a beautiful property of the curve, and all the more interesting that Clerk Maxwell discovered it when he was a boy*.

(2) The following method is useful and easy when we have a portion of a single whorl, such as to shew both its inner and its outer edge. A broken whorl of an Ammonite, a curved shell such as *Dentalium*, or a horn of similar form to the latter, will fall under this head. We have merely to draw a tangent, GEH, to the outer whorl at any point E; then draw to the inner whorl a tangent parallel to GEH, touching the curve in some point F. The straight line joining the points of contact, EF, must evidently pass through the pole: and, accordingly, the angle GEF is the angle required. In shells which bear *longitudinal* striae or other ornaments, any pair of these will suffice for our purpose, instead of the actual boundaries of the whorl. But it is obvious that this method will be apt to fail us when the angle α is very small; and when, consequently, the points E and F are very remote.

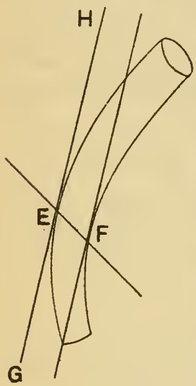


Fig. 381.

(3) In shells (or horns) shewing rings or other *transverse* ornamentation, we may take it that these ornaments are set at

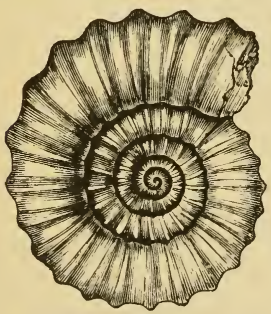


Fig. 382. An Ammonite, to shew corrugated surface-pattern.

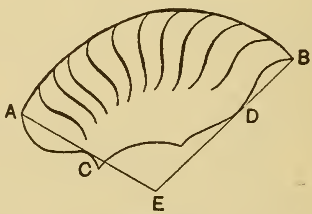


Fig. 383.

* Clerk Maxwell, On the theory of rolling curves, *Trans. R.S.E.* XVI, pp. 519–540, 1849; *Sci. Papers*, I, pp. 4–29.

a constant angle to the spire, and therefore to the radii. The angle (θ) between two of them, as AC, BD, is therefore equal to the angle θ between the polar radii from A and B, or from C and D; and therefore $BD/AC = e^{\theta \cot \alpha}$, which gives us the angle α in terms of known quantities.

(4) If only the outer edge be available, we have the ordinary geometrical problem—given an arc of an equiangular spiral, to find its pole and spiral angle. The methods we may employ depend (i) on determining directly the position of the pole, and (ii) on determining the radius of curvature.

The first method is theoretically simple, but difficult in practice; for it requires great accuracy in determining the points. Let AD, DB be two tangents drawn to the curve. Then a circle drawn through the points A, B, D will pass through the pole O, since the angles OAD, OBE (the supplement of OBD) are equal. The point O may be determined by the intersection of two such circles; and the angle DBO is then the angle, α, required.

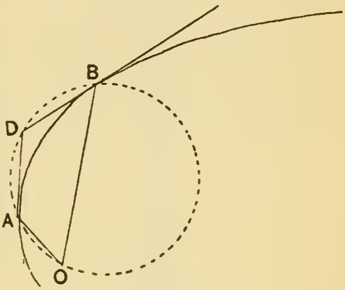


Fig. 384.

Or we may determine graphically, at two points, the radii of curvature $\rho_1 \rho_2$. Then, if s be the length of the arc between them (which may be determined with fair accuracy by rolling the margin of the shell along a ruler),

$$\cot \alpha = (\rho_1 - \rho_2)/s.$$

The following method*, given by Blake, will save actual determination of the radii of curvature.

Measure along a tangent to the curve the distance, AC, at which a certain small offset, CD, is made by the curve; and from another point B, measure the distance at which the curve makes an equal offset. Then, calling the offset μ; the arc AB, s; and AC, BE, respectively x_1, x_2, we have

$$\rho_1 = \frac{x_1^2 + \mu^2}{2\mu}, \text{ approximately,}$$

and
$$\cot \alpha = \frac{x_2^2 - x_1^2}{2\mu s}.$$

Of all these methods by which the mathematical constants, or specific characters, of a given spiral shell may be determined, the

* For an example of this method, see Blake, *loc. cit.* p. 251.

only one of which much use has been made is that which Moseley first employed, namely, the simple method of determining the relative breadths of the whorl at distances separated by some convenient vectorial angle such as 90°, 180°, or 360°.

Very elaborate measurements of a number of Ammonites have been made by Naumann*, by Grabau, by Sandberger†, and by Müller, among which we may choose a couple of cases for consideration‡. In the following table I have taken a portion of Grabau's

Ammonites intuslabiatus

Breadth of whorls (180° apart)	Ratio of breadth of successive whorls (360° apart)	The angle (α) as calculated
0·30 mm.	—	— —
0·30	1·333	87° 23′
0·40	1·500	86 19
0·45	1·500	86 19
0·60	1·444	86 39
0·65	1·417	86 49
0·85	1·692	85 13
1·10	1·588	85 47
1·35	1·545	86 2
1·70	1·630	85 33
2·20	1·441	86 40
2·45	1·432	86 43
3·15	1·735	85 0
4·25	1·683	85 16
5·30	1·482	86 25
6·30	1·519	86 12
8·05	1·635	85 32
10·30	1·416	86 50
11·40	1·252	87 57
12·90	—	— —
	Mean	86° 15′

* C. F. Naumann, Ueber die Spiralen von Conchylien, *Abh. k. sächs. Ges.* 1846, pp. 153–196; Ueber die cyclocentrische Conchospirale u. über das Windungsgesetz von *Planorbis corneus, ibid.* I, pp. 171–195, 1849; Spirale von Nautilus u. *Ammonites galeatus, Ber. k. sächs. Ges.* II, p. 26, 1848; Spirale von *Amm. Ramsaueri, ibid.* XVI, p. 21, 1864. Oken, reviewing Naumann's work (in *Isis*, 1847, p. 867) foretold how some day the naturalist and the mathematician would each learn of the other: "Um die Sache zu Vollendung zu bringen wird der Mathematiker Zoolog und Physiolog, und diese Mathematiker werden müssen."

† G. Sandberger, *Clymenia subnautilina, Jahresber. d. Ver. f. Naturk. im Herzogth. Nassau*, 1855, p. 127; Spiralen des *Ammonites Amaltheus, A. Gaytani* und *Goniatites intumescens, Ztschr. d. d. Geolog. Gesellsch.* X, pp. 446–449, 1858. Also Müller, Beitrag zur Konchyliometrie, *Poggend. Ann.* LXXXVI, p. 533, 1850; *ibid.* XC, p. 323, 1853. These two authors upheld the logarithmic law against Naumann and Grabau.

‡ See also Chr. Petersen, *Das Quotientengesetz, eine biologisch-statistische Untersuchung*, 119 pp., Copenhagen, 1921; E. Sporn, Ueber die Gesetzmässigkeit im Baue der Muschelgehaüser, *Arch. f. Entw. Mech.* CVIII, pp. 228–242, 1926.

determinations of the breadth of the whorls in *Ammonites* (*Arcestes*) *intuslabiatus*; these measurements Grabau gives for every 45° of arc, but I have only set forth successive whorls measured along one diameter on both sides of the pole. The ratio between *alternate* measurements is therefore the same ratio as Moseley adopted, namely the ratio of breadth between *contiguous whorls* along a radius vector. I have then added to these observed values the corresponding calculated values of the angle α, as obtained from our usual formula.

There is considerable irregularity in the ratios derived from these measurements, but it will be seen that this irregularity only implies a variation of the angle of the spiral between about 85° and 87°; and the values fluctuate pretty regularly about the mean, which is 86° 15′. Considering the difficulty of measuring the whorls, especially towards the centre, and in particular the difficulty of determining with precise accuracy the position of the pole, it is clear that in such a case as this we are not justified in asserting that the law of the equiangular spiral is departed from.

Ammonites tornatus

Breadth of whorls (180° apart)	Ratio of breadth of successive whorls (360° apart)	The spiral angle (α) as calculated
0·25 mm.	—	— —
0·30	1·400	86° 56′
0·35	1·667	85 21
0·50	2·000	83 42
0·70	2·000	83 42
1·00	2·000	83 42
1·40	2·100	83 16
2·10	2·179	82 56
3·05	2·238	82 42
4·70	2·492	81 44
7·60	2·574	81 27
12·10	2·546	81 33
19·35	—	— —
Mean	2·11	83° 22′

In some cases, however, it is undoubtedly departed from. Here for instance is another table from Grabau, shewing the corresponding ratios in an Ammonite of the group of *Arcestes tornatus*. In this case we see a distinct tendency of the ratios to increase as we pass from the centre of the coil outwards, and consequently for the values of the angle α to diminish. The case is comparable to that of a cone with slightly curving sides: in which, that is to say, there is a slight acceleration of growth in a transverse as compared with the longitudinal direction.

In a tubular spiral, whether plane or helicoid, the consecutive whorls may either be (1) isolated and remote from one another; or (2) they may precisely meet, so that the outer border of one and the inner border of the next just coincide; or (3) they may overlap, the vector plane of each outer whorl cutting that of its immediate predecessor or predecessors.

Looking, as we have done, upon the spiral shell as being essentially a cone rolled up*, it is plain that, for a given spiral angle, intersection or non-intersection of the successive whorls will depend upon *the apical angle* of the original cone. For the wider the cone, the more will its inner border tend to encroach on the preceding whorl. But it is also plain that the greater the apical angle of the cone, and the broader, consequently, the cone itself, the greater difference will there be between the total *lengths* of its inner and outer borders. And, since the inner and outer borders are describing precisely the same spiral about the pole, we may consider the inner border as being *retarded* in growth as compared with the outer, and as being always identical with a smaller and earlier part of the latter.

If λ be the ratio of growth between the outer and the inner curve, then, the outer curve being represented by

$$r = ae^{\theta \cot \alpha},$$

the equation to the inner one will be

$$r' = a\lambda e^{\theta \cot \alpha},$$

or

$$r' = ae^{(\theta - \gamma) \cot \alpha},$$

* To speak of a cone "rolling up," and becoming a nautiloid spiral by doing so, is a rough and non-mathematical description; nor is it easy to see how a cone of wide angle could roll up, and yet remain a cone. But if (i) the centre of a sphere move along a straight line and its radius keep proportional to the distance the centre has moved, the sphere generates as its envelope a circular cone of which the straight line is the axis; and so, similarly, if (ii) the centre of a sphere move along an equiangular spiral and its radius keep proportional to the arc-distance along the spiral back to the pole, the sphere generates as its envelope a self-similar shell-surface, or nautiloid spiral.

and γ may then be called the angle of retardation, to which the inner curve is subject by virtue of its slower rate of growth.

Dispensing with mathematical formulae, the several conditions may be illustrated as follows:

In the diagrams (Fig. 385), $OP_1P_2P_3$, etc. represents a radius, on which P_1, P_2, P_3 are the points attained by the outer border of the tubular shell after as many entire consecutive revolutions. And P_1', P_2', P_3' are the points similarly intersected by the inner border; OP/OP' being always $= \lambda$, which is the ratio of growth, or "cutting-down factor." Then, obviously, (1) when OP_1 is less than

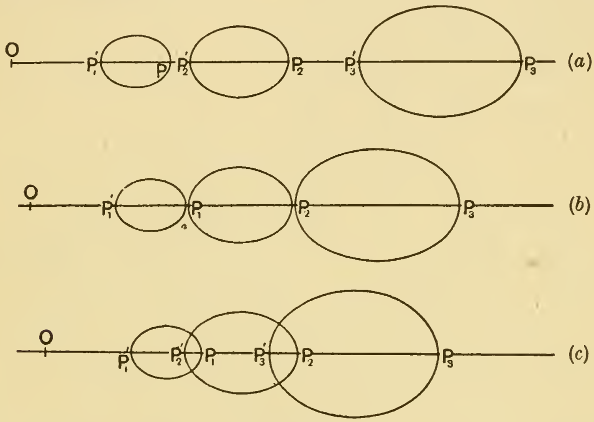


Fig. 385.

OP_2' the whorls will be separated by an interspace (a); (2) when $OP_1 = OP_2'$ they will be in contact (b), and (3) when OP_1 is greater than OP_2' there will be a greater or less extent of overlapping, that is to say of concealment of the surfaces of the earlier by the later whorls (c). And as a further case (4), it is plain that if λ be very large, that is to say if OP_1 be greater, not only than OP_2' but also than OP_3', OP_4', etc., we shall have complete, or all but complete, concealment by the last formed whorl of the whole of its predecessors. This latter condition is completely attained in *Nautilus pompilius*, and approached, though not quite attained, in *N. umbilicatus*; and the difference between these two forms, or "species," is constituted accordingly by a difference in the value of λ. (5) There is also a final case, not easily distinguishable externally from (4), where P' lies on the opposite side of the radius vector to P, and is therefore imaginary. This final condition is exhibited in *Argonauta*.

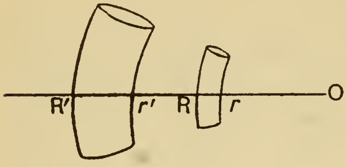


Fig. 386.

The limiting values of λ are easily ascertained.

In Fig. 386 we have portions of two successive whorls, whose corresponding points on the same radius vector (as R and R') are, therefore, at a distance apart corresponding to 2π. Let r and r' refer to the inner, and R, R' to the outer sides of the two whorls. Then, if we consider

$$R = ae^{\theta \cot \alpha},$$

it follows that

$$R' = ae^{(\theta+2\pi)\cot \alpha},$$

$$r = \lambda ae^{\theta \cot \alpha} = ae^{(\theta-\gamma)\cot \alpha},$$

and

$$r' = \lambda ae^{(\theta+2\pi)\cot \alpha} = ae^{(\theta+2\pi-\gamma)\cot \alpha}.$$

Now in the three cases (a, b, c) represented in Fig. 385, it is plain that $r' \gtreqless R$, respectively. That is to say,

$$\lambda ae^{(\theta+2\pi)\cot \alpha} \gtreqless ae^{\theta \cot \alpha},$$

and

$$\lambda e^{2\pi \cot \alpha} \lesseqgtr 1.$$

The case in which $\lambda e^{2\pi \cot \alpha} = 1$, or $-\log \lambda = 2\pi \cot \alpha \log e$, is the case represented in Fig. 385, b: that is to say, the particular case, for each value of α, where the consecutive whorls just touch, without interspace or overlap. For such cases, then, we may tabulate the values of λ as follows:

Constant angle α of spiral	Ratio (λ) of rate of growth of inner border of tube, as compared with that of the outer border
89°	0·896
88	0·803
87	0·720
86	0·645
85	0·577
80	0·330
75	0·234
70	0·1016
65	0·0534

We see, accordingly, that in plane spirals whose constant angle lies, say, between 65° and 70°, we can only obtain contact between consecutive whorls if the rate of growth of the inner border of the tube be a small fraction—a tenth or a twentieth—of that of the outer border. In spirals whose constant angle is 80°, contact is attained when the respective rates of growth are, approximately, as 3 to 1; while in spirals of constant angle from about 85° to 89°, contact is attained when the rates of growth are in the ratio of from about $\frac{3}{5}$ to $\frac{9}{10}$.

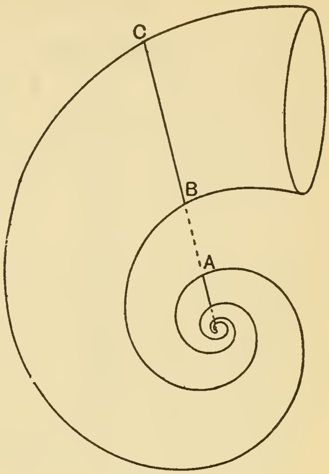


Fig. 387.

If on the other hand we have, for any given value of α, a value of λ greater or less than the value given in the above table, then we have, respectively, the conditions of separation or of overlap which are exemplified in Fig. 385, *a* and *c*. And, just as we have constructed this table for the particular case of simple contact, so we could construct similar tables for various degrees of separation or of overlap.

For instance, a case which admits of simple solution is that in which the interspace between the whorls is everywhere a mean proportional between the breadths of the whorls themselves (Fig. 387). In this case, let us call $OA = R$, $OC = R_1$, and $OB = r$. We then have

$$R_1 = OA = ae^{(\theta \cot \alpha)},$$

$$R_2 = OC = ae^{(\theta + 2\pi) \cot \alpha},$$

$$R_1 R_2 = ae^{2(\theta + \pi) \cot \alpha} = r^2 *.$$

And $$r^2 = (1/\lambda)^2 \,.\, \epsilon^{2\theta \cot \alpha},$$

whence, equating, $$1/\lambda = e^{\pi \cot \alpha}.$$

* It has been pointed out to me that it does not follow at once and obviously that, because the interspace AB is a mean proportional between the breadths of the adjacent whorls, therefore the whole distance OB is a mean proportional between OA and OC. This is a corollary which requires to be proved; but the proof is easy.

The corresponding values of λ are as follows:

Constant angle (α)	Ratio (λ) of rates of growth of outer and inner border, such as to produce a spiral with interspaces between the whorls, the breadth of which interspaces is a mean proportional between the breadths of the whorls themselves
90°	1·00 (imaginary)
89	0·95
88	0·89
87	0·85
86	0·81
85	0·76
80	0·57
75	0·43
70	0·32
65	0·23
60	0·18
55	0·13
50	0·090
45	0·063
40	0·042
35	0·026
30	0·016

As regards the angle of retardation, γ, in the formula

$$r' = \lambda e^{\theta \cot \alpha}, \text{ or } r' = e^{(\theta - \gamma)\cot \alpha},$$

and in the case

$$r' = e^{(2\pi - \gamma)\cot \alpha}, \text{ or } -\log \lambda = (2\pi - \gamma)\cot \alpha,$$

it is evident that when $\gamma = 2\pi$, that will mean that $\lambda = 1$. In other words, the outer and inner borders of the tube are identical, and the tube is constituted by one continuous line.

When λ is a very small fraction, that is to say when the rates of growth of the two borders of the tube are very diverse, then γ will tend towards infinity—tend that is to say towards a condition in which the inner border of the tube never grows at all. This condition is not infrequently approached in nature. I take it that *Cypraea* is such a case. But the nearly parallel-sided cone of *Dentalium*, or the widely separated whorls of *Lituites*, are cases where λ nearly approaches unity in the one case, and is still large in the other, γ being correspondingly small; while we can easily find cases where γ is very large, and λ is a small fraction, for instance in *Haliotis*, in *Calyptraea*, or in *Gryphaea*.

For the purposes of the morphologist, then, the main result of this last general investigation is to shew that all the various types of "open" and "closed" spirals, all the various degrees of separation or overlap of the successive whorls, are simply the outward expression of a varying ratio in the *rate of growth* of the outer as compared with the inner border of the tubular shell.

The foregoing problem of contact, or intersection, of successive whorls is a very simple one in the case of the discoid shell but a more complex one in the turbinate. For in the discoid shell contact will evidently take place when the retardation of the inner as compared with the outer whorl is just 360°, and the shape of the whorls need not be considered.

As the angle of retardation diminishes from 360°, the whorls stand further and further apart in an open coil; as it increases beyond 360°, they overlap more and more; and when the angle of retardation is infinite, that is to say when the true inner edge of the whorl does not grow at all, then the shell is said to be completely involute. Of this latter condition we have a striking example in *Argonauta*, and one a little more obscure in *Nautilus pompilius*.

In the turbinate shell the problem of contact is twofold, for we have to deal with the possibilities of contact on the *same* side of the axis (which is what we have dealt with in the discoid) and also with the new possibility of contact or intersection on the *opposite* side; it is this latter case which will determine the presence or absence of an open *umbilicus*. It is further obvious that, in the case of the turbinate, the question of contact or no contact will depend on the shape of the generating curve; and if we take the simple case where this generating curve may be considered as an ellipse, then contact will be found to depend on the angle which the major axis of this ellipse makes with the axis of the shell. The question becomes a complicated one, and the student will find it treated in Blake's paper already referred to.

When one whorl overlaps another, so that the generating curve cuts its predecessor (at a distance of 2π) on the same radius vector, the locus of intersection will follow a spiral line upon the shell, which is called the "suture" by conchologists. It is one of that *ensemble* of spiral lines in space of which, as we have seen, the whole shell may be conceived to be constituted; and we might call it a "contact-spiral," or "spiral of intersection." In discoid shells, such as an *Ammonite* or a *Planorbis*, or in *Nautilus umbilicatus*, there are obviously two such contact-spirals, one on each side of the shell, that is to say one on each side of a plane perpendicular to the axis. In turbinate shells such a condition is also possible, but is somewhat rare. We have it for instance in *Solarium perspectivum*, where the one contact-spiral is visible on the exterior of

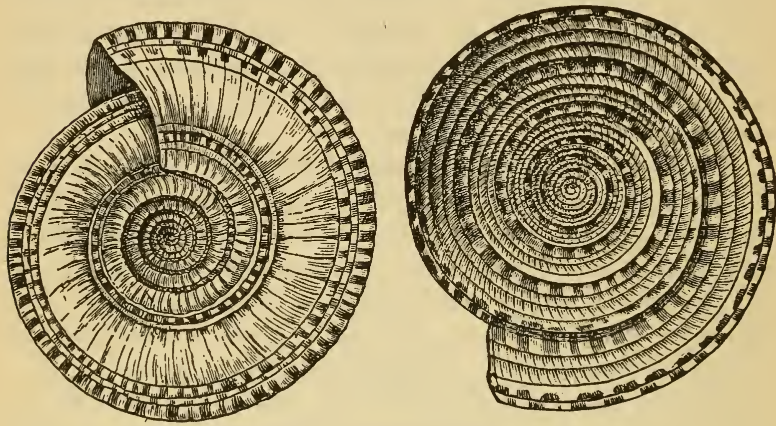


Fig. 388. *Solarium perspectivum.*

the shell, and the other lies internally, winding round the open cone of the umbilicus*; but this second contact-spiral is usually imaginary, or concealed within the whorls of the turbinated shell.

Fig. 389. *Haliotis tuberculata* L.; the ormer, or ear shell.

Fig. 390. *Scalaria pretiosa* L.; the wentletrap. From Cooke's *Spirals.*

Again, in *Haliotis*, one of the contact-spirals is non-existent, because of the extreme obliquity of the plane of the generating curve. In

* A beautiful construction: *stupendum Naturae artificium,* Linnaeus.

Scalaria pretiosa and in *Spirula** there is no contact-spiral, because the growth of the generating curve has been too slow in comparison with the vector rotation of its plane. In *Argonauta* and in *Cypraea* there is no contact-spiral, because the growth of the generating curve has been too quick. Nor, of course, is there any contact-spiral in *Patella* or in *Dentalium*, because the angle α is too small

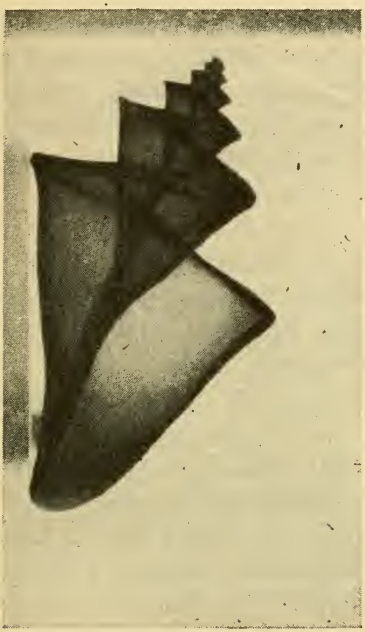


Fig. 391. *Thatcheria mirabilis* Angas; from a radiograph by Dr A. Müller.

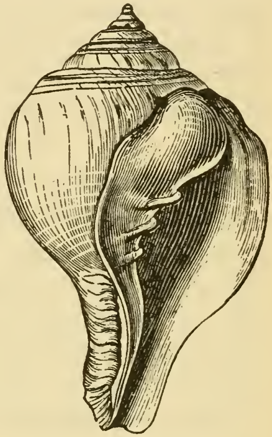


Fig. 392. *Turbinella napus* Lam.; an Indian chank-shell. From Chenu.

ever to give us a complete revolution of the spire. *Thatcheria mirabilis* is a peculiar and beautiful shell, in which the outline of the lip is sharply triangular, instead of being a smooth curve: with the result that the apex of the triangle forms a conspicuous "generating spiral", which winds round the shell and is more conspicuous than the suture itself.

In the great majority of helicoid or turbinate shells the innermost

* "It [*Spirula*] is curved so as its roundness is kept, and the Parts do not touch one another": R. Hooke, *Posthumous Works*, 1745, p. 284.

or axial portions of the whorls tend to form a solid axis or "columella"; and to this is attached the columellar muscle which on the one hand withdraws the animal within its shell, and on the other hand provides the controlling force or trammel, by which (in the gastropod) the growing shell is kept in its spiral course. This muscle is apt to leave a winding groove upon the columella (Fig. 373); now and then the muscle is split into strands or bundles, and then it leaves parallel grooves with ridges or pleats between, and the number of these folds or pleats may vary with the species, as in the Volutes, or even with race or locality. Thus, among the curiosities of conchology, the chank-shells on the Trincomali coast have four columellar folds or ridges; but all those from Tranquebar, just north of Adam's Bridge, have only three (Fig. 392)*.

The various forms of straight or spiral shells among the Cephalopods, which we have seen to be capable of complete definition by the help of elementary mathematics, have received a very complicated descriptive nomenclature from the palaeontologists. For instance, the straight cones are spoken of as *orthoceracones* or *bactriticones*, the loosely coiled forms as *gyroceracones* or *mimoceracones*, the more closely coiled shells, in which one whorl overlaps the other, as *nautilicones* or *ammoniticones*, and so forth. In such a series of forms the palaeontologist sees undoubted and unquestioned evidence of ancestral descent. For instance we read in Zittel's *Palaeontology*†: "The bactriticone obviously represents the primitive or primary radical of the Ammonoidea, and the mimoceracone the next or secondary radical of this order"; while precisely the opposite conclusion was drawn by Owen, who supposed that the straight chambered shells of such fossil Cephalopods as *Orthoceras* had been produced by the gradual unwinding of a coiled nautiloid shell‡. *The mathematical study of the forms of shells lends no support to these*

* Cf. R. Winckworth, *Proc. Malacol. Soc.* XXIII, p. 345, 1939.

† English edition, 1900, p. 537. The chapter is revised by Professor Alpheus Hyatt, to whom the nomenclature is largely due. For a more copious terminology, see Hyatt, *Phylogeny of an Acquired Characteristic*, 1894, p. 422 *seq.* Cf. also L. F. Spath, The evolution of the Cephalopoda, *Biol. Reviews*, VIII, pp. 418–462, 1933.

‡ This latter conclusion is adopted by Willey, *Zoological Results*, 1902, p. 747. Cf. also Graham Kerr, on *Spirula*: *Dana Reports*, No. 8, Copenhagen, 1931.

*or any suchlike phylogenetic hypotheses**. If we have two shells in which the constant angle of the spire be respectively 80° and 60°, that fact in itself does not at all justify an assertion that the one is more primitive, more ancient, or more "ancestral" than the other. Nor, if we find a third in which the angle happens to be 70°, does that fact entitle us to say that this shell is intermediate between the other two, in time, or in blood relationship, or in any other sense whatsoever save only the strictly formal and mathematical one. For it is evident that, though these particular arithmetical constants manifest themselves in visible and recognisable differences of form, yet they are not necessarily more deep-seated or significant than are those which manifest themselves only in difference of magnitude; and the student of phylogeny scarcely ventures to draw conclusions as to the relative antiquity of two allied organisms on the ground that one happens to be bigger or less, or longer or shorter, than the other.

At the same time, while it is obviously unsafe to rest conclusions upon such features as these, unless they be strongly supported and corroborated in other ways—for the simple reason that there is unlimited room for *coincidence*, or separate and independent attainment of this or that magnitude or numerical ratio—yet on the other hand it is certain that, in particular cases, the evolution of a race has actually involved gradual increase or decrease in some one or more numerical factors, magnitude itself included—that is to say increase or decrease in some one or more of the actual and relative velocities of growth. When we do meet with a clear and unmistakable series of such progressive magnitudes or ratios, manifesting themselves in a progressive series of "allied" forms, then we have the phenomenon of "*orthogenesis*." For orthogenesis is simply that phenomenon of continuous lines or series of form (and also of functional or physiological capacity),

* Phylogenetic speculation, fifty years ago the chief preoccupation of the biologist, has had its caustic critics. Cf. (*int. al.*) Rhumbler, in *Arch. f. Entw. Mech.* VII, p. 104, 1898: "Phylogenetische Speculationen...werden immer auf Anklang bei den Fachgenossen rechnen dürfen, sofern nicht ein anderer Fachgenosse auf demselben Gebiet mit gleicher Kenntniss der Dinge und mit gleicher Scharfsinn zufällig zu einer anderen Theorie gekommen ist....Die Richtigkeit 'guter' phylogenetischer Schlüsse lässt sich im schlimmsten Fälle anzweifeln, aber direkt widerlegen lässt sich in der Regel nicht."

which was the foundation of the Theory of Evolution, alike to Lamarck and to Darwin and Wallace; and which we see to exist whatever be our ideas of the "origin of species," or of the nature and origin of "functional adaptations." And to my mind, the mathematical (as distinguished from the purely physical) study of morphology bids fair to help us to recognise this phenomenon of orthogenesis in many cases where it is not at once patent to the eye; and, on the other hand, to warn us in many other cases that even strong and apparently complex resemblances in form may be capable of arising independently, and may sometimes signify no more than the equally accidental numerical coincidences which are manifested in identity of length or weight or any other simple magnitudes.

I have already referred to the fact that, while in general a very great and remarkable regularity of form is characteristic of the molluscan shell, yet that complete regularity is apt to be departed from. We have clear cases of such a departure in *Pupa*, *Clausilia* and various *Bulimi*, where the spire is not conical, but its sides are curved and narrow in.

The following measurements of three specimens of *Clausilia* shew a gradual change in the ratio to one another of successive whorls, or in other words a marked departure from the logarithmic law:

Clausilia lamellosa. (From Chr. Petersen*.)

	Width of successive whorls (mm.)				Ratios, or "quotients" of successive whorls			
	I	II	III		I	II	III	Mean
a	2·42	2·51	2·49	*a/b*	1·43	1·45	1·42	1·44
b	1·69	1·72	1·75	*b/c*	1·36	1·33	1·31	1·33
c	1·24	1·30	1·33	*c/d*	1·21	1·29	1·23	1·24
d	1·02	1·00	1·08	*d/e*	1·22	1·20	1·26	1·23
e	0·83	0·83	0·86					

In many ammonites, where the helicoid factor does not enter into the case, we have a clear illustration of how gradual and marked

* From Chr. Petersen, *Das Quotientengesetz,* p. 36. After making a careful statistical study of 1000 Clausilias, Peterson found the following mean ratios of the successive whorls, *a/b*, *b/c*, etc.: 1·37, 1·33, 1·27, 1·24, 1·22, 1·19.

changes in the spiral angle may be detected even in ammonites which present nothing abnormal to the eye. But let us suppose that the spiral angle increases somewhat rapidly; we shall then get a spiral with gradually narrowing whorls, which condition is characteristic of *Oekotraustes*, a subgenus of *Ammonites*. If on the other hand, the angle α gradually diminishes, and even falls away to zero, we shall have the spiral curve opening out, as it does in *Scaphites*, *Ancyloceras*

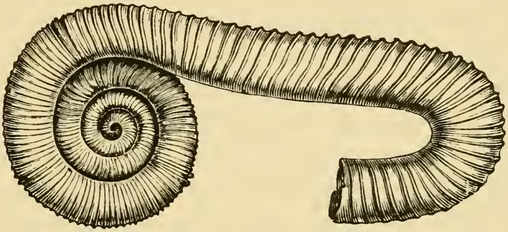


Fig. 393. An ammonitoid shell (*Macroscaphites*) to shew change of curvature.

and *Lituites*, until the spiral coil is replaced by a spiral curve so gentle as to seem all but straight. Lastly, there are a few cases, such as *Bellerophon expansus* and some *Goniatites*, where the outer spiral does not perceptibly change, but the whorls become more "embracing" or the whole shell more involute. Here it is the angle of retardation, the ratio of growth between the outer and inner parts of the whorl, which undergoes a gradual change.

In order to understand the relation of a close-coiled shell to its straighter congeners, to compare (for example) an *Ammonite* with an *Orthoceras*, it is necessary to estimate the length of the right cone which has, so to speak, been coiled up into the spiral shell. Our problem is, to find the length of a plane equiangular spiral, in terms of the radius and the constant angle α. Then, if OP be a radius vector, OQ a line of reference perpendicular to OP, and PQ a tangent to the curve, PQ, or sec α, is equal in length to the spiral arc OP. In other words, the arc measured from the pole is equal to the polar tangent*. And this is practically obvious: for

* Descartes made this discovery, and records it in a letter to Mersenne, 1638. The equiangular spiral was thus the first transcendental curve to be "rectified."

$PP'/PR' = ds/dr = \sec\alpha$, and therefore $\sec\alpha = s/r$, or the ratio of arc to radius vector.

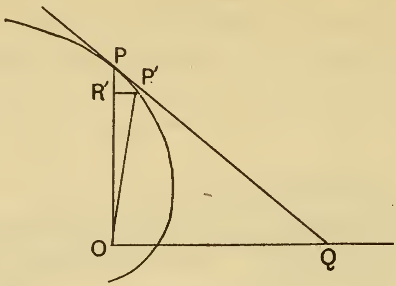


Fig. 394.

Accordingly, the ratio of l, the total length, to r, the radius vector up to which the total length is to be measured, is expressed by a simple table of secants; as follows:

α	l/r	α	l/r
5°	1·004	87°	19·1
10	1·015	88	28·7
20	1·064	89	57·3
30	1·165	89° 10′	68·8
40	1·305	20	85·9
50	1·56	30	114·6
60	2·0	40	171·9
70	2·9	50	343·8
75	3·9	55	687·5
80	5·8	59	3437·7
85	11·5	90	Infinite
86	14·3		

Putting the same table inversely, so as to shew the total length in terms of the radius, we have as follows:

Total length (in terms of the radius)	Constant angle
2	60°
3	70 31′
4	75 32
5	78 28
10	84 16
20	87 8
30	88 6
40	88 34
50	88 51
100	89 26
1000	89 56′ 36″
10,000	89 59 30

Accordingly, we see that (1), when the constant angle of the spiral is small, the shell (or for that matter the tooth, or horn or claw) is scarcely to be distinguished from a straight cone or cylinder; and this remains pretty much the case for a considerable increase of angle, say from 0° to 20° or more; (2) for a considerably greater increase of the constant angle, say to 50° or more, the shell would still only have the appearance of a gentle curve; (3) the characteristic close coils of the Nautilus or Ammonite would be typically represented only when the constant angle lies within a few degrees on either side of about 80°. The coiled up spiral of a Nautilus, with a constant angle of about 80°, is about six times the length of its radius vector, or rather more than three times its own diameter; while that of an Ammonite, with a constant angle of, say, from 85° to 88°, is from about six to fifteen times as long as its own diameter. And (4) as we approach an angle of 90° (at which point the spiral vanishes in a circle), the length of the coil increases with enormous rapidity. Our spiral would soon assume the appearance of the close coils of a Nummulite, and the successive increments of breadth in the successive whorls would become inappreciable to the eye.

The geometrical form of the shell involves many other beautiful properties, of great interest to the mathematician but which it is not possible to reduce to such simple expressions as we have been content to use. For instance, we may obtain an equation which shall express completely the surface of any shell, in terms of polar or of rectangular coordinates (as has been done by Moseley and by Blake), or in Hamiltonian vector notation*. It is likewise possible (though of little interest to the naturalist) to determine the area of a conchoidal surface or the volume of a conchoidal solid, and to find the centre of gravity of either surface or solid†. And Blake has further shewn, with considerable elaboration, how we may deal with the symmetrical distortion due to pressure which fossil shells are often found to have undergone, and how we may reconstitute by calculation their original undistorted form—a problem which, were the available methods only a little easier, would be

* Cf. H. W. L. Hime's *Outlines of Quaternions*, 1894, pp. 171–173.

† See Moseley, *op. cit.* p. 361 *seq.* Also, for more complete and elaborate treatment, Haton de la Goupillière, *op. cit.* 1908, pp. 5–46, 69–204.

very helpful to the palaeontologist; for, as Blake himself has shewn, it is easy to mistake a symmetrically distorted specimen of (for instance) an Ammonite for a new and distinct species of the same genus. But it is evident that to deal fully with the mathematical problems contained in, or suggested by, the spiral shell, would require a whole treatise, rather than a single chapter of this elementary book. Let us then, leaving mathematics aside, attempt to summarise, and perhaps to extend, what has been said about the general possibilities of form in this class of organisms.

The univalve shell: a summary

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.

When the envelope of the shell is a right cone—and it is seldom far from being so—then our helico-spiral is a loxodromic curve, and is obviously identical with a projection, parallel with the axis, of the logarithmic spiral of the base. As this spiral cuts all radii at a constant angle, so its orthogonal projection on the surface intersects all generatrices, and consequently all parallel circles, under a constant angle: this being the definition of a loxodromic curve on a surface of revolution. Guido Grandi describes this curve for the first time in a letter to Ceva, printed at the end of his *Demonstratio theorematum Hugenianorum circa...logarithmicam lineam*, 1701 *.

* See R. C. Archibald, *op. cit.* 1918. Olivier discussed it again (*Rev. de géom. descriptive*, 1843) calling it a "conical equiangular" or "conical logarithmic"

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. 396) 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*. Its form is seldom open to easy mathematical expression, save when it is an actual circle or

Fig. 395. Section of a spiral univalve, *Triton corrugatus* Lam. From Woodward.

spiral. Paul Serret (*Th. nouv...des lignes à double courbure*, 1860, p. 101) called it "*hélice cylindroconique*"; Haton de la Goupillière calls it a "*cônhélice*." It has also been studied by (*int. al.*) Tissot, *Nouv. ann. de mathém.* 1852; G. Pirondini, *Mathesis*, XIX, pp. 153–8, 1899; etc.

* 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*, VI, p. 411, 1895; *Zoological Results*, 1902, p. 742.)

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 $r = a(1 + \cos\theta)$.

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

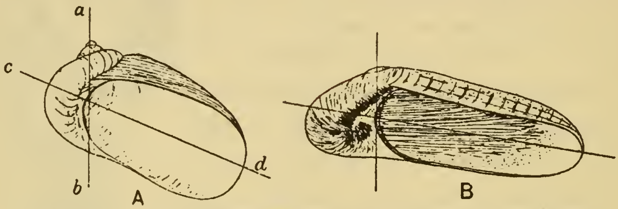


Fig. 396. A, *Lamellaria perspicua*; B, *Sigaretus haliotoides*. After Woodward.

curve is so oblique to the axis of the shell that the latter appears to grow by additions to one margin only (cf. Fig. 362), as in the case of the opercula of *Turbo* and *Nerita* referred to on p. 775; and this is what Moseley supposed it to do.

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, as has been sufficiently explained, by the ratios of certain velocities of growth. These angles are (1) the constant angle of the 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 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*.

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, as we have seen, 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*.

Directly related to the angle α is the ratio which subsists between the breadths of successive whorls. The following table gives a few

* 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.

illustrations of this ratio in particular cases, in addition to those which we have already studied.

Ratio of breadth of consecutive whorls

Pointed Turbinates		Obtuse Turbinates and Discoids	
Telescopium fuscum	1·14	*Conus virgo*	1·25
Terebra subulata	1·16	‡*Clymenia laevigata*	1·33
**Turritella terebellata*	1·18	*Conus litteratus*	1·40
**Turritella imbricata*	1·20	*Conus betulinus*	1·43
Cerithium palustre	1·22	‡*Clymenia arietina*	1·50
Turritella duplicata	1·23	‡*Goniatites bifer*	1·50
Melanopsis terebralis	1·23	**Helix nemoralis*	1·50
Cerithium nodulosum	1·24	**Solarium perspectivum*	1·50
**Turritella carinata*	1·25	*Solarium trochleare*	1·62
Terebra crenulata	1·25	*Solarium magnificum*	1·75
Terebra maculata (Fig. 397)	1·25	**Natica aperta*	2·00
**Cerithium lignitarum*	1·26	*Euomphalus pentangulatus*	2·00
Terebra dimidiata	1·28	*Planorbis corneus*	2·00
Cerithium sulcatum	1·32	*Solaropsis pellis-serpentis*	2·00
Fusus longissimus	1·34	*Dolium zonâtum*	2·10
**Pleurotomaria conoidea*	1·34	‡*Goniatites carinatus*	2·50
Trochus niloticus (Fig. 398)	1·41	**Natica glaucina*	3·00
Mitra episcopalis	1·43	*Nautilus pompilius*	3·00
Fusus antiquus	1·50	*Haliotis excavatus*	4·20
Scalaria pretiosa	1·56	*Haliotis parvus*	6·00
Fusus colosseus	1·71	*Delphinula atrata*	6·00
Phasianella australis	1·80	*Haliotis rugoso-plicata*	9·30
Helicostyla polychroa	2·00	*Haliotis viridis*	10·00

Those marked * from Naumann; ‡ from Müller; the rest from Macalister†.

In the case of turbinate shells, we must take into account the angle β, in order to determine the spiral angle α from the ratio of the breadths of consecutive whorls; for the short table given on p. 791 is only applicable to discoid shells, in which the angle β is an angle of 90°. Our formula, as mentioned on p. 771, now becomes

$$R = \epsilon^{2\pi \sin\beta \cot\alpha}.$$

For this formula I have worked out the following table.

† Alex. Macalister, Observations on the mode of growth of discoid and turbinated shells, *Proc. R.S.* XVIII, pp. 529–532, 1870; *Ann. Mag. N.H.* (6), IV, p 160, 1870. Cf. also his Law of Symmetry as exemplified in animal form, *Journ. R. Dublin Soc.* 1869, p. 327.

Table shewing values of the spiral angle α corresponding to certain ratios of breadth of successive whorls of the shell, for various values of the apical semi-angle β

Ratio $R/1$	$\beta=5°$	10°	15°	20°	30°	40°	50°	60°	70°	80°	90°
1·1	80° 8′	85° 0′	86° 44′	87° 28′	88° 16′	88° 39′	88° 52′	89° 0′	89° 4′	89° 7′	89° 8′
1·25	67 51	78 27	82 11	84 5	85 56	86 50	87 21	87 39	87 50	87 56	87 58
1·5	53 30	69 37	76 0	79 21	82 39	84 16	85 13	85 44	86 4	86 15	86 18
2·0	38 20	57 35	66 55	73 11	77 34	80 16	81 52	82 45	83 18	83 37	83 42
2·5	30 53	50 0	60 35	67 0	73 45	77 13	79 19	80 26	81 11	81 35	81 42
3·0	26 32	44 50	56 0	63 0	70 45	74 45	77 17	78 35	79 28	79 56	80 5
3·5	23 37	41 5	52 25	59 50	68 15	72 45	75 35	77 2	78 1	78 33	78 43
4·0	21 35	38 10	49 35	57 15	66 10	71 3	74 9	75 42	76 47	77 22	77 34
4·5	20 0	36 0	47 15	55 5	64 25	69 35	72 54	74 33	75 43	76 20	76 35
5·0	18 45	34 10	45 20	53 15	62 55	68 15	71 48	73 31	74 45	75 25	75 38
10·0	13 25	25 20	35 15	43 5	53 45	60 20	64 57	67 4	68 42	69 35	69 53
20·0	10 25	20 0	28 30	35 45	46 25	53 25	58 52	61 10	63 6	64 10	64 31
50·0	8 0	15 35	22 35	28 50	38 45	45 55	52 1	54 18	56 28	57 42	58 6
100·0	6 50	13 20	19 30	25 5	34 20	41 15	47 35	49 45	52 3	53 20	53 46

From this table, by interpolation, we may easily fill in the approximate values of α, as soon as we have determined the apical angle β and measured the ratio R; as follows:

	R	β	α
Turritella sp.	1·12	7°	81°
Cerithium nodulosum ...	1·24	15	82
Conus virgo	1·25	70	88
Mitra episcopalis	1·43	16	78
Scalaria pretiosa	1·56	26	81
Phasianella australis ...	1·80	26	80
Solarium perspectivum ...	1·50	53	85
Natica aperta	2·00	70	83
Planorbis corneus ...	2·00	90	84
Euomphalus pentangulatus	2·00	90	84

We see from this that shells so different in appearance as *Cerithium*, *Solarium*, *Natica* and *Planorbis* differ very little indeed in the magnitude of the spiral angle α, that is to say in the relative velocities of radial and tangential growth. It is upon the angle β that the difference in their form mainly depends.

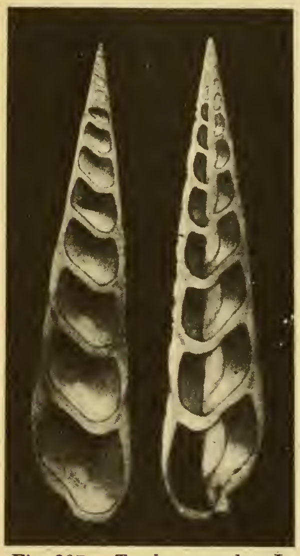


Fig. 397. *Terebra maculata* L.

The angle, or rather semi-angle (β), of the tangent cone may be taken as 90° in the discoid shells, such as *Nautilus* and *Planorbis*. It is still a large angle, of 70° or 75°, in *Conus* or in *Cymba*, somewhat less in *Cassis*, *Harpa*, *Dolium* or *Natica*; it is about 50° to 55° in the various species of *Solarium*, about 35° in the typical *Trochi*, such as *T. niloticus* or *T. zizyphinus*, and about 25° or 26° in *Scalaria pretiosa* and *Phasianella bulloides*; it becomes a very acute angle, of 15°, 10°, or even less, in *Eulima*, *Turritella* or *Cerithium*. The British species of '*Fusus*' form a series in which the apical angle ranges from about 28° in *F. antiquus*, through *F. Norvegicus*, *F. berniciensis*, *F. Turtoni*, *F. Islandicus*, to about 17° in *F. gracilis*. It varies much among the Cones; and the costly *Conus gloria-maris*, one of the great treasures of the conchologist, differs from its congeners in no important particular save in the somewhat "produced" spire, that is to say in the comparatively low value of the angle β.

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

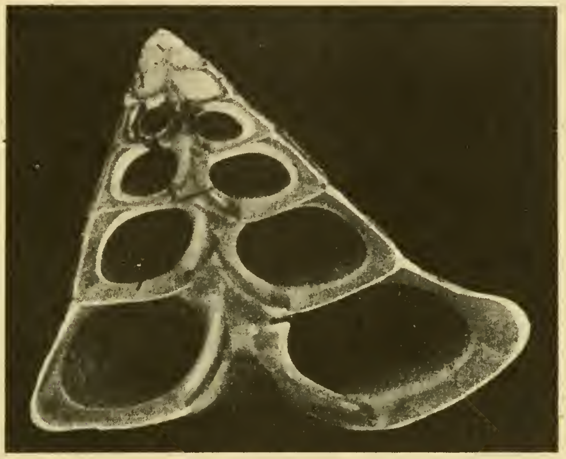


Fig. 398. *Trochus niloticus* L.

it in *Cerithium*, and in the cusp-like spire of *Cassis*, *Dolium* and some Cones, is much the commoner of the two*.

In the vast majority of spiral univalves the shell winds to the right, or turns clockwise, as we look along it in the direction in which the animal crawls and puts out its head. The thread of a carpenter's screw (except in China) runs the same way, and we call it a "right-handed screw." Save that it takes a right-handed movement to

* Many measurements of the linear dimensions of univalve shells have been made of late years, and studied by statistical methods in order to detect local races and other instances of variation and variability. But conchological statisticians seem to be content with some arbitrary linear ratio as a measure of "squatness" or the reverse; and the measurements chosen give little or no help towards the determination either of the apical or of the spiral angle. Cf. (e.g.) A. E. Boycott, Conchometry, *Proc. Malacol. Soc.* XVII, p. 8, 1928; C. Price-Jones, *ibid.* XIX, p. 146, 1930; etc. See also G. Duncker, Methode der Variations-Statistik, *Arch. f. Entw. Mech.* VIII, pp. 112–183, 1899.

drive in a "right-handed" screw, the terms right-handed and left-handed are purely conventional; and the mathematicians and the naturalists, unfortunately, use them in opposite ways. Thus the mathematicians call the snail-shell or the joiner's screw *leiotropic*; and Listing for one has much to say about lack of precision or even confusion on the part of the conchologists and the botanists, from Linnaeus downwards, in their attempts to deal with right-handed and left-handed spirals or screws*. The convolvulus twines to the right, the hop to the left; vine-tendrils are said to be mostly right-handed. At any rate, Clerk Maxwell spoke of *hop-spirals* and *vine-spirals*, trying to avoid the confusion or ambiguity of left and right. Some climbing plants are one and some the other; and the architect shews little preference, but builds his spiral staircases or twisted columns either way. But in all these, shells and all, the spiral runs *one way*; it is *isotropic*, while the fir-cone shews spirals running both ways at once, and we call them *heterotropic*, or *diadromic*.

When we find a "reversed shell," a whelk or a snail winding the wrong way, we describe it mathematically by the simple statement that the apical angle (β) has changed sign. Such left-handed shells occur as a well-known but rare abnormality; and the men who handle snails in the Paris market or whelks in Billingsgate keep a sharp look-out for them. In rare instances they become common. While left-handed whelks (*Buccinum* or *Neptunea*) are very rare nowadays, it was otherwise in the epoch of the Red Crag; for *Neptunea* was then extremely common, but right-handed specimens were as rare as left-handed are today. In the beautiful genus *Ampullaria*, or apple-snails, which inhabit tropical and sub-tropical rivers, there is unusual diversity; for the spire turns to the right in some species, and to the left in others, and again some are flat or "discoid," with no spire at all; and there are plenty of half-way stages, with right and left-handed spires of varying steepness or acuteness†; in short, within the limits of this singular genus the apical angle (β) may vary from about $\pm 35°$ to $\pm 125°$. But we need not imagine that the direction of growth actually changes over from right-handed to left-handed; it is enough to suppose

* See Listing's *Topologie*, p. 36; and cf. Clerk Maxwell's *Electricity and Magnetism*, I, p. 24.

† See figures in Arnold Lang's *Comparative Anatomy* (English translation), II, p. 161, 1902.

that the skew movement along the axis has changed its direction. For if I take a roll of tape and push the core out to one side or to the other, or if I keep the centre of the roll fixed and push the rim to the one side or to the other, I thereby convert the flat roll into a hollow cone, or (in other words) a plane into a gauche spiral. Whether we push one way or other, whether the spiral coil be plane or gauche, positively or negatively deformed, it remains right-handed or left-handed as the case may be; but it does change its direction as soon as we *turn it upside down*, or as soon as the animal does so in assuming its natural attitude. The linear spirals within and without the cone may change places but must remain congruent with one another; for they are merely the two edges of the ribbon, and as such are inseparable and identical twins. But of the shell itself we may reasonably say that a right-handed has given place to a left-handed spiral. Of these, the one is a mirror-image of the other; and the passing from one to the other through the plane of symmetry (which has no "handedness") is an operation which Listing called *perversion*. The flat or discoid apple-snails are like our roll of tape, which can be *converted* into a conical spire and *perverted* in one direction or the other; and in this genus, by a rare exception, it seems wellnigh as easy to depart one way as the other from the plane of symmetry. But why, in the general run of shells, all the world over, in the past and in the present, one direction of twist is so overwhelmingly commoner than the other, no man knows.

The phenomenon of reversal, or "sinistrality," has an interest of its own from the side of development and heredity. For careful study of certain pond-snails has shewn that dextral and sinistral varieties appear, not one by one, but by whole broods of the one sort or the other; a discovery which goes some way to account for the predominant left-handedness of *Fusus ambiguus* in the Red Crag. The right-handed, or ordinary form, is found to be "dominant" to the other; but the Mendelian heredity is of a curious and complicated kind. For the direction of the twist appears to be predetermined in the germ even prior to its fertilisation; and a left-handed pond-snail will produce a brood of left-handed young even when fertilised by a normal, or right-handed, individual*.

* See A. E. Boycott and others, Abnormal forms of *Limnaea peregra*...and their inheritance, *Phil. Trans.* (B), CCXXIX, p. 51, 1930; and other papers.

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. But with these phenomena we have already dealt sufficiently.

The beautiful shell of the paper-nautilus (*Argonauta argo* L.) differs in sundry ways both from the Nautilus and from ordinary univalves. Only the female Argonaut possesses it; it is not attached to its owner, but is (so to speak) worn loose; it is rather a temporary cradle for the young than a true shell or bodily covering; and it is not secreted in the usual way, but is plastered on from the outside by two of the eight arms of the little Octopus to which it belongs. The shell shews a single whorl, or but little more; and the spiral is hard to measure, for this reason. It has been supposed by some to obey a law other than the logarithmic spiral. For my part I have made no special study of it, nor has any one else, to my knowledge, of recent years; but the simple fact that it conserves its shape as it grows, or that each increment is a gnomon to the rest, is enough to shew that this delicate and beautiful shell is mathematically, though not morphologically, homologous with all the others.

Of bivalve shells

Hitherto we have dealt only with univalve shells, and it is in these that all the mathematical problems connected with the spiral, or helico-spiral, configuration are best illustrated. But the case of the bivalve shell, whether of the lamellibranch or the brachiopod, presents no essential difference, save only that we have here to do with two conjugate spirals, whose two axes have a definite relation to one another, and some independent freedom of rotatory movement relatively to one another.

The bivalve or lamellibranch mollusca are very different creatures from the rest. The univalves or gastropods, like their cousins the cephalopods, go about their business and get their living in an ordinary way; but the bivalves are unintelligent, "acephalous" animals, and imbibe the invisible plankton-food which ciliary currents bring automatically to their mouths. There is something

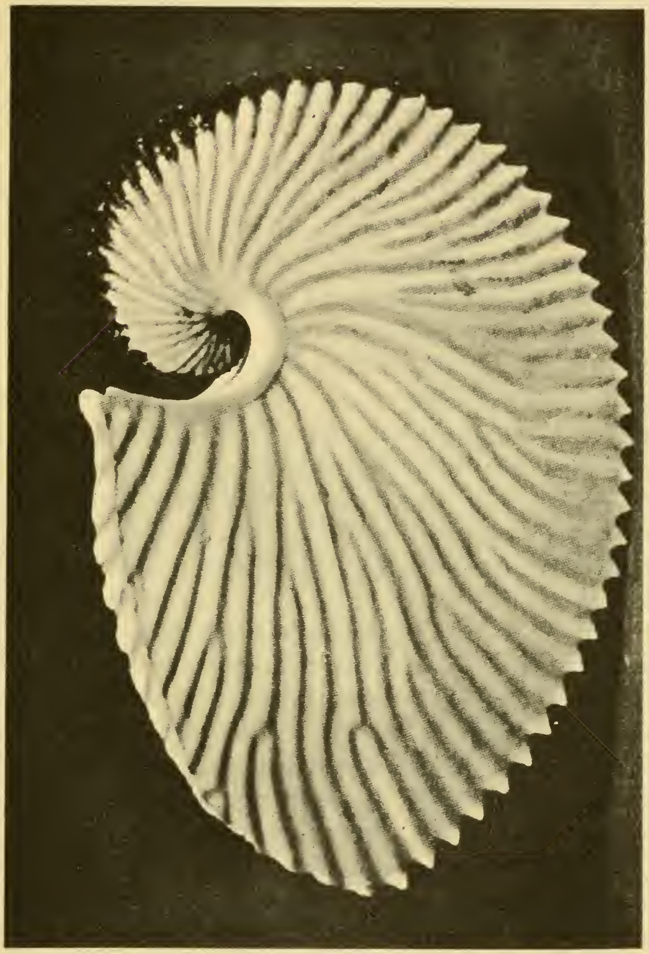


Fig. 399. *Argonauta argo* L. The paper-nautilus. From Cooke's *Spirals in Nature and Art.*

to be said for withdrawing them, as brachiopods and others have been withdrawn, from Cuvier's great class of the Mollusca. But whether bivalves and univalves be near relations or no is not the question. Both of them secrete a shell, and in both the shell grows by the successive addition of similar parts, gnomon after gnomon; so that in both the equiangular spiral makes, and is bound to make, its appearance. There is a mathematical analogy between the two; but it has no more bearing on zoological classification than has the still closer likeness between Nautilus and the nautiloid Foraminifera.

The generating curve is particularly well seen in the bivalve, where it simply constitutes what we call "the outline of the shell." It is for the most part a plane curve, but not always; for there are forms such as *Hippopus*, *Tridacna* and many Cockles, or *Rhynchonella* and *Spirifer* among the Brachiopods, in which the edges of the two valves interlock, and others, such as *Pholas*, *Mya*, etc., where they gape asunder. In such cases as these the generating curves, though not plane, are still conjugate, having a similar relation, but of opposite sign, to a median plane of reference or of projection. There are a few exceptional cases, e.g. *Arca* (*Parallelepipedon*) *tortuosa*, where there is no median plane of symmetry, but the generating curve, and therefore the outline of the shell itself, is a tortuous curve in three dimensions.

A great variety of form is exhibited among the bivalves by these generating curves. In many cases the curve or outline is all but circular, as in *Anomia*, *Sphaerium*, *Artemis*, *Isocardia*; it is nearly semicircular in *Argiope*; it is approximately elliptical in *Anodon*, *Lutraria*, *Orthis*; it may be called semi-elliptical in *Spirifer*; it is a nearly rectilinear triangle in *Lithocardium*, and a curvilinear triangle in *Mactra*. Many apparently diverse but more or less related forms may be shewn to be deformations of a common type, by a simple application of the mathematical theory of "transformations," which we shall have to study in a later chapter. In such a series as is furnished, for instance, by *Gervillea*, *Perna*, *Avicula*, *Modiola*, *Mytilus*, etc., a "simple shear" accounts for most, if not all, of the apparent differences.

Upon the surface of the bivalve shell we usually see with great clearness the "lines of growth" which represent the successive margins of the shell, or in other words the successive positions assumed during growth by the growing generating curve; and we have a good illustration, accordingly, of how it is characteristic of the generating curve that it should constantly increase, while never altering its geometric similarity.

Underlying these lines of growth, which are so characteristic of a molluscan shell (and of not a few other organic formations), there is, then, a law of growth which we may attempt to enquire into and which may be illustrated in various ways. The simplest cases are those in which we can study the lines of growth on a more or less flattened shell, such as the one valve of an oyster, a *Pecten* or a *Tellina*, or some such bivalve mollusc. Here around an origin, the so-called "umbo" of the shell, we have a series of curves, sometimes nearly circular, sometimes elliptical, often asymmetrical; and such curves are obviously not "concentric," though we are often apt to call them so, but have a common centre of similitude. This arrangement may be illustrated by various analogies. We might for instance compare it to a series of waves, radiating outwards from a point, through a medium which offered a resistance increasing, with the angle of divergence, according to some simple law. We may find another and perhaps a simpler illustration as follows:

In a simple and beautiful theorem, Galileo shewed that, if we imagine a number of inclined planes, or gutters, sloping downwards (in a vertical plane) at various angles from a common starting-point, and if we imagine a number of balls rolling each down its own gutter under the influence of gravity (and without hindrance from friction), then, at any given instant, the locus of all these moving bodies is a circle passing through the point of origin. For the acceleration along any one of the sloping paths, for instance AB (Fig. 400), is such that

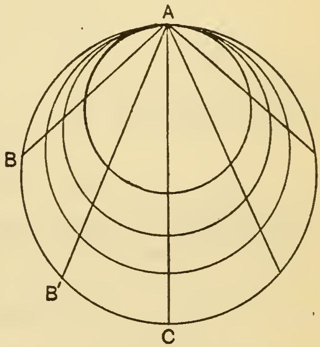


Fig. 400.

$$AB = \tfrac{1}{2}g\cos\theta\,.\,t^2$$
$$= \tfrac{1}{2}g\,.\,AB/AC\,.\,t^2.$$

Therefore $$t^2 = 2/g\,.\,AC.$$

That is to say, all the balls reach the circumference of the circle at the same moment as the ball which drops vertically from A to C.

Where, then, as often happens, the generating curve of the shell is approximately a circle passing through the point of origin, we may consider the acceleration of growth along various radiants to be governed by a simple mathematical law, closely akin to that simple law of acceleration which governs the movements of a falling body. And, *mutatis mutandis*, a similar definite law underlies the cases where the generating curve is continually elliptical, or where it assumes some more complex, but still regular and constant form.

It is easy to extend the proposition to the particular case where the lines of growth may be considered elliptical. In such a case we have $x^2/a^2 + y^2/b^2 = 1$, where a and b are the major and minor axes of the ellipse.

Or, changing the origin to the vertex of the figure,

$$\frac{x^2}{a^2} - \frac{2x}{a} + \frac{y^2}{b^2} = 0, \quad \text{giving} \quad \frac{(x-a)^2}{a^2} + \frac{y^2}{b^2} = 1.$$

Then, transferring to polar coordinates, where $r.\cos\theta = x$, $r.\sin\theta = y$, we have

$$\frac{r.\cos^2\theta}{a^2} - \frac{2\cos\theta}{a} + \frac{r.\sin^2\theta}{b^2} = 0,$$

which is equivalent to

$$r = \frac{2ab^2\cos\theta}{b^2\cos^2\theta + a^2\sin^2\theta},$$

or, simplifying, by eliminating the sine-function,

$$r = \frac{2ab^2\cos\theta}{(b^2 - a^2)\cos^2\theta + a^2}.$$

Obviously, in the case when $a = b$, this gives us the circular system which we have already considered. For other values, or ratios, of a and b, and for all values of θ, we can easily construct a table, of which the following is a sample:

Chords of an ellipse, whose major and minor axes (a, b) are in certain given ratios

θ	$a/b = 1/3$	1/2	2/3	1/1	3/2	2/1	3/1
0°	1·0	1·0	1·0	1·0	1·0	1·0	1·0
10	1·01	1·01	1·002	0·985	0·948	0·902	0·793
20	1·05	1·03	1·005	0·940	0·820	0·695	0·485
30	1·115	1·065	1·005	0·866	0·666	0·495	0·289
40	1·21	1·11	0·995	0·766	0·505	0·342	0·178
50	1·34	1·145	0·952	0·643	0·372	0·232	0·113
60	1·50	1·142	0·857	0·500	0·258	0·152	0·071
70	1·59	1·015	0·670	0·342	0·163	0·092	0·042
80	1·235	0·635	0·375	0·174	0·078	0·045	0·020
90	0·0	0·0	0·0	0·0	0·0	0·0	0·0

The ellipses which we then draw, from the values given in the table, are such as are shewn in Fig. 401 for the ratio $a/b = \frac{3}{1}$, and in Fig. 402 for the ratio $a/b = \frac{1}{2}$; these are fair approximations to the actual outlines, and to the actual arrangement of the lines of growth, in such forms as *Solecurtus* or *Cultellus*, and in *Tellina* or *Psammobia*. It is not difficult to introduce a constant into our equation to meet the case of a shell which is somewhat unsymmetrical on either side of the median axis. It is a somewhat more troublesome matter, however, to bring these configurations into relation with a "law of growth," as was so easily done in the case of the circular figure: in other words, to formulate a law of acceleration according to which points starting from the origin O, and moving along radial lines, would all lie, at any future epoch, on an ellipse passing through O; and this calculation we need not enter into.

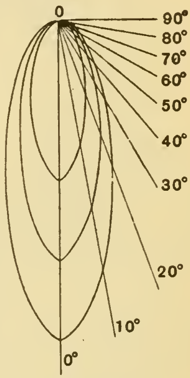


Fig. 401.

All that we are immediately concerned with is the simple fact that where a velocity, such as our rate of growth, varies with its direction—varies that is to say as a function of the angular divergence from a certain axis—then, in a certain simple case, we get lines of growth laid down as a system of coaxial circles, and, in somewhat less simple cases, we obtain a system of ellipses or of other more complicated coaxial figures, which may or may not be symmetrical on either side of the axis. Among our bivalve mollusca we shall find the lines of growth to be approximately circular in, for instance, *Anomia*; in *Lima* (e.g. *L. subauriculata*) we have a system of nearly symmetrical ellipses with the vertical axis about twice the transverse; in *Solen pellucidus*, we have again a system of lines of growth which are not far from being symmetrical ellipses,

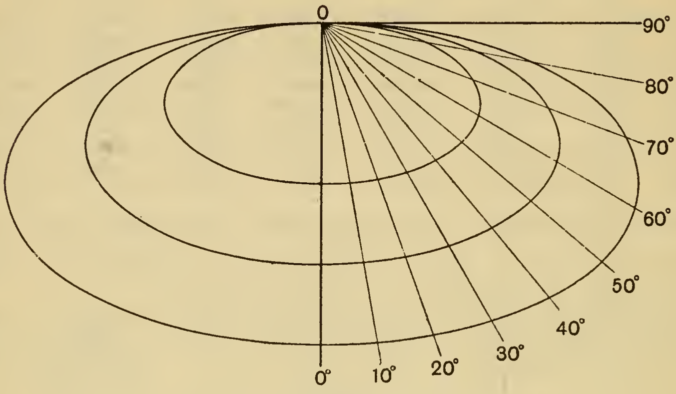


Fig. 402.

in which however the transverse is between three and four times as great as the vertical axis. In the great majority of cases, we have a similar phenomenon with the further complication of slight, but occasionally very considerable, lateral asymmetry.

In the above account of the mathematical form of the bivalve shell, we have supposed, for simplicity's sake, that the pole or origin of the system is at a point where all the successive curves touch one another. But such an arrangement is neither theoretically probable, nor is it actually the case; for it would mean that in a certain direction growth fell, not merely to a minimum, but to zero. As a matter of fact, the centre of the system (the "umbo" of the conchologists) lies not at the edge of the system, but very near to it; in other words, there is a certain amount of growth all round. But to take account of this condition would involve more troublesome mathematics, and it is obvious that the foregoing illustrations are a sufficiently near approximation to the actual case.

In certain little Crustacea (of the genus *Estheria*) the carapace takes the form of a bivalve shell, closely simulating that of a lamellibranchiate mollusc, and bearing lines of growth in all respects analogous to or even identical with those of the latter. The explanation is very curious and interesting. In ordinary Crustacea the carapace, like the rest of the chitinised and calcified integument, is shed off in successive moults, and is restored again as a whole. But in *Estheria* (and one or two other small crustacea) the moult is incomplete: the old carapace is retained, and the new, growing up underneath it, adheres to it like a lining, and projects beyond its edge: so that in course of time the margins of successive old carapaces appear as "lines of growth" upon the surface of the shell. In this mode of formation, then (but not in the usual one), we obtain a structure which "is partly old and partly new," and whose successive increments are all similar, similarly situated, and enlarged

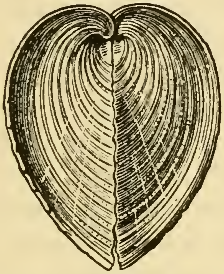


Fig. 403. *Hemicardium inversum* Lam. From Chenu.

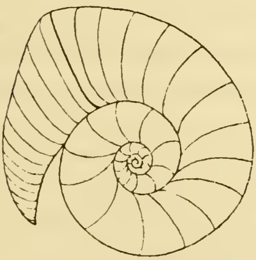


Fig. 404. *Caprinella adversa.* After Woodward.

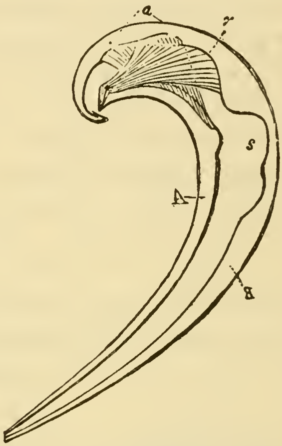


Fig. 405. Section of *Productus* (*Strophonema*) sp. From Woods.

in a continued progression. We have, in short, all the conditions appropriate and necessary for the development of a logarithmic spiral; and this logarithmic spiral (though it is one of small angle) gives its own character to the structure, and causes the little carapace to partake of the characteristic conformation of the molluscan shell.

Among the bivalves the spiral angle (α) is very small in the flattened shells, such as *Orthis*, *Lingula* or *Anomia*. It is larger, as a rule, in the Lamellibranchs than in the Brachiopods, but in the latter it is of considerable magnitude among the Pentameri.

Among the Lamellibranchs it is largest in such forms as *Isocardia* and *Diceras*, and in the very curious genus *Caprinella*; in all of these last-named genera its magnitude leads to the production of a spiral shell of several whorls, precisely as in the univalves. The angle is usually equal, but of opposite sign, in the two valves of the Lamellibranch, and usually of opposite sign but unequal in the two valves of the Brachiopod. It is very unequal in many Ostreidae, and especially in such forms as *Gryphaea*, or in *Caprinella*, which is a kind of exaggerated *Gryphaea*; in the cretaceous genus *Requienia*, the two valves of the shell closely resemble a turbinate gastropod with its flat calcified operculum. Occasionally it is of the same sign in both valves (that is to say, both valves curve the same way) as we see sometimes in *Anomia*, and better in *Productus* or *Strophonema*.

It will be observed, and it may not be difficult to explain, that the more the bivalve shell curves in the one direction the more it curves in the other; each valve tends to be spheroidal, or ellipsoidal, rather than cylindroidal. The cylindroidal form occurs, exceptionally, in *Solen*. But *Pecten*, *Gryphaea*, *Terebratula* are all cases of bivalve shells where one valve is flat and the other curved from *side to side*; and the flat valve tends to remain flat in the longitudinal direction also, while the curved valve grows into its logarithmic spiral.

In the genus *Gryphaea*, an oyster-like bivalve from the Jurassic, the creature lay on its side with its left valve downward, as oysters and scallops also do; and this valve adhered to the ground while the animal was young. The upper valve stays flat, and looks like a mere operculum; but the lower or deep valve grows into a more or less pronounced spiral. So is it also in the neighbouring genus *Pecten*, where *P. Jacobaeus* has its under-valve much deeper and more curved than, say, *P. opercularis*; but *Gryphaea incurva* is more spirally curved than any of these, and *G. arcuata* has a spiral angle very near to that of *Nautilus* itself. In both the spiral is a typical equiangular one, built up of a succession of gnomonic increments, which in turn depend on a constant ratio between the expansion of a generating figure and its rotation about a centre of similitude. *Rate of growth* is at the root of the whole matter. Now *Gryphaea*, like some Ammonites of which we spoke before, is one of those cases in which not only does the form of the shell vary, but geologists recognise, now and then, a *trend*, or progressive sequence of variation, from one stratum or one "horizon" to another. In short, *as time goes on*, we seem to see the shell growing thicker or wider, or more and more spirally curved, before our eyes. What meaning shall we give, what importance should we assign, to these changes, and what sort or grade of evolution do they imply? Some hold that these palaeontological features are "strictly comparable with those on which the geneticist bases his factorial studies"; and that as such they may shew "linkage of characters," as when "in the evolution of *Gryphaea* the area of attachment retrogresses as the arching progresses"*. These are debatable matters. But in so far as the changes depend on mere gradations of magnitude, they lead indeed to variety but fall short of the full concept of evolution. For to quote Aristotle once again (though we need not go to Aristotle to learn it): "some things shew increase but suffer no alteration; because increase is one thing and alteration is another."

The so-called "spiral arms" of *Spirifer* and many other Brachiopods are not difficult to explain. They begin as a single structure, in the form of a loop of shelly substance, attached to the dorsal valve of the shell, in the neighbourhood of the hinge, and forming a skeletal support for two ciliate and tentaculate arms. These grow to a considerable length, coiling up within the shell that they may do so. In *Terebratula* the loop remains short and simple, and is merely flattened and distorted somewhat by the restraining pressure of the ventral valve; but in *Spirifer*, *Atrypa*, *Athyris* and many more it forms a watchspring coil on either side, corresponding to the close-coiled arms of which it was the support and skeleton. In these curious and characteristic structures we see no sign of progressive

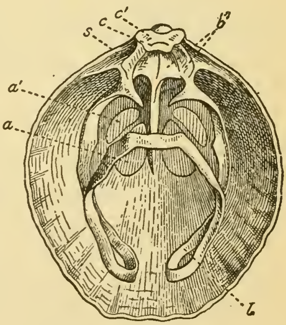


Fig. 406. Skeletal loop of *Terebratula*. From Woods.

* H. H. Swinnerton, Unit characters in fossils, *Biol. Reviews*, VII, pp. 321–335, 1932; cf. A. E. Truman, *Geol. Mag.* LIX, p. 258, LXI, p. 358, 1922–24.

growth, no successional increments, no "gnomons," no self-similarity in the figure. In short it has nothing to do with a logarithmic or equiangular spiral, but is a mere twist, or tapering helix, and it points now one way, now another. The cases in which the helicoid spires point towards, or point away from, the middle line are ascribed, in zoological classification, to particular "families" of Brachiopods, the former condition defining (or helping to define) the Atrypidae and the latter the Spiriferidae

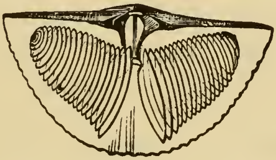


Fig. 407. Spiral arms of *Spirifer*.

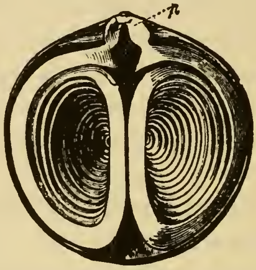


Fig. 408. Inwardly directed spiral arms of *Atrypa*.

and Athyridae. It is obvious that the incipient curvature of the arms, and consequently the form and direction of the spirals, will be influenced by the surrounding pressures, and these in turn by the general shape of the shell. We shall expect, accordingly, to find the long outwardly directed spirals associated with shells which are transversely elongated, as *Spirifer* is; while the more rounded *Atrypa* will tend to the opposite condition. In a few cases, as in *Cyrtina* or *Reticularia*, where the shell is comparatively narrow but long, and where the uncoiled basal support of the arms is long also, the coils into which the latter grow are turned backwards, in the direction where there is most room for them. And in the few cases where the shell is very considerably flattened, the spirals (if they find room to grow at all) will be constrained to do so in a discoid or nearly discoid fashion, and this is actually the case in such flattened forms as *Koninckina* or *Thecidium*.

The shells of Pteropods

While mathematically speaking we are entitled to look upon the bivalve shell of the Lamellibranch as consisting of two distinct elements, each comparable to the entire shell of the univalve, we have no biological grounds for such a statement; for the shell arises from a single embryonic origin, and afterwards becomes split into portions which constitute the two separate valves. We can perhaps throw some indirect light upon this phenomenon, and upon several other phenomena connected with shell-growth, by a consideration of the simple conical or tubular shells of the Pteropods. The shells of the latter are in few cases suitable for simple mathematical investigation, but nevertheless they are of very considerable interest in connection with our general problem. The morphology of the Pteropods is bv no means well understood, and in speaking of them

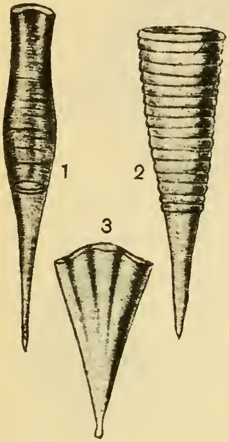


Fig. 409. Pteropod shells: (1) *Cuvierina columnella*; (2) *Cleodora chierchiae*; (3) *C. pygmaea*. After Boas.

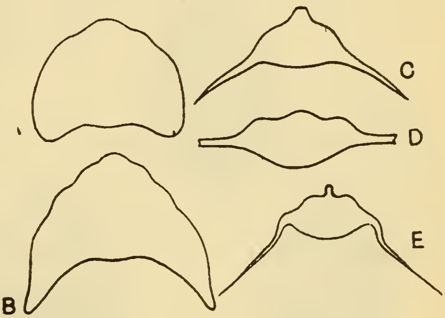


Fig. 410. Diagrammatic transverse sections, or outlines of the mouth, in certain Pteropod shells: A, B, *Cleodora australis*; C, *C. pyramidalis*; D, *C. balantium*; E, *C. cuspidata*. After Boas.

I will assume that there are still grounds for believing (in spite of Boas' and Pelseneer's arguments) that they are directly related to, or may at least be directly compared with, the Cephalopoda*.

The simplest shells among the Pteropods have the form of a tube, more or less cylindrical (*Cuvierina*), more often conical (*Creseis*, *Clio*); and this tubular shell (as we have already had occasion to remark, on p. 416), frequently tends, when it is very small and delicate, to assume the character of an unduloid. (In such a case it is more than likely that the tiny shell, or that portion of it which

* We need not assume a *close* relationship, nor indeed any more than such a one as permits us to compare the shell of a *Nautilus* with that of a Gastropod.

constitutes the unduloid, has not grown by successive increments or "rings of growth," but has developed as a whole.) A thickened "rib" is often, perhaps generally, present on the dorsal side of the little conical shell. In a few cases (*Limacina*, *Peraclis*) the tube becomes spirally coiled, in a normal equiangular spiral or helicospiral.

In certain cases (e.g. *Cleodora*, *Hyalaea*) the tube or cone is curiously modified. In the first place, its cross-section, originally circular or nearly so, becomes flattened or compressed dorsoventrally; and

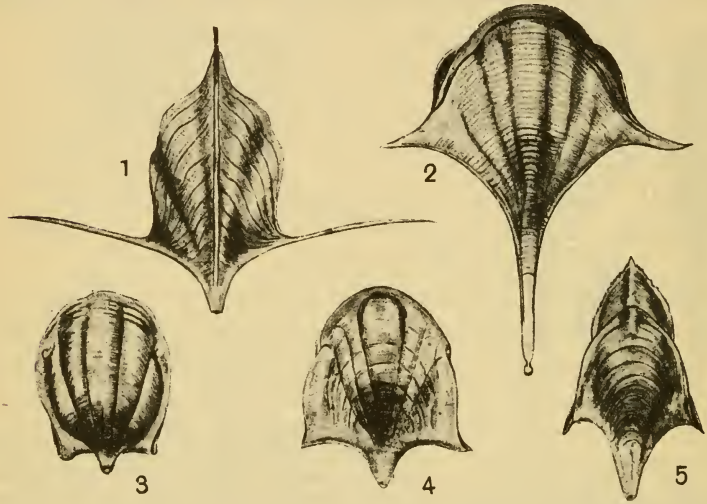


Fig. 411. Shells of thecosome Pteropods (after Boas). (1) *Cleodora cuspidata*; (2) *Hyalaea trispinosa*; (3) *H. globulosa*; (4) *H. uncinata*; (5) *H. inflexa*.

the angle, or rather edge, where dorsal and ventral walls meet, becomes more and more drawn out into a ridge or keel. Along the free margin, both of the dorsal and the ventral portion of the shell, growth proceeds with a regularly varying velocity, so that these margins, or lips, of the shell become regularly curved or markedly sinuous. At the same time, growth in a transverse direction proceeds with an acceleration which manifests itself in a curvature of the sides, replacing the straight borders of the original cone. In other words, the cross-section of the cone, or what we have been calling the generating curve, increases its dimensions more rapidly than its distance from the pole.

In the above figures, for instance in that of *Cleodora cuspidata*, the markings of the shell which represent the successive edges of the lip at former stages of growth furnish us at once with a "graph"

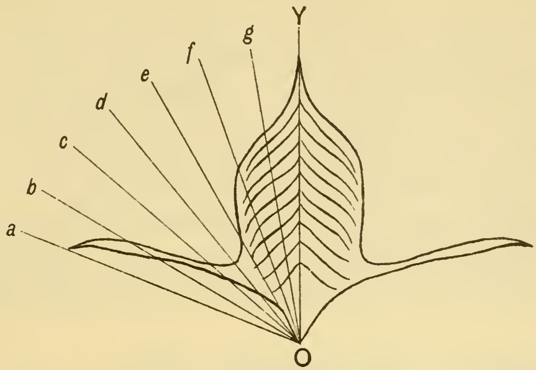


Fig. 412. *Cleodora cuspidata.*

of the varying velocities of growth as measured, radially, from the apex. We can reveal more clearly the nature of these variations in the following way, which is simply tantamount to converting our radial into rectangular coordinates. Neglecting curvature (if any)

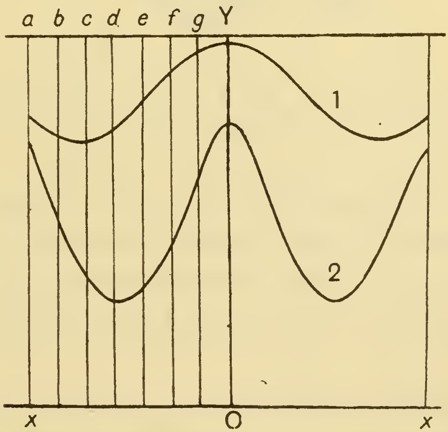


Fig. 413. Curves obtained by transforming radial ordinates, as in Fig. 412, into vertical equidistant ordinates. 1, *Hyalaea trispinosa*; 2, *Cleodora cuspidata*.

of the sides and treating the shell (for simplicity's sake) as a right cone, we lay off equal angles from the apex O, along the radii Oa, Ob, etc. If we then plot, as vertical equidistant ordinates, the magnitudes Oa, Ob ... OY, and again on to Oa', we obtain a diagram such as follows in Fig. 413: by help of which we not only see more clearly the way in which the growth-rate varies from point to point, but we also recognise better than before the nature of the law which governs this variation in the different species.

Furthermore, the young shell having become differentiated into a dorsal and a ventral part, marked off from one another by a lateral edge or keel, and the inequality of growth being such as to cause each portion to increase most rapidly in the median line, it follows that the entire shell will appear to have been split into a dorsal and a ventral plate, both connected with, and projecting from, what remains of the original undivided cone. Putting the same thing in other words, we may say that the generating figure, which

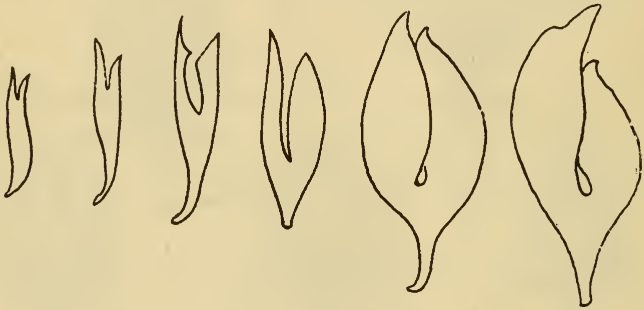


Fig. 414. Development of the shell of *Hyalaea* (*Cavolinia*) *tridentata* Forskal: the earlier stages being the "*Pleuropus longifilis*" of Troschel. After Tesch.

lay at first in a plane perpendicular to the axis of the cone, has now, by unequal growth, been sharply bent or folded, so as to lie approximately in two planes, parallel to the anterior and posterior faces of the cone. We have only to imagine the apical connecting portion to be further reduced, and finally to disappear or rupture, and we should have a *bivalve shell* developed out of the original simple cone.

In its outer and growing portion, the shell of our Pteropod now consists of two parts which, though still connected together at the apex, may be treated as growing practically independently. The shell is no longer a simple tube, or simple cone, in which regular inequalities of growth will lead to the development of a spiral; and this for the simple reason that we have now two opposite maxima of growth, instead of a maximum on the one side and a minimum on the other side of our tubular shell. As a matter of fact, the dorsal and the ventral plate tend to curve in opposite directions, towards the middle line, the dorsal curving ventrally and the ventral curving towards the dorsal side.

In the case of the Lamellibranch or the Brachiopod, it is quite possible for both valves to grow into more or less pronounced spirals, for the simple reason that they are *hinged* upon one another; and each growing edge, instead of being brought to a standstill by the growth of its opposite neighbour, is free to move out of the way, by the rotation about the hinge of the plane in which it lies.

But where there is no such hinge, as in the Pteropod, the dorsal and ventral halves of the shell (or dorsal and ventral valves, if we

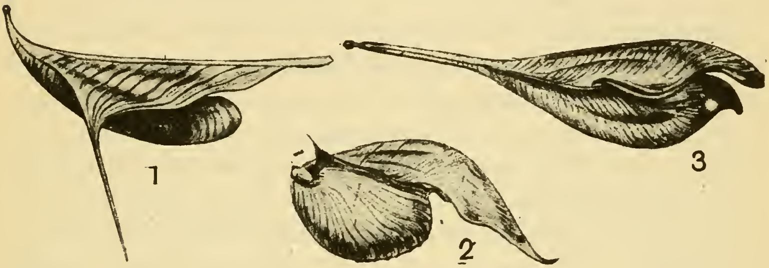


Fig. 415. Pteropod shells, from the side: (1) *Cleodora cuspidata*; (2) *Hyalaea longirostris*; (3) *H. trispinosa*. After Boas.

may call them so) would soon interfere with one another's progress if they curved towards one another (as they do in a cockle), and the development of a pair of conjugate spirals would become impossible. Nevertheless, there is obviously, in both dorsal and ventral valve, a *tendency* to the development of a spiral curve, that of the ventral valve being more marked than that of the larger and overlapping dorsal one, exactly as in the two unequal valves of *Terebratula*. In many cases (e.g. *Cleodora cuspidata*), the dorsal valve or plate, strengthened and stiffened by its midrib, is nearly straight, while the curvature of the other is well displayed. But the case will be materially altered and simplified if growth be arrested or retarded in either half of the shell. Suppose for instance that the dorsal valve grew so slowly that after a while, in comparison with the other, we might speak of it as being absent altogether:

or suppose that it merely became so reduced in relative size as to form no impediment to the continued growth of the ventral one; the latter would continue to grow in the direction of its natural curvature, and would end by forming a complete and coiled logarithmic spiral. It would be precisely analogous to the spiral shell of *Nautilus*, and, in regard to its ventral position, concave towards the dorsal side, it would even deserve to be called directly homologous with it. Suppose, on the other hand, that the ventral valve were to be greatly reduced, and even to disappear, the dorsal valve would then pursue its unopposed growth; and, were it to be markedly curved, it would come to form a logarithmic spiral, concave towards the ventral side, as is the case in the shell of *Spirula**. Were the dorsal valve to be destitute of any marked curvature (or in other words, to have but a low spiral angle), it would form a simple plate, as in the shells of *Sepia* or *Loligo*. Indeed, in the shells of these latter, and especially in that of *Sepia*, we seem to recognise a manifest resemblance to the dorsal plate of the Pteropod shell, as we have it (e.g.) in *Cleodora* or *Hyalaea*; the little "rostrum" of *Sepia* is but the apex of the primitive cone, and the rounded anterior extremity has grown according to a law precisely such as that which has produced the curved margin of the dorsal valve in the Pteropod. The ventral portion of the original cone is nearly, but not wholly, wanting; it is represented by the so-called posterior wall of the "siphuncular space." In many decapod cuttle-fishes also (e.g. *Todarodes*, *Illex*, etc.) we still see at the posterior end of the "pen" a vestige of the primitive cone, whose dorsal margin only has continued to grow; and the same phenomenon, on an exaggerated scale, is represented in the *Belemnites*.

It is not at all impossible that we may explain on the same lines the development of the curious "operculum" of the Ammonites. This consists of a single horny plate (*Anaptychus*), or of a thicker, more calcified plate divided into two symmetrical halves (*Aptychi*), often found inside the terminal chamber of the Ammonite, and occasionally to be seen lying *in situ*, as an operculum which partially closes the mouth of the shell; this structure is known to exist even

* Cf. Owen, "These shells [*Nautilus* and Ammonites] are revolutely spiral or coiled over the back of the animal, not involute like *Spirula*": *Palaeontology*, 1861, p. 97; cf. *Memoir on the Pearly Nautilus*, 1832; also *P.Z.S.* 1878, p. 955.

in connection with the early embryonic shell. In form the Anaptychus, or the pair of conjoined Aptychi, shew an upper and a lower border, the latter strongly convex, the former sometimes slightly concave, sometimes slightly convex, and usually shewing a median projection or slightly developed rostrum. From this rostral border the curves of growth start, and course round parallel to, finally constituting, the convex border. It is this convex border which fits into the free margin of the mouth of the Ammonite's shell, while the other is applied to and overlaps the preceding whorl of the spire. Now this relationship is precisely what we should expect, were we to imagine as our starting-point a shell similar to that of *Hyalaea*: in which however the dorsal part of the split cone had become separate from the ventral half, had remained flat, and had grown comparatively slowly, while at the same time it kept slipping forward over the growing and coiling spire into which the ventral half of the original shell develops*. In short, I think there is reason to believe, or at least to suspect, that we have in the shell and Aptychus of the Ammonites, two portions of a once united structure; of which other Cephalopods retain not both parts but only one or other, one as the ventrally situated shell of *Nautilus*, the other as the dorsally placed shell for example of *Sepia* or of *Spirula*.

In the case of the bivalve shells of the Lamellibranchs or of the Brachiopods, we have to deal with a phenomenon precisely analogous to the split and flattened cone of our Pteropods, save only that the primitive cone has been split into two portions, not incompletely, as in the Pteropod (*Hyalaea*), but completely, so as to form two separate valves. Though somewhat greater freedom is given to growth now that the two valves are separate and hinged, yet still the two valves oppose and hamper one another, so that in the longitudinal direction each is capable of only a moderate curvature. This curvature, as we have seen, is recognisable as an equiangular spiral, but only now and then does the growth of the spiral continue so far as to develop successive coils: as it does in a few symmetrical forms such as *Isocardia cor*; and as it does still more conspicuously in a few others, such as *Gryphaea* and *Caprinella*, where one of the

* The case of *Terebratula* or of *Gryphaea* would be closely analogous, if the smaller valve were less closely connected and co-articulated with the larger.

two valves is stunted, and the growth of the other is (relatively speaking) unopposed.

Of septa

Before we leave the subject of the molluscan shell, we have still another problem to deal with, in regard to the form and arrangement of the septa which divide up the tubular shell into chambers, in the Nautilus, the Ammonite and their allies.

The existence of septa in a nautiloid shell may probably be accounted for as follows. We have seen that it is a property of a cone that, while growing by increments at one end only, it conserves its original shape: therefore the animal within, which (though growing by a different law) also conserves its shape, will continue to fill the shell if it actually fills it to begin with: as does a snail or other Gastropod. But suppose that our mollusc fills a part only of a conical shell (as it does in the case of *Nautilus*); then, unless it alter its shape, it must move upward as it grows in the growing cone, until it comes to occupy a space similar in form to that which it occupied before: just, indeed, as a little ball drops far down into the cone, but a big one must stay farther up. Then, when the animal after a period of growth has moved farther up in the shell, the mantle-surface continues or resumes its secretory activity, and that portion which had been in contact with the former septum secretes a septum anew. In short, at any given epoch, the creature is not secreting a tube and a septum by separate operations, but is secreting a shelly case about its rounded body, of which case one part appears as the continuation of the tube, and the other part, merging with it by indistinguishable boundaries, appears as the septum*.

The various forms assumed by the septa in spiral shells† present us with a number of problems of great beauty, simple in their essence, but whose full investigation would soon lead us into difficult mathematics.

* "It has been suggested, and I think in some quarters adopted as a dogma, that the formation of successive septa [in *Nautilus*] is correlated with the recurrence of reproductive periods. This is not the case, since, according to my observations, propagation only takes place after the last septum is formed"; Willey, *Zoological Results*, 1902, p. 746.

† Cf. Henry Woodward, On the structure of camerated shells, *Pop. Sci. Rev.* XI, pp. 113–120, 1872.

We do not know how these septa are laid down in an Ammonite, but in the Nautilus the essential facts are clear*. The septum begins as a very thin cuticular membrane (composed of a substance called conchyolin), which is secreted by the skin, or mantle-surface, of the animal; and upon this membrane nacreous matter is gradually laid down on the mantle-side (that is to say between the animal's body and the cuticular membrane which has been thrown off from it), so that the membrane remains as a thin pellicle over the *hinder* surface of the septum, and so that, to begin with, the membranous septum is moulded on the flexible and elastic surface of the animal, within which the fluids of the body must exercise a uniform, or nearly uniform pressure.

Let us think, then, of the septa as they would appear in their uncalcified condition, formed of, or at least superposed upon, an elastic membrane. They must follow the general law, applicable to all elastic membranes under uniform pressure, that the tension varies inversely as the radius of curvature; and we come back once more to our old equation of Laplace and Plateau, that

$$P = T\left(\frac{1}{r} + \frac{1}{r'}\right).$$

Moreover, since the cavity below the septum is practically closed, and is filled either with air or with water, P will be constant over the whole area of the septum. And further, we must assume, at least to begin with, that the membrane constituting the incipient septum is homogeneous or isotropic.

Let us take first the case of a straight cone, of circular section, more or less like an *Orthoceras*; and let us suppose that the septum is attached to the shell in a plane perpendicular to its axis. The septum itself must then obviously be spherical. Moreover the extent of the spherical surface is constant, and easily determined. For obviously, in Fig. 417, the angle LCL' equals the supplement of the angle (LOL') of the cone; that is to say, the circle of contact subtends an angle at the centre of the spherical surface, which is constant, and which is equal to $\pi - 2\beta$. The case is not excluded where, owing to an asymmetry of tensions, the septum meets the

* See Willey, *op. cit.*, p. 749. Cf. also Bather, Shell-growth in Cephalopoda, *Ann. Mag. N.H.* (6), I, pp. 298–310, 1888; *ibid.* pp. 421–427, and other papers by Blake, Riefstahl, etc. quoted therein.

side walls of the cone at other than a right angle, as in Fig. 416; and here, while the septa still remain portions of spheres, the geometrical construction for the position of their centres is equally easy.

If, on the other hand, the attachment of the septum to the inner walls of the cone be in a plane oblique to the axis, then the outline of the septum will be an ellipse, but its surface will still be spheroidal. If

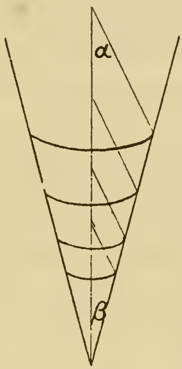


Fig. 416.

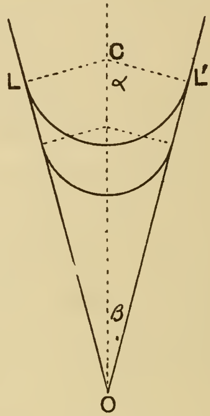


Fig. 417.

the attachment of the septum be not in one plane, but forms a sinuous line of contact with the cone, then the septum will be a saddle-shaped surface, of great complexity and beauty. In all cases, provided only that the membrane be isotropic, the form assumed will be precisely that of a soap-bubble under similar conditions of attachment: that is to say, it will be (with the usual limitations or conditions) a surface of minimal area, and of constant mean curvature.

If our cone be no longer straight, but curved, then the septa will by symmetrically deformed in consequence. A beautiful and interesting case is afforded us by *Nautilus* itself. Here the outline of the septum, referred to a plane, is approximately bounded by two elliptic curves, similar and similarly situated, whose areas are to one another in a definite ratio, namely as

$$\frac{A_1}{A_2} = \frac{r_1 r'_1}{r_2 r'_2} = \epsilon^{-4\pi \cot \alpha},$$

and a similar ratio exists in Ammonites and all other close-whorled spirals, in which however we cannot always make the simple assumption of elliptical form. In a median section of *Nautilus*, we see each septum forming a tangent to the inner and to the outer wall, just as it did in a section of the straight *Orthoceras*; but the

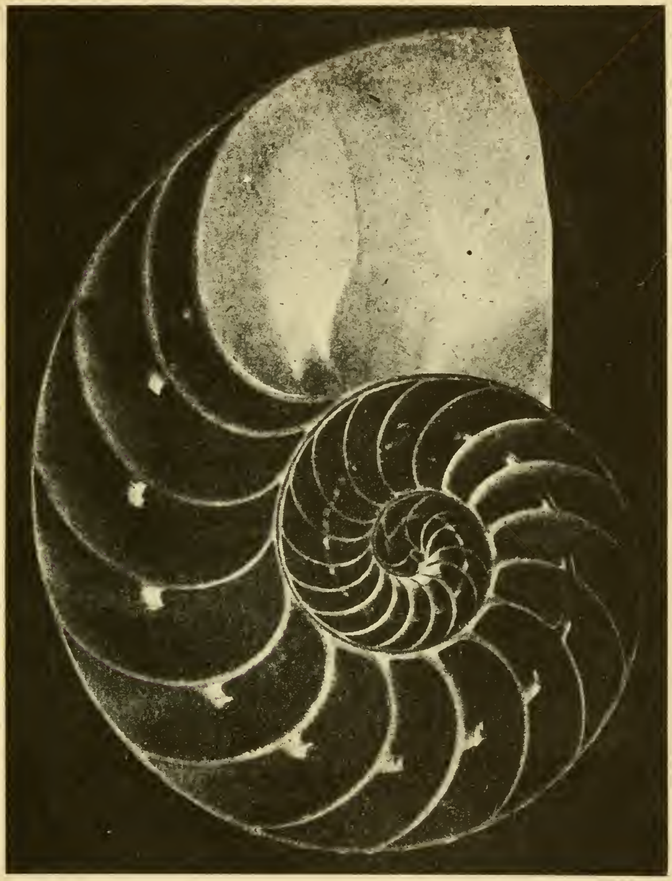


Fig. 418. Section of *Nautilus*, shewing the contour of the septa in the median plane.

curvatures in the neighbourhood of these two points of contact are not identical, for they now vary inversely as the radii, drawn from the pole of the spiral shell. The contour of the septum in this median plane is a spiral curve—the conformal spiral transformation of the spherical septum of the rectilinear Orthoceratite.

But while the outline of the septum in median section is simple and easy to determine, the curved surface of the septum in its entirety is a very complicated matter, even in *Nautilus* which is one of the simplest of actual cases. For, in the first place, since the form of the septum, as seen in median section, is that of a logarithmic spiral, and as therefore its curvature is constantly

Fig. 419. Cast of the interior of *Nautilus*: to shew the contours of the septa at their junction with the shell-wall.

altering, it follows that, in successive *transverse* sections, the curvature is also constantly altering. But in the case of *Nautilus*, there are other aspects of the phenomenon, which we can illustrate, but only in part, in the following simple manner. Let us imagine a pack of cards, in which we have cut out of each card a similar concave arc of a logarithmic spiral, such as we actually see in the median section of the septum of a *Nautilus*. Then, while we hold the cards together, foursquare, in the ordinary position of the pack, we have a simple "ruled" surface, which in any longitudinal section has the form of a logarithmic spiral but in any transverse section is a straight horizontal line. If we shear or slide the cards upon one another, thrusting the middle cards of the pack forward in advance of the others, till the one end of the pack is a convex, and the other a concave, ellipse, the cut edges which combine to represent our septum will now form a curved surface of much greater complexity; and this is part, but not by any means all, of the deformation produced as a direct consequence of the form in *Nautilus* of the section of the tube within which the septum has to lie. The complex curvature of the surface will be manifested in a sinuous outline of the edge, or line of attachment of the septum to the tube, and will vary according to the configuration of the latter. In the case of *Nautilus*, it is easy to shew empirically (though not perhaps easy to demonstrate mathematically), that the sinuous or saddle-shaped contour of the "suture" (or line of attachment of the septum to the tube) is such as can be precisely accounted for in this manner; and we may find other forms, such as *Ceratites*, where the septal outline is only a little more sinuous, and still precisely analogous to that of *Nautilus*. It is also easy to see that, when the section of the tube (or "generating curve") is more complicated in form, when it is flattened, grooved, or otherwise ornamented, the curvature of the septum and the outline of its sutural attachment will become very complicated indeed*; but it will be comparatively simple in the case of the first few sutures of the young shell, laid down before any overlapping of whorls has taken place, and this comparative simplicity of the first-formed sutures is a marked feature among Ammonites†.

* The "lobes" and "saddles" which arise in this manner, and on whose arrangement the modern classification of the nautiloid and ammonitoid shells largely depends, were first recognised and named by Leopold von Buch, *Ann. Sci. Nat.* XXVII, XXVIII, 1829.

† Blake has remarked upon the fact (*op. cit.* p. 248) that in some Cyrtocerata we may have a curved shell in which the ornaments approximately run at a constant angular distance from the pole, while the septa approximate to a radial direction; and that "thus one law of growth is illustrated by the inside, and another by the outside." In this there is nothing at which we need wonder. It is merely a case where the generating curve is set very obliquely to the axis of the shell; but where the septa, which have no necessary relation to the *mouth* of the shell, take their places, as usual, at a certain definite angle to the *walls* of the tube. This relation of the septa to the walls of the tube arises after the tube itself is fully formed, and the obliquity of growth of the open end of the tube has no relation to the matter.

We have other sources of complication, besides those which are at once introduced by the sectional form of the tube. For instance, the siphuncle, or little inner tube which perforates the septa, exercises a certain amount of tension, sometimes evidently considerable, upon the latter: which tension is made manifest in *Spirula* (and slightly so even in *Nautilus*) by a dip in the septal floor where it meets the siphuncle. We can no longer, then, consider each septum as an isotropic surface under uniform pressure; and there may be other structural modifications, or inequalities, in that portion of the

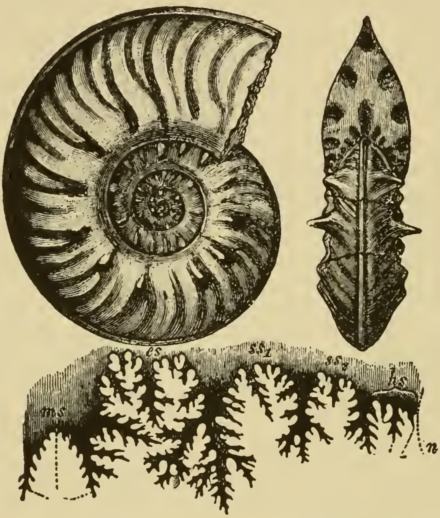


Fig. 420. *Ammonites Sowerbyi.* From Zittel.

animal's body with which the septum is in contact, and by which it is conformed. It is hardly likely, for all these reasons, that we shall ever attain to a full and particular explanation of the septal surfaces and their sutural outlines throughout the whole range of Cephalopod shells; but in general terms, the problem is probably not beyond the reach of mathematical analysis. The problem might be approached experimentally, after the manner of Plateau's experiments, by bending a wire into the complicated form of the suture-line, and studying the form of the liquid film which constitutes the corresponding surface *minimae areae*.

In certain Ammonites the septal outline is further complicated in another way. Superposed upon the usual sinuous outline, with its "lobes" and "saddles," we have here a minutely ramified, or arborescent outline, in which all the branches terminate in wavy, more or less circular arcs—looking just like the "landscape marble" from the Bristol Rhaetic. We have no difficulty in recognising in this a surface-tension phenomenon. The figures are precisely such as we can imitate (for instance) by pouring a few drops of milk upon a greasy plate, or of oil upon an alkaline solution*; they are what Charles Tomlinson called "cohesion figures."

Fig. 421. Suture-line of a Triassic Ammonite (*Pinacoceras*). From Zittel.

We must not forget that while the nautilus and the ammonite resemble one another, and are mathematically identical in their spiral curves, they are really very different things. The one is an external, the other an internal shell. The nautilus occupies the large terminal chamber of the many-chambered shell, and "Still as the spiral grew, He left the past year's dwelling for the new." But even the largest ammonites never contained the body of the animal, but lay hidden, as *Spirula* does, deep within the substance of the mantle. How the complicated septa and septal outlines of the ammonites are produced I do not know†.

We have very far from exhausted, we have perhaps little more than begun, the study of the logarithmic spiral and the associated curves which find exemplification in the multitudinous diversities of molluscan shells. But, with a closing word or two, we must now bring this chapter to an end.

* "The Fimbriae, or Edges, appeared on the Surface like the Outlines of some curious Foliage. This, upon Examination of them, I found to proceed from the Fulness of the Edges of the Diaphragms, whereby the Edges were waved or plaited somewhat in the manner of a Ruff" (R. Hooke, *op. cit.*).

† In certain rare cases the complicated sutural pattern of an ammonite is found *upside down*, but unchanged otherwise. Cf. Otto Haas, A case of inversion of suture lines in *Hysteroceras*, *Amer. Jl. of Sci.* CCXXXIX, p. 661, 1941.

In the spiral shell we have a problem, or a phenomenon, of growth, immensely simplified by the fact that each successive increment is no sooner formed than it is fixed irrevocably, instead of remaining in a state of flux and sharing in the further changes which the organism undergoes. In such a structure, then, we have certain primary phenomena of growth manifested in their original simplicity, undisturbed by secondary and conflicting phenomena. What actually *grows* is merely the lip of an orifice, where there is produced a ring of solid material, whose form we have discussed under the name of the generating curve; and this generating curve grows in magnitude without alteration of its form. Besides its increase in areal magnitude, the growing curve has certain strictly limited degrees of freedom, which define its motions in space. And, though we may know nothing whatsoever about the actual velocities of any of these motions, we do know that they are so correlated together that their *relative* velocities remain constant, and accordingly the form and symmetry of the whole system remain in general unchanged.

But there is a vast range of possibilities in regard to every one of these factors: the generating curve may be of various forms, and even when of simple form, such as an ellipse, its axes may be set at various angles to the system; the plane also in which it lies may vary, almost indefinitely, in its angle relatively to that of any plane of reference in the system; and in the several velocities of growth, of rotation and of translation, and therefore in the ratios between all these, we have again a vast range of possibilities. We have then a certain definite type, or group of forms, mathematically isomorphous, but presenting infinite diversities of outward appearance: which diversities, as Swammerdam said, *ex sola nascüntur diversitate gyrationum*; and which accordingly are seen to have their origin in differences of rate, or of magnitude, and so to be, essentially, neither more nor less than *differences of degree*.

In nature, we find these forms presenting themselves with but little relation to the character of the creature by which they are produced. Spiral forms of certain particular kinds are common to Gastropods and to Cephalopods, and to diverse families of each; while outside the class of molluscs altogether, among the Foraminifera and among the worms (as in *Spirorbis*, *Spirographis*, and in the *Dentalium*-like shell of *Ditrupa*), we again meet with similar and corresponding spirals.

Again, we find the same forms, or forms which (save for external ornament) are mathematically identical, repeating themselves in all periods of the world's geological history; and we see them mixed up, one with another, irrespective of climate or local conditions, in the depths and on the shores of every sea. It is hard indeed (to my mind) to see in such a case as this where Natural Selection necessarily enters in, or to admit that it has had any share whatsoever in the production of these varied conformations. Unless indeed we use the term Natural Selection in a sense so wide as to deprive it of any purely biological significance; and so recognise as a sort of natural selection whatsoever nexus of causes suffices to differentiate between the likely and the unlikely, the scarce and the frequent, the easy and the hard: and leads accordingly, under the peculiar conditions, limitations and restraints which we call "ordinary circumstances," one type of crystal, one form of cloud, one chemical compound, to be of frequent occurrence and another to be rare*.

* Cf. Bacon, *Advancement of Learning*, Bk. II (p. 254): "Doth any give the reason, why some things in nature are so common and in so great mass, and others so rare and in so small quantity?"