TECHNIQUE FOR SCALE MODELLING OF CEPHALOPOD SHELLS

by JOHN A. CHAMBERLAIN, JR.

ABSTRACT. Previous work by Raup on the mathematical description of coiled shells provides a foundation for the construction of three-dimensional scale models of cephalopod shells. A computer programme, based on the method of Raup, has been developed which contours planispiral surfaces of the cephalopod type. The computer output is then used to construct plastic models of these surfaces. The morphological range covered by this programme includes the entire suite of planispiral cephalopod forms. Provision is made for the simulation of both actual fossil species and hypothetical morphologies. In addition, mathematical simulation of accretionary growth allows the modelling of different stages of ontogenetic series.

THE term 'scale model' has been used to describe those models which are physical reproductions of a prototype. Most scale models are used to adjust the dimensions of the prototype to a size more readily or accurately studied. Size change is not essential, however, as scale models with dimensions similar to those of the prototype may be employed if the prototype itself is unsuitable. Scale models are real, physical objects and thus differ from mathematical models in that the latter are abstractions. The two are not exclusive, however, since a scale model may be based upon a mathematical model. The scale cephalopod models figured in this paper, for example, are true scale models, but their construction is formulated on Raup's (1961, 1963, 1966) mathematical model of shell coiling.

The experimental use of scale models has become a technique of considerable importance to the physical sciences and engineering. Due primarily to the greater complexity of the organic world, problems concerning organisms are not yet as amenable to the scale-model approach as are purely physical phenomena. Our understanding of organic mechanics and the level of modelling technology are usually inadequate to deal with the intricate nature of organic mechanisms. Where the requirements for model-building are reasonable, however, the scale-model technique can be productive.

COMPUTER TECHNIQUE FOR CEPHALOPOD SHELLS

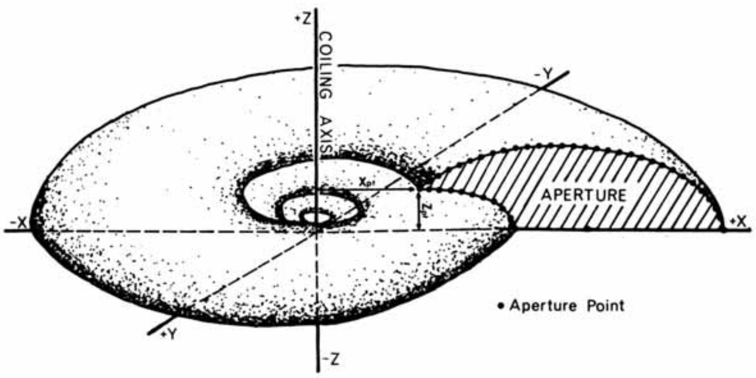
It has been known since the work of Moseley (1838, 1842) that the logarithmic spiral is fundamental to the molluscan shell plan. Not until the work of Raup (1961, 1963, 1966) and Raup and Chamberlain (1967), however, were the cumbersome mathematics of earlier workers replaced by equations which could be readily applied to actual shells. According to Raup, the basic form of a spiral shell may be defined by four parameters: the shape of the generating curve (S); the whorl expansion rate (W); the distance from the generating curve to the coiling axis (D); and the translation rate along the coiling axis (T). These parameters are further defined and the mathematical methodology set forth in the above papers. Raup (1962) and Raup and Michelson (1965) have demonstrated the utility of these parameters in the application of both digital and analog computers to the investigation of shell geometry. The equations used here to simulate

[Palaeontology, Vol. 12, Part 1, 1969, pp. 48–55, pl. 7.]

cephalopod morphology are based on Raup's mathematical model and his previous work with computers.

A computer programme, written in Fortran IV and intended for use in the I.B.M. S/360 machine, has been developed by the author. This programme yields, as plotter output, contour maps of planispiral surfaces. These maps are then used in constructing laminated plastic replicas of planispiral cephalopods. Each lamina is parallel to the median plane and has a thickness equal to the contour interval. The programme has been deposited in the reprint files (reprint no. 227) of the Department of Geological Sciences, University of Rochester, Rochester, N.Y., and is available upon request.

Since cephalopod shells are bilaterally symmetrical, the mathematical reconstruction of an entire surface is unwarranted; instead this programme considers the median plane as a base and treats only a single side. Symmetry is restored by duplicating this one half during the actual construction of the model. The models herein described are thus three-dimensional reproductions of planispiral surfaces.



TEXT-FIG. 1. Cephalopod sectioned along median plane to show the fundamental relationships for computer simulation.

While the programme itself is relatively involved, it preserves simplicity in its input requirements. The user is required to include as input data only three of Raup's parameters (T is zero for planispiral forms and so is excluded here), and the value of a few constants and logical variables. An orthogonal grid system is assumed in defining the position of the surface in space (text-fig. 1). The coiling axis lies at the centre of the system perpendicular to the $Z = 0$ plane. The aperture has the coordinates of distance from the coiling axis (X), and distance above the median plane (Z). The shape of the generating curve is taken as the outline of the aperture above the median plane, and is defined by a series of points whose (X, Z) coordinates are either directly read in as input, or calculated from the equations of simple geometric curves whose half axes and distance to the coiling axis constitute the input data. Other input parameters include the whorl expansion rate (W), and the length of the spiral expressed in numbers of whorls.

The computer defines new planes, the number of which depends on the Z coordinate of the highest point on the aperture. These planes lie above the median plane and parallel to it such that a constant interplanar distance is maintained. The Z coordinate of each aperture point is compared to each plane in turn. If a point lies below a given plane, it is ignored; if it lies on or above the plane, its intersection with the plane is calculated from the logarithmic decay of its Z coordinate using the following equations:

$$Z_{\text{plane}} = Z_{\text{pt}} \,.\, e^{a\theta},$$
$$\theta = [\ln(Z_{\text{plane}}) - \ln(Z_{\text{pt}})]/a. \qquad (1)$$

In the above, which are simply different forms of the equation of a logarithmic spiral, Z_{plane} is the Z coordinate of the plane and Z_{pt} is the Z coordinate of the aperture point. e is the base of the natural logarithms. θ is the angle, expressed in radians, through which the aperture point must be rotated so that the Z coordinate of the point will be the same as the Z value of the plane. a is the spiral constant and is equal to cot α, where α is the spiral angle of Thompson (1942). a may be further expressed as $a = \ln W/2\pi$ or $W = e^{2\pi a}$, where W is the whorl expansion rate of Raup. In equation 1, since $Z_{\text{pt}} \geqslant Z_{\text{plane}}$ and $a > 0$, θ will always be negative or zero. The latter case is trivial, however, as no rotation is involved. Since θ is thus actually negative, the planispiral surface is constructed inward from the aperture rather than outward from the first generating curve, which in molluscs is that portion of the shell immediately adoral to the protoconch. A negative θ permits mathematical consideration of the easily measured aperture, and eliminates the critical drawback, inherent in nearly all previous work, of a positive θ requiring a set of equations based on the shape of the minute and often unavailable first generating curve. The importance of a negative θ to the mathematical analysis of real shells has been further demonstrated by Raup and Chamberlain (1967). Once θ is known, the X and Y coordinates for Z_{plane}, the new Z coordinate, may be calculated from the following:

$$X_{\text{plane}} = X_{\text{pt}} \cdot e^{a\theta} \cdot \sin\theta,$$
$$Y_{\text{plane}} = X_{\text{pt}} \cdot e^{a\theta} \cdot \cos\theta,$$

where X_{plane} and Y_{plane} are the new (X, Y) coordinates respectively, and X_{pt} is the X coordinate of the undecayed aperture point. Other terminology is as before. The (X, Y) coordinates of all logarithmically decayed aperture points for a given Z plane are scaled and fed into a Calcomp plotter which then plots them. A sagittal section

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EXPLANATION OF PLATE 7

Lateral and anterior views of some cephalopod models. Figs. 1–6 show various stages in the assembly of a model. Figs. 7–12 show three members of a hypothetical ontogenetic series: $W = 2{\cdot}0$, $D = 0{\cdot}2$.

Figs. 1–2. Specimen of *Lytoceras fimbriatum* (Sowerby) from which measurements for model in figs. 3–6 were taken. The shell is severed 0·4 whorls from the aperture. ×0·3.

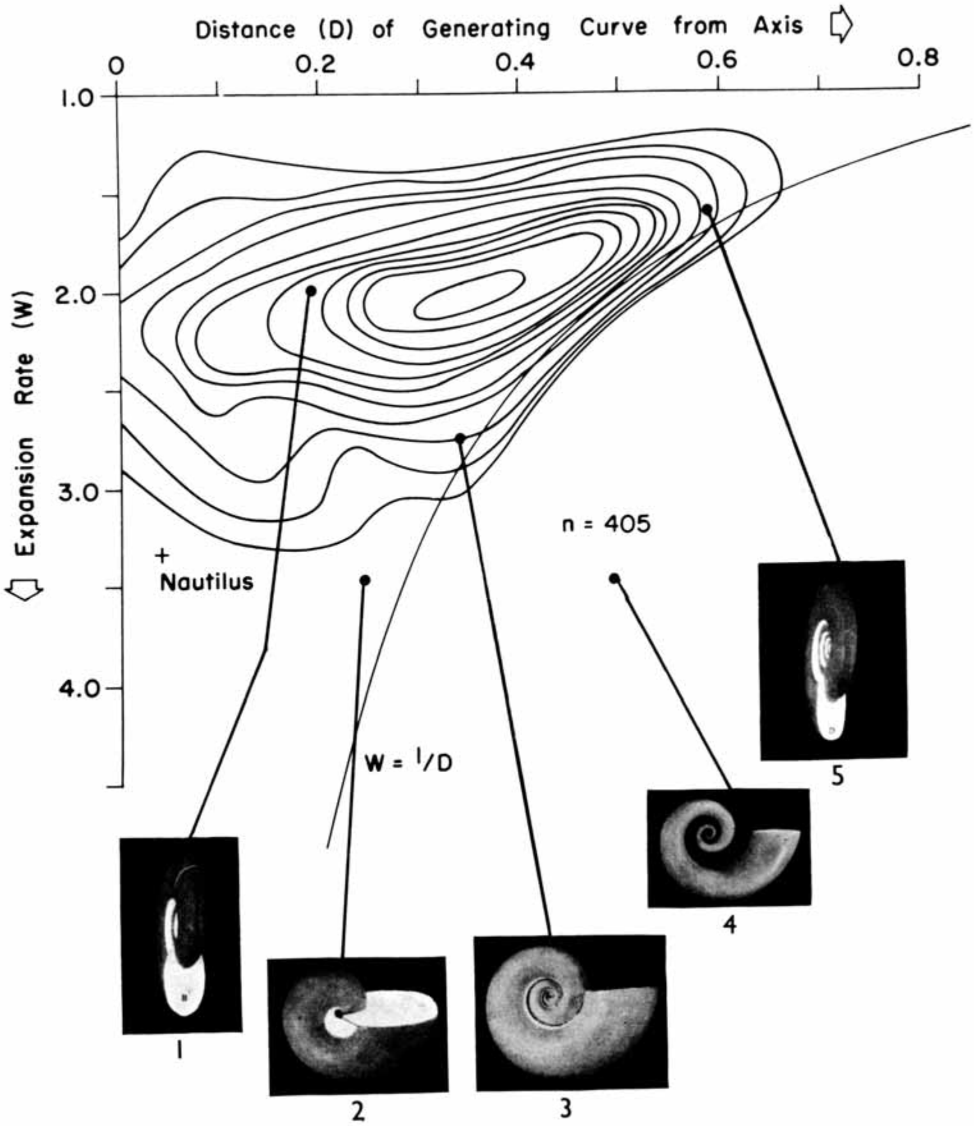
Figs. 3–4. Unfinished model showing contoured Plexiglas surface. Reference points for section alignment appear near section numbers: 12, 15, 19, 25, 28, in fig. 3. ×0·4.

Figs. 5–6. Finished model showing smooth epoxy surface. White portion of umbilical area in this and other models has no morphological significance, it is used merely as a means of emphasizing surface relief. ×0·4.

Figs. 7–8. Model A, 2·4 whorls, growth increment = −0·6. ×0·4.

Figs. 9–10. Model B, 3·0 whorls, growth increment = 0·0; stage A adapical of line BA. ×0·4.

Figs. 11–12. Model C, 3·4 whorls, growth increment = 0·4; stage B adapical of line BC, stage A adapical of line BA. ×0·4.



TEXT-FIG. 2. Position of various models on a contoured density graph of the natural occurrence of planispiral ammonoids (adapted from text-fig. 4 of Raup 1967). Contour parameters are *W* and *D*. 90% of sample lies inside outermost contour. Sample size is 405 species. All models but 3, which is the model of *L. fimbriatum*, have hypothetical morphologies. All models ×0·2.

lying above the median plane of line a distance of Z_{plane} is thus formed. Moreover, since all points on a given sagittal section have identical elevations (Z_{plane}), each plot is actually a contour line, and the plots for all Z planes form a contour map. Plate 7, figs. 3 and 4, shows the contoured surface of an unfinished model.

In addition to the mathematical treatment described above, the computer programme incorporates several operations which provide for the reproduction of most of the variations observed among cephalopod shells. The simulation of all types of smooth planispiral shells (involute to gyroconic and cyrtoconic) is created by the inclusion of a number of options for inputting Raup's parameters to the computer. Among these, the options for defining aperture shape make possible the modelling of real species or completely hypothetical and, in terms of real animals, non-existent morphologies. Plate 7, figs. 1–6, shows a specimen of *Lytoceras fimbriatum* (Sowerby) and a model constructed from measurements taken from it. Text-fig. 2 shows several models with hypothetical morphologies.

The wide range in size displayed by coiled cephalopods is accommodated in the programme by scaling. The size of a model is independent of other input data and depends only on the operator's prescribed size instructions. There are thus no restrictions on the size of a prototype (where real shells are being copied) except those concerning precision in measurement. Models are limited by the width of the plotter paper to a maximum diameter of 10 in., although if the computer output is used in conjunction with a blue-print enlarger this size may be exceeded.

Although scaling accounts for a wide range of variation, it does not duplicate the accretionary nature of size increase in cephalopods. The ontogenetic development of the shells of these animals occurs by addition of shell material along the margins of the aperture; there is no uniform expansion of the entire shell, as is accomplished by scaling. To alleviate this deficiency, a mathematical simulation of accretionary growth has been built into the programme and functions when instructed by the operator. Plate 7, figs. 7–12, shows three members of a hypothetical ontogenetic series produced by making three computer runs, each time varying the magnitude of the growth increment while keeping other input data constant.

Although the programme can reproduce, and in some respects exceed, much of the morphological range of normal cephalopods, it retains certain limitations which prevent simulation of all cephalopod types. Since its operation is founded on the equation of a logarithmic spiral, which by definition is a spiral without translation, helicoid forms, such as those morphologies characterized by non-planispiral heteromorphs, are excluded. These exceptions do not notably detract from the over-all scope of the programme as the morphological range of the great majority of fossil species is still reproducible.

While the basic shape of planispiral forms may be simulated, the surface texture and much of the shell sculpture can not. Except for prominent spiral ornamentation, such as keels, no ornamentation can be rigorously duplicated. This includes the many kinds of radial sculpture (e.g. ribs, spines, tubercles) and apertural contrivances (e.g. rostra, lappets). Ornamentation of this sort is not readily susceptible to objective mathematical treatment, nor is the precision of the assembly technique adequate to reproduce the finer sculpture. Sculptured models are not precluded, however, since surface ornamentation may be added once the smooth surface is finished.

The programme is also not in strict accord with nature in its implicit assumption of ontogenetic constancy in the whorl expansion rate and in the shape of the generating curve. Ontogenetic variation in both of these parameters is well known among cephalopods, especially ammonoids.

The length of time required for a complete computer run depends primarily on the maximum thickness of a model, since more sagittal sections are required for a thick model than for a thin one. All models illustrated in this paper consumed less than ten minutes of computer time, and for most, the average run took about seven minutes.

TECHNIQUE FOR MODEL ASSEMBLY

The computer sagittal sections are traced on to sheets of clear Plexiglas. The thickness of the sheets used in the construction of these models is 0·031 in., 0·001 in. less than the section spacing. Other thicknesses can be handled by the computer, but this one was considered best for the purpose at hand since it combines precision with practicality. A second Plexiglas sheet of equal thickness is temporarily glued over those inscribed with the sections. This allows both model halves to be shaped at once—the reason for the treatment in the programme of only one symmetrical side. The sections are then cut out of the double sheets with an electric band-saw and trimmed with a rotary sander. A model 2 Moto-Tool, manufactured by the Dremel Mfg. Co., Racine, Wisconsin, was found to be ideal for trimming. The Plexiglas sagittal sections are separated from one another and divided into two stacks, one for each half of the model. They are then fastened permanently to one another with a layer of acrylic cement, the thickness of which is estimated at 0·001 in. When this thickness is added to that of the Plexiglas sheets, the sum equals the Z spacing defined in the programme. Section alignment and positioning are controlled by reference points, which are part of the computer output and appear at the same place (have the same (X, Y) coordinates) on all plotted sections and plastic templates (Pl. 7, fig. 3). Distortion due to section displacement is thus minimal. Plate 7, figs. 3 and 4, shows that at this stage of assembly, models have a contoured surface. In order to simulate more closely the surface of cephalopod shells, the edges are smoothed by infilling the steps with plastic resin. The common type of epoxy plastic, Epoxi-Patch Kit3X, made by the Hysol Chemical Co., Olean, N.Y., was found to be well suited for this purpose. The steps are filled in rather than sanded down because it is the upper edges of the templates that lie on the computed surface. When mixed, the epoxy is a viscous paste that may be easily applied with small spatulas. The model is coated with epoxy and placed in an oven at 140 °F to 170 °F for two hours, after which the hardened model is removed and the surface sanded down until the edges of the Plexiglas reappear. If necessary, a second and third coat is applied, each time removing the excess epoxy, until a smooth, even surface is produced. Finally the model is painted. The construction time varies with the size and thickness of the model and with the number of applications of epoxy. Generally, however, assembly requires 10–20 working hours from the receipt of the computer output to the finished model.

APPLICATIONS

These cephalopod models illustrate a number of advantageous properties possessed by scale models of fossil organisms. Perhaps their most significant feature is that they can, in a sense, act as a substitute for a thorough theoretical or mathematical understanding of a problem. For example, the forces acting on the hull of a moving ship still defy complete mathematical description. Thus, in designing hulls, reliance has been placed not so much upon theory as upon scale models of hulls, the reason being that while the physical interrelationships may not be totally understood, the use of scale models enables the important ones to be studied and conclusions to be drawn. The history of experimental physics shows that scale models can be used to derive empirically laws which escape theoretical analysis because of inadequate data. The same holds true for many areas of palaeoecology, particularly those dealing with the palaeoautecological problems of function and adaptation. Although scale models may supplant conceptual depth, their use does not presume complete *naïveté*, as there must be sufficient understanding of basic relationships to build models and design appropriate experiments.

A second important attribute of fossil scale models is functionability, a property which actual fossils, in their lithified state, do not have. Thus, Rudwick (1961) used a working model of *Prorichthofenia* instead of inoperable specimens. Preservation is important here since even so-called excellent preservation is rarely adequate to maintain a shell as it was in life. One of the reasons the present author is using models such as these in experiments on cephalopod hydrodynamics is that they do not possess the common deformities of real fossil shells. Models are not distorted, fragmentary, or embedded in sediment.

Scale models can be used to simulate actual species or hypothetical morphologies. Models therefore provide for a wider range of morphologic variability than actual fossils. They facilitate the study of evolutionary trends, as models of hypothetical morphologies may be used in tracing the evolution of function and adaptation from one real form to another. Hypothetical forms are also useful in evaluating the function of characters which do appear in real animals since they allow the relative advantages of real and non-real characters to be compared. This is especially significant in determining the characters which delimit a taxon's morphological range. The work of Raup (1966, 1967) illustrates the value of hypothetical shell forms in this type of functional morphologic research and the importance of investigation of characters not exhibited by actual fossils.

The value of models is further demonstrated by their utility in studying the effects of changes in morphological characters. It is often difficult or impossible to isolate individual characters for study, particularly in the case of many fossil taxa, where functionable specimens are rare and sample size necessarily small. Modelling facilitates investigations of this sort since models varying from one another in only a single character may be constructed. Use of models frees the investigator from dependence on fossil material. Such autonomy is important since it eliminates the problem of scarcity of serviceable fossils and the laborious and often unrewarding process of searching the various museums and repositories for usable specimens.

Models can be designed to fit the experiment, whereas prototypes may possess characters—perhaps size, weight, or surface texture—in magnitudes detrimental to their use. In cases where only a portion of a fossil or a particular set of characters is being studied, experimentation on the whole fossil, especially if it is morphologically complex, may conceal the desired effects or make the work unnecessarily complicated. It is not mandatory to construct models patterned after fossils in every detail; it is sufficient to build models that resemble the prototypes only in those characters being investigated. The practicality of model construction should therefore depend on the number and nature of the characters involved rather than on the complexity of the fossil as a whole.

While the models figured here are designed for hydrodynamic research, adaptations of the technique could provide models suitable for other purposes, as for example, shell strength experiments similar to those of Raup and Takahashi (1966), and Denton and Gilpin-Brown (1966), or the orientation work of Reyment (1958). Although the computer programme was designed specifically for the simulation of cephalopod morphology, it retains sufficient versatility to simulate other planispiral forms as well. Of particular interest is its ability to reproduce many of the forms exhibited by brachiopods, scaphopods, and planispiral foraminifera. By including the appropriate equations for translation, it could be adapted to reproduce the helicoid form of bivalves, gastropods, and many foraminifera.

Acknowledgements. The writer acknowledges the assistance of David M. Raup, who offered valuable advice at various stages of this study and with S. M. Stanley reviewed the manuscript. This research was supported by the National Science Foundation, through its traineeship programme, and by the Petroleum Research Fund, administered by the American Chemical Society. The computer work was done at the University of Rochester Computer Center. R. M. Eaton prepared the figures.

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J. A. CHAMBERLAIN, JR.
Department of Geological Sciences
University of Rochester
Rochester, New York

Typescript received 31 May 1968


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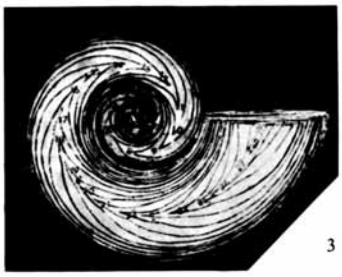
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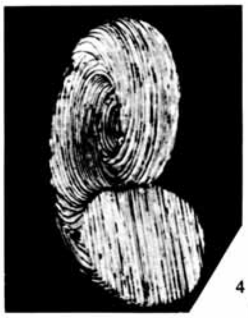
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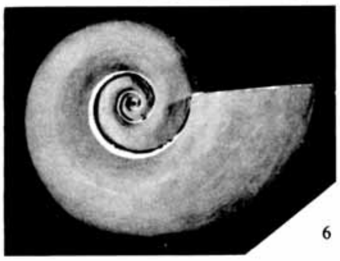
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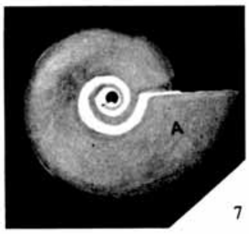

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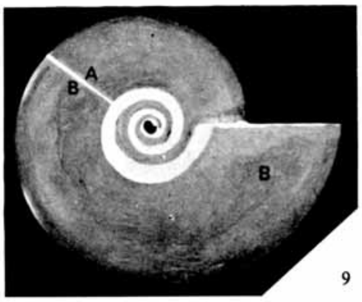

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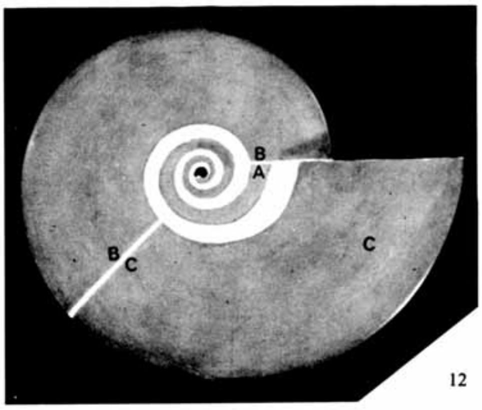

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