ANALYSIS OF HETEROMORPH AMMONOIDS BY DIFFERENTIAL GEOMETRY

by TAKASHI OKAMOTO

ABSTRACT. The complicated shell form of heteromorph ammonoids can be considered simply as an integration of *ad hoc* accretional growth of the aperture, without defining any coordinate system. This 'growing tube model' is newly developed herein, using differential geometry, and is applicable to the growth pattern of any coiled shell. Using the model, any coiled shell with a circular cross-section can be analysed and described by three differential parameters: *E*, radius enlarging ratio; *C*, standardized curvature; and *T*, standardized torsion. I applied the growing tube model to eight nostoceratid species of heteromorph ammonoid and analysed growth patterns and ontogenetic change; stable stages and transitional intervals are clearly recognizable during growth. Morphologies of real specimens can be produced using computer graphics. A particular advantage of the model is that perfect similitude is kept at any growth stage because growth patterns are described relative to whorl radius. This is the most appropriate model for the study of comparative morphology and function of free tubular shells.

THE mode of coiling of heteromorph ammonoids often looks complicated and is commonly used as a diagnostic character for species and genera. Yet it is difficult to express exactly their various coiling patterns with current morphological terms. I present here a newly developed method for describing and analysing three-dimensional coiling patterns, using differential geometry.

The method can be illustrated quite simply by imagining a curved highway with a car moving at constant speed; this curve can be described using a fixed coordinate system, of course, but there is another method. The driver of the car must steer right or left to stay on the highway; if the steering operation is recorded exactly through time, the shape of the highway can be reconstructed by tracing the path of the car, without recourse to a fixed coordinate system.

Each heteromorph ammonoid whorl approaches a smoothly curved tube of gradually increasing radius. The ammonoid shell and the living organism responsible for it are comparable with our highway and the car, the former being just a trace of the latter. It is, therefore, possible to analyse differentially the shell coiling of various heteromorph ammonoids at any growth stage. This new method provides an effective approach for the investigation of the particular coiling mechanisms of heteromorph ammonoids, and of coiling patterns in general.

PREVIOUS WORK ON SHELL COILING

Moseley (1838) proposed a geometric model for the coiling of a shell, based on the equiangular spiral (a curve in which the angle between the radius and tangential line is constant at any point; also called a Bernoulli spiral after its discoverer). Thompson (1942) reviewed this and other early studies on the coiling of molluscs and foraminiferans, which all invoked a geometrical approach. Fukutomi (1953) pointed out that the equiangular spiral equation is not only applicable to gastropods and nautiloids but also to bivalves.

Raup's model. Raup (1966) was able to express the shell form of most gastropods, cephalopods, and bivalves using just four parameters: *W*, whorl expansion rate; *D*, distance between the coiling axis and generating curve; *T*, whorl translation rate; and *S*, shape of the generating curve. These parameters are defined as simple ratios (see text-fig. 1). Raup's model is characterized by a circular generating curve revolving around a fixed coiling axis. The model can be applied only to a shell form with isometric growth around such a coiling axis. Raup (1967) applied his model to normally coiled ammonoids and discussed their theoretical morphology. Tanabe *et al.*

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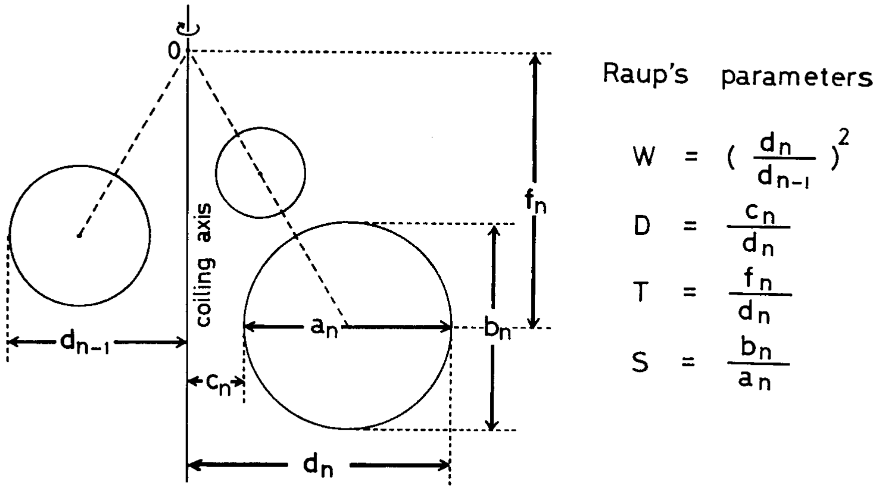


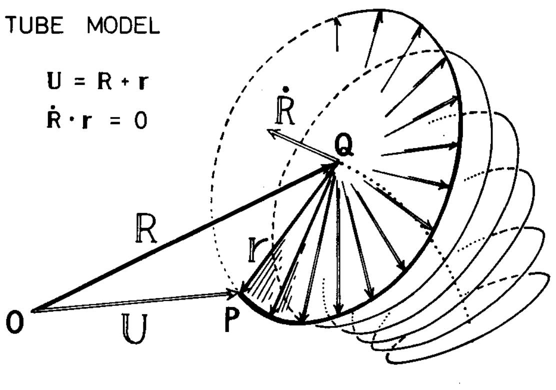
TEXT-FIG. 1. Raup's (1966) model, expressed by four simple ratio parameters in cylindrical coordinates.

(1981) later used Raup's parameters to express the coiling of some heteromorph species, but only some helicoid and open planispiral forms or growth stages could be accommodated. The coiling of many other heteromorphs cannot be satisfactorily defined by a fixed coiling axis and such simple parameters.

Tube model. Recently (Okamoto 1984), I proposed a tube model that is applicable to all types of shell coiling. Because this work appeared in a Japanese journal of limited distribution, the method and results are briefly summarized here, and the merits and limitation of the model discussed. In this model the cross-section of a coiling shell is regarded as a circle. Generally, a tubular body with circular cross-section can be expressed by the following equations (see text-fig. 2):

$$\mathbf{U} = \mathbf{R}+\mathbf{r}, \qquad \mathbf{r}\cdot\dot{\mathbf{R}} = 0 \text{ [inner product]},$$

R is a position vector to the centre of the tube; **r**, a radius of the tube; **U**, a position vector to the surface of the tube; and $\dot{\mathbf{R}}$, the total differential of **R**, showing the growing direction of the tube. Using these vectors, I analysed the

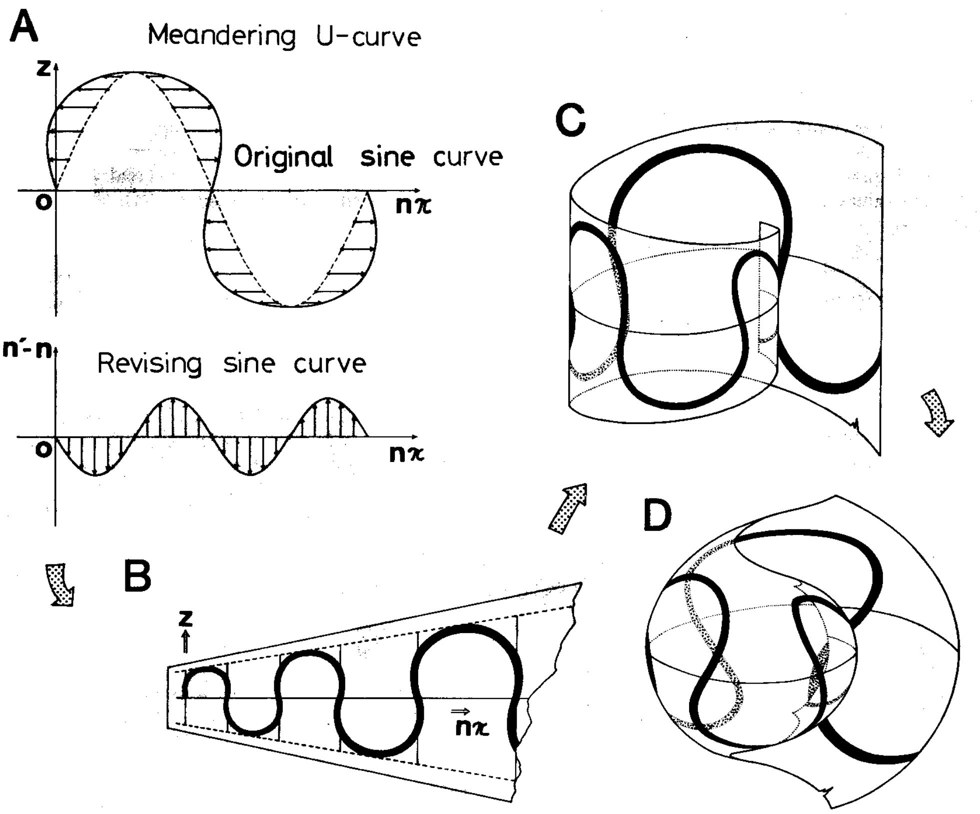


TEXT-FIG. 2. Tube model, composed of two elements **R** and **r**. **R**, tube centre line; **r**, corresponding tube radius; **U**, tube surface vector. Adapted from Okamoto (1984).

coiling of the Cretaceous heteromorph ammonoid *Nipponites*. An approximation to the shape of real specimens was achieved in four stages (text-fig. 3):

1. The basic meandering U-shaped curve of *Nipponites* was obtained by the synthesis of two synchronized sine curves (text-fig. 3A).

2. Although the wave height of the meandering U-shaped curve increased during growth, the wave length, which also increased, can be regarded as constant against the revolution angle (text-fig. 3B).



TEXT-FIG. 3. Construction of the tube centre line for *Nipponites*. A, approximation of the meandering U-curve by the synthesis of two sine curves. B, increasing the wave length and amplitude exponentially. C, cylindrical model in which the amplified meandering U-curve is rolled up around a coiling axis, so as to show an equiangular spiral in transverse section. D, transformation from the cylindrical model to the spherical model.

3. The 'amplified meandering U-shaped curve' revolves around a coiling axis Z, so that its projection on to the X–Y plane becomes an equiangular spiral (text-fig. 3C).

4. The length of vector **R** does not increase constantly because of the oscillation of the tube parallel to the coiling axis. In actual specimens, the increasing ratio of **R** seems to be nearly constant. Then the X and Y coordinates are transformed to maintain a constant increasing ratio of **R** without changing the values of Z and revolution angle. This procedure geometrically transforms a cylindrical model to a spherical model, as shown in text-fig. 3D.

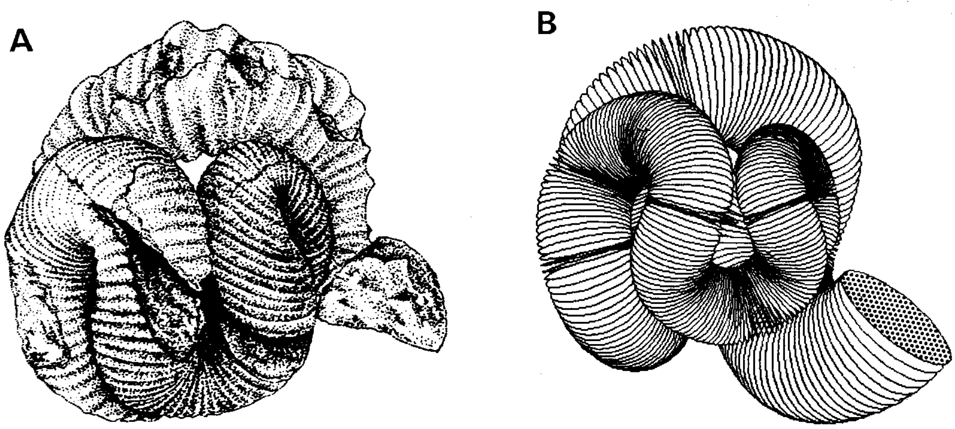
Consequently, the following equations are obtained:

$$\mathbf{R} = (x, y, z)$$
$$x = \sqrt{100^{an+a_0} - z^2} \cdot \cos n'\pi,$$
$$y = \sqrt{100^{an+a_0} - z^2} \cdot \sin n'\pi,$$
$$z = 10^{bn+b_0} \sin dn\pi, \qquad n' = n - f \sin 2dn\pi,$$

where a and b are the rates of increase of **R** and meandering amplitude, a_0 and b_0 are their exponentials at the initial stage, d is the meandering frequency, and f is its intensity index. The radius of whorl cross-section has a constant growth ratio to the revolution angle as follows:

$$\|\mathbf{r}\| = 10^{cn+c_0}.$$

The eight coefficients used in this tube model describe completely the coiling of *Nipponites.* Using measured specimens of *N. mirabilis,* I calculated actual values of these coefficients to analyse its geometry. In order to test the adequacy of the model, computer graphics were applied to these equations using real values for the coefficient values; the resulting computer-produced figure matches well with the coiling pattern of the holotype (text-fig. 4).



TEXT-FIG. 4. Comparison between an actual specimen and a tube model of *Nipponites.* A, sketch of the holotype of *N. mirabilis,* UMUT MM7560. B, figure produced by computer from the theoretical formulae and calculated parameters.

Traditional analyses of shell coiling, using rectangular or polar coordinates, are characterized by the adoption of fixed axes. How significant is such a fixed coordinate system for organisms with accretionally growing shells? The coiling axis in Raup's model may have some biological significance for many gastropods, planispiral ammonoids, and the like because, during accretionary growth, this axis maintains an invariable direction relative to the aperture or growing direction of the whorl, and because it is always in the plane of the generating curve. But no such coiling axis can be defined for heteromorph ammonoids. However complicated the coiling pattern, of course, it would be possible to simulate it in a fixed coordinate system with a suitable number of parameters. But it is important to note that any fixed coordinate system is no more than an artificial framework imposed upon the coiling pattern. For the living organisms, at least, fixed coordinates are irrelevant to the fundamental mechanism of coiling. Therefore, the *Nipponites* graphic (text-fig. 4B) is merely a model for 'pattern matching', useful for the description of shell form, but no more. In order to recognize the *mechanism* of shell coiling, especially in heteromorph ammonoids, it is necessary to abandon the traditional concept of a fixed coordinate system.

GROWING TUBE MODEL

Natural equations of space curves

The shell of every heteromorph ammonoid can be regarded as an elongated conical tube with a circular cross-section. The tube is defined by two components: 1, the locus of the centre of the whorl cross-section; and 2, the radius of the tube corresponding to it. For simplicity, consider a curved wire which represents the centre of the tube. To understand the mode of coiling in this wire model, we can analyse the differential property of its curvature. At the point $x(\lambda)$ on the space curve, we define a coordinate system having an origin at $x(\lambda)$ and an axis along the tangent of the curve at the same point. This coordinate system is composed of three unit vectors at a given point on the space curve; **t**, the tangent; **n**, the principal normal; and **b**, the binormal vectors, which all move on the space curve. Thus, we can describe any smooth space curves without using a fixed coordinate system.

If arc length λ is a parameter of the equation of space curve C, then

$$C:\mathbf{X}(\lambda) = (x(\lambda), y(\lambda), z(\lambda))$$

has direction with the progress of parameter λ. Therefore, the three unit vectors **t**, **n**, and **b**, which intersect each other perpendicularly and form a right-hand system of coordinates, are expressed as follows (text-fig. 5):

$$\mathbf{t} = \mathbf{t}(\lambda) = \dot{\mathbf{X}}(\lambda),$$
$$\mathbf{n} = \mathbf{n}(\lambda) = \frac{\dot{\mathbf{t}}(\lambda)}{\|\dot{\mathbf{t}}(\lambda)\|},$$
$$\mathbf{b} = \mathbf{b}(\lambda) = \mathbf{t}(\lambda) \times \mathbf{n}(\lambda) \text{ [outer product].}$$

These unit vectors move on the space curve with the motion of the position vector $\mathbf{X}(\lambda)$. Here, the set $(\mathbf{X}, \mathbf{t}, \mathbf{n}, \mathbf{b})$ is called the 'Frenet frame' or 'moving frame'.

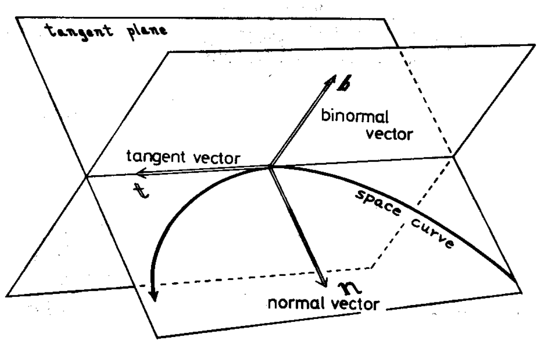
Now the differentials of these equations, which are given by:

$$\dot{\mathbf{X}} = \mathbf{t}, \quad \begin{aligned} \dot{\mathbf{t}} &= \kappa\mathbf{n} \\ \dot{\mathbf{n}} &= -\kappa\mathbf{t} + \tau\mathbf{b} \\ \dot{\mathbf{b}} &= -\tau\mathbf{n} \end{aligned}$$

express the changing condition of the unit vectors, and are called 'Frenet's equations', where the coefficients κ and τ represent curvature and torsion, respectively.

When the points $\mathbf{X}(\lambda)$ and $\mathbf{X}(\lambda + \Delta\lambda)$ exist on the space curve, and $\Delta\theta$ is the angle between the two unit tangent vectors, the curvature $\kappa(\lambda)$ is given by:

$$\kappa(\lambda) = \lim_{\Delta\lambda \to 0} \frac{\Delta\theta}{\Delta\lambda}.$$



TEXT-FIG. 5. Frenet frame for a space curve. This frame, which moves along the space curve, is composed of three unit vectors: **t**, tangent; **n**, normal; and **b**, binormal.

When $\Delta\varphi$ is the angle between the two tangent planes at the above two points, the torsion $\tau(\lambda)$ is given by:

$$\tau(\lambda)^2 = \lim_{\Delta\lambda \to 0} \left(\frac{\Delta\varphi}{\Delta\lambda}\right)^2$$

This theorem shows that curvature κ and torsion τ respectively indicate the revolution rates of the unit tangent vector and the tangent plane with the change of arc length λ.

On the other hand, if the differentiable functions $\kappa(\lambda)$ (> 0) and $\tau(\lambda)$ are given in the interval I, there is a definite regular space curve, in which the curvature and torsion are given by κ and τ with arc length λ, respectively. If we regard the curves, which fit each other by revolution and parallel dislocation, as identical, there is only one space curve fitting the given condition. Generally speaking, there are many formulae for expressing a space curve, e.g. $z = f(x, y)$; $x = f(t)$, $y = g(t)$, $z = h(t)$, and so on. But these equations show different forms in accordance with the setting of a coordinate system. On the contrary, $\kappa(\lambda)$ and $\tau(\lambda)$ with a parameter of arc length have geometrical significance, and define a unique space curve independent of any coordinate axis. Therefore, $\kappa = \kappa(\lambda)$ and $\tau = \tau(\lambda)$ can be regarded as equations of a space curve. They may be called 'natural equations of a space curve'.

Standardization of moving frame

The tube model for real coiling has an increasing whorl radius r throughout growth. To describe the pattern of heteromorph coiling geometry more precisely, it is necessary to consider not only the locus of the tube centre but also the tube radius. It is, therefore, impossible to use the natural equations of a space curve directly for a growing tube. In order to establish a method of differential geometric analysis for a coiling shell, it is necessary to devise some modifications of these parameters λ, κ, and τ.

In a Frenet frame, each coordinate axis is defined as a unit vector $\mathbf{t}$, $\mathbf{n}$, or $\mathbf{b}$. This frame is not suitable for a coiling tube because it is independent of the tube size. In this case, the unit length of a moving frame at an arbitrary stage should be defined as a length proportional to the tube radius. Therefore, I adopt three dimensional vectors $r\mathbf{t}$, $r\mathbf{n}$ and $r\mathbf{b}$ as a standardized moving frame instead of Frenet's. These may be adequate standards to estimate the mode of coiling corresponding to shell size and growth stage. Use of these vectors enables arc length, curvature, and torsion to be standardized as set out below.

Growth stage s

In the description of any growth pattern, time might be considered the most appropriate parameter. Among fossil organisms, however, time scale in the growing process cannot be detected. In the natural equations of a space curve, curvature κ and torsion τ are expressed as the functions of arc length λ. But arc length is not always a suitable parameter for expressing the growth of a coiling shell because it is independent of size. The description of growth should reflect an organism's size at any time. The concept of *relative growth* developed by Huxley (1932) is based upon this principle. If the concept of relative growth is applied to the tube model, scale can be defined differentially. For the analysis of tube coiling, I introduce a parameter s that indicates the *growth stage* of the coiling tube instead of λ. In the time interval from t to $t + dt$, the increase of the growth stage $ds(t)$ is related to the increase of arc length $d\lambda(t)$ and tube radius $r(t)$ as follows:

$$\frac{d}{dt}s(t) = \frac{1}{r(t)} \cdot \frac{d}{dt}\lambda(t)$$

Radius enlarging ratio E

The *radius enlarging ratio* is based upon the radii at two growth stages. If a slight advance of growth stage from s to $s + \varepsilon$ produces a change in tube radius from r to $r + \Delta r$, then the radius enlarging ratio E is given by:

$$E^{\varepsilon} = \frac{r + \Delta r}{r} \qquad \text{or} \qquad \ln E = \frac{d}{ds}(\ln r)$$

In this definition, E is a function of s, and prescribes the size of r at the next stage. On the other hand, the value of r is influenced by change in s, by which the radius enlarging ratio E is defined. Note that E and s are determined recurrently. This definition is generally more suitable for describing the mode of growth of a coiling shell.

Standardized curvature and torsion

The helicoid, gastropod-like model tube in text-fig. 6A appears to have a constant mode of coiling throughout growth, but the curvature κ and torsion τ calculated along the tube centre are not constant. Although the figure shows a proportional spiral curve, κ and τ must decrease with growth. The three tubes shown in text-fig. 6B–D are instructive: B and C show the same curvature of their centre line but have different radii, while B and D are similar in shape but different in size. Thus D must have a different value of curvature κ from B and C. In the tube model, however, it would be more convenient for B and D to be the same in their mode of coiling, and different from C. The curvature and torsion of a tube can be standardized so that the differential parameters are constant in such proportional growth as shown in text-fig. 6A, and so that text-fig. 6B and D have the same values. Therefore, I introduce new parameters *standardized curvature* C and *standardized torsion* T instead of κ and τ. The curvature and torsion of the tube model can be defined as the revolution rate of the standardized moving frame. Finally, the parameters C and T are given by:

$$C = r\kappa, \qquad T = r\tau.$$

By using these parameters, all geometrically similar figures can be expressed as the same coiling pattern.

Description of a growing tube

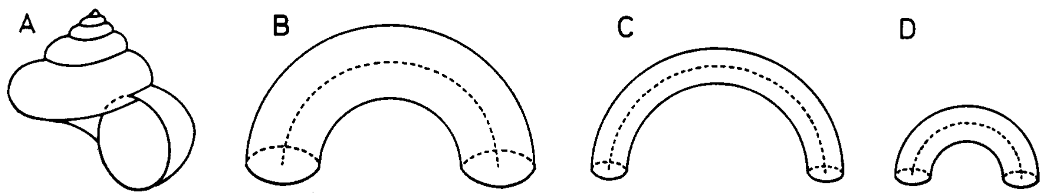
In the new tube model, I have now defined three parameters: E, radius enlarging ratio; C, standardized curvature; and T, standardized torsion. These describe the differential characters of a coiling tube in general, and are given by the parameter s, indicating growth stage, as follows:

$$E = E(s), \qquad C = C(s), \qquad T = T(s)$$

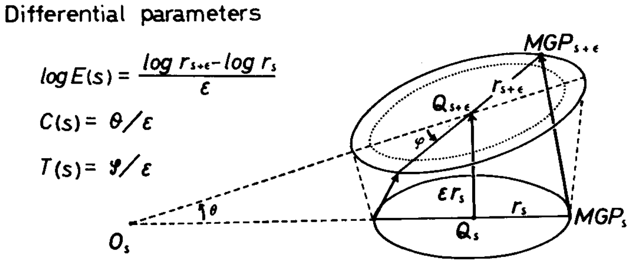
These three equations describe only the mode of coiling, not its size. For the description of shell size, a constant r_0 indicating initial tube radius must be introduced. If the three equations and one constant are given, a unique tube conforming with the conditions is obtained. Finally, the combination of $E(s)$, $C(s)$, $T(s)$, and r_0 may be regarded as a natural equation of the tube model. To the extent that a tube grows proportionally, the parameters E, C, and T are constants.

Moving frame analysis for the growing tube model

One of my main purposes here is to establish a method of analysis and description of the regular but free coiling of heteromorph ammonoids. Text-fig. 7 makes the geometric meaning of the parameters of the growing tube model more explicit. Given a circular generating curve with centre Q_s and radius r_s



TEXT-FIG. 6. Four hypothetical tubes. A, a proportional spiral, like a gastropod. B and C have the same curvature of the tube centre line, but a different tube radius. B and D are similar in shape but different in size.



TEXT-FIG. 7. Growing tube model showing the three differential parameters E, C, and T. In this theory the three parameters are calculated as a limit value of $\varepsilon = 0$.

at growth stage s, at the next growth stage $s+\varepsilon$ the centre of the circular generating curve shifts to $Q_{s+\varepsilon}$ along a line normal to this circle's plane. This direction indicates the tangential vector of the standardized moving frame. On the generating curve, there is a special point MGP_s which signifies the point of maximum growth at this growth stage. The normal vector of the standardized moving frame indicates the point MGP_s from Q_s. Then we can define the standardized moving frame $(r_s\mathbf{t}, r_s\mathbf{n}, r_s\mathbf{b})$ forming a right-hand system at an arbitrary growth stage.

Consequently, the generating curve can be explained as follows: 1, during growth of the tube from s to $s+\varepsilon$, the centre of the generating curve Q_s moves εr_s in length (θ radians) around the point O_s, in the tangent plane; 2, in the normal plane, the maximum growth point MGP_s revolves φ radians around Q_s; 3, the radius of the generating curve increases from r_s to $r_{s+\varepsilon}$. In this growth model for a generating curve, the parameters E, C, and T are given by:

$$\ln E = (\ln r_{s+\varepsilon} - \ln r_s)/\varepsilon$$
$$C = \theta/\varepsilon$$
$$T = \varphi/\varepsilon$$

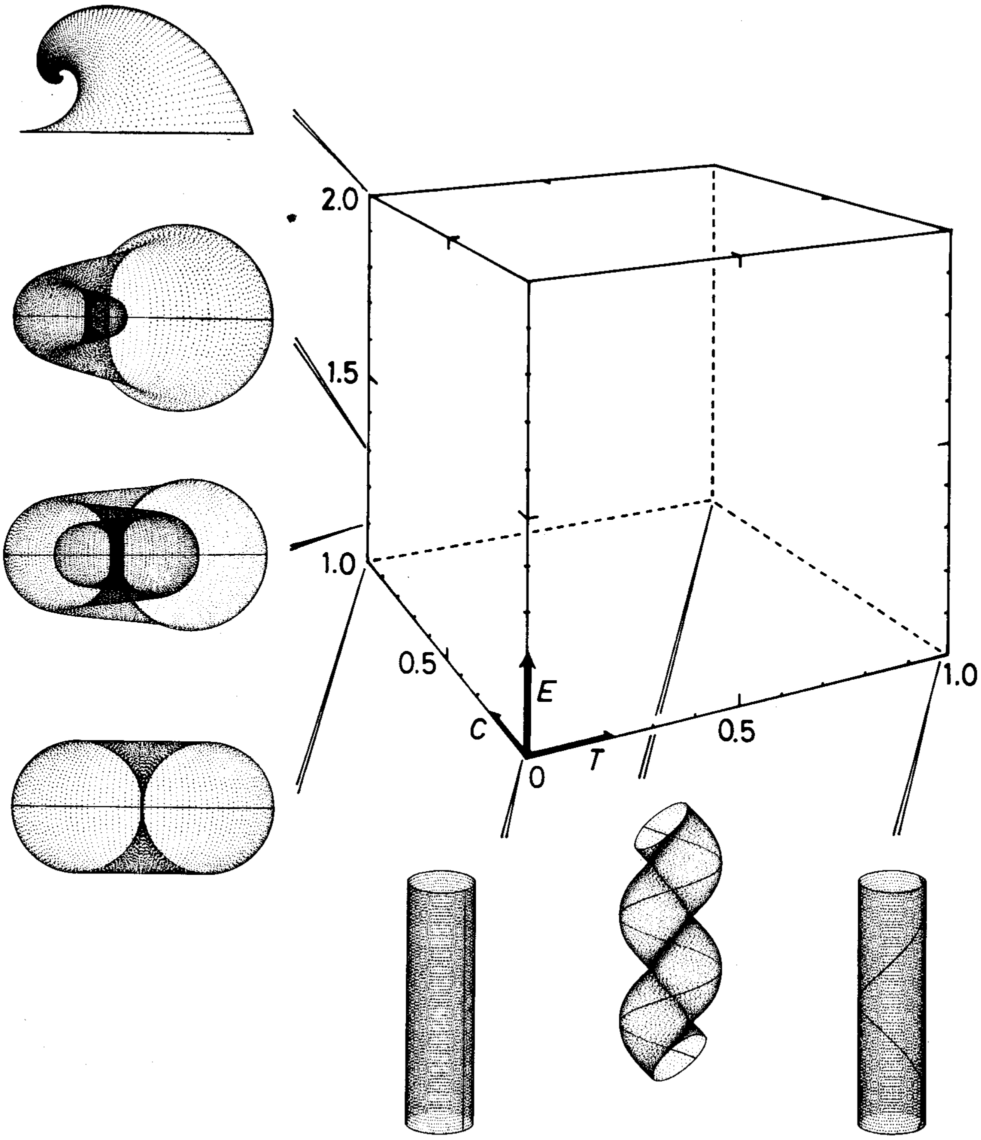
When the limit value ($\varepsilon = 0$) is taken, the three parameters can be defined more accurately. I have written a computer program SNAKY by which the above growing process can be visualized for different values of the three differential parameters E, C, and T (see Appendix). Text-figs. 8 and 9 show index figures produced by microcomputer; these diagrams correspond to Raup's (1966) representations.

E represents the ratio of enlargement of tube radius. So in the growing tube model, $E \geqq 1$ (when $E = 1$, tube radius is invariable). If E is extremely large, the aperture of the tube rapidly enlarges, like a limpet or pelecypod valve. If the ratio were smaller than 1, tube radius would decrease.

C represents the degree of tube bending. The theoretical range of this value is $0 \leqq C \leqq 1$. When $C = 0$, the shell grows straight, like an orthoconic cephalopod. When $C = 1$, however, the centre of revolution in the tangent plane lies at the inner margin of the generating curve. If $C > 1$, this point would lie inside the generating curve, a state never found in real coiled shells.

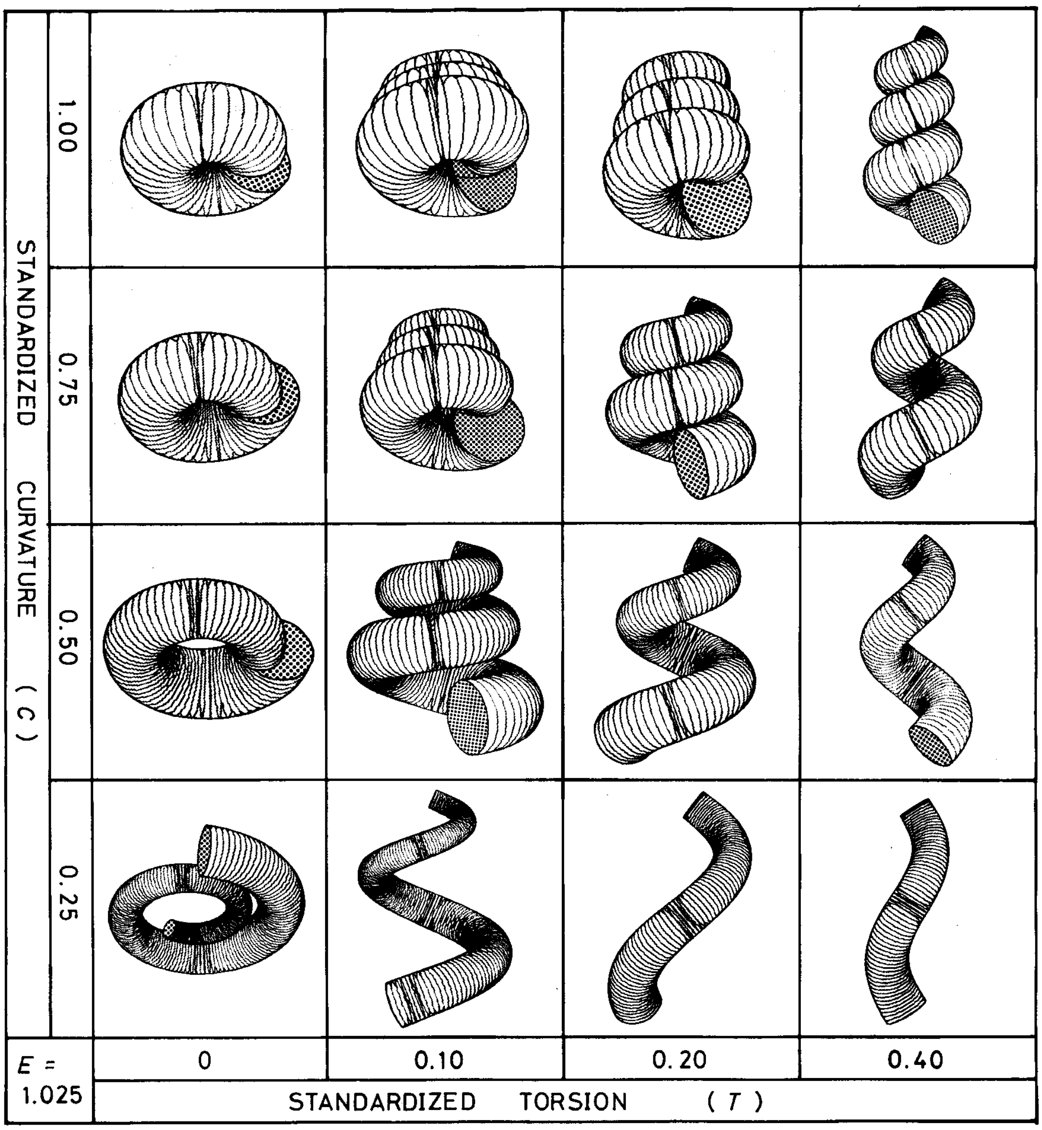
T represents the revolution rate of MGP (maximum growth point) in the generating curve, to which there is no theoretical limit. Whether coiling is dextral or sinistral is determined by the sign of T, and if $T = 0$ the tube is planispiral.

The moving frame in this growing tube model means a coordinate system that is always situated at the last generating curve, i.e. at the aperture of a coiling shell. In other words, this frame travels along the centre line of the coiling tube throughout its growth. Therefore, moving frame analysis is a method, using three parameters E, C, and T, that describes how the frame behaves in space. By applying this method to actual coiling shells, it is possible to analyse and express not only complex shell coiling but also any ontogenetic changes in mode of coiling. One of the striking merits of moving frame analysis in the growing tube model is its ability to determine uniquely the changing pattern of $E(s)$, $C(s)$, and $T(s)$, corresponding to each growth stage. Traditional methods, using a fixed coordinate



TEXT-FIG. 8. Three-dimensional block diagram showing the spectrum of hypothetical shells, when the three differential parameters E, C, and T are changed.

system, require extremely variable formulae according to slight differences of the fitting model. Furthermore, even for one and the same tube model, many equations are possible, dependent on different definitions of the axis or coordinate system. In the growing tube model, by contrast, any gently curved tube can be visually expressed by a diagram showing the change of the three parameters during growth. The more accurate the computer graphics representation becomes, the more closely a graph of the three parameters must approach a single pattern.



TEXT-FIG. 9. Spectrum of computer-produced hypothetical shell forms with various values of *C* and *T*, and a constant value of *E*. This corresponds to a horizontal section through the block diagram in text-fig. 8, near the base.

APPLICATION TO HETEROMORPH AMMONOIDS

Many well-preserved heteromorph ammonoids from the Upper Cretaceous of Hokkaido were described by Yabe (1904), Matsumoto (1967, 1977), Matsumoto and Kanie (1967), and others. Some species, especially those belonging to the Nostoceratidae and Diplomoceratidae, show peculiar three-dimensional coiling patterns; Tanabe *et al.* (1981) and Okamoto (1984) studied their coiling geometry. Here I analyse by moving frame analysis the growth patterns of several characteristic species of Nostoceratidae and Diplomoceratidae. The repositories of specimens are as follows: UMUT, University Museum, University of Tokyo; GK, Department of Geology, Kyushu University; WEA, Institute of Earth Science, Waseda University; and KPMG, Kanagawa Prefectural Museum.

Several methods can be used to estimate values for the parameters *E*, *C*, and *T* from actual specimens. One is to calculate them directly from specimen measurements. This method is effective for the estimation of standardized curvature *C* or radius enlarging ratio *E* in certain growth stages, but these values are difficult to measure continuously throughout growth: moreover, it is almost impossible to estimate the standardized torsion *T* by this method because the maximum growth point *MGP* is not evident on the shell surface. Alternatively, we can employ the tube model to model a specimen using a fixed coordinate system to obtain the equations of the centre line of the tube and its radius. The coefficients in the equations can then be determined from measurements of actual specimens. When the equations of the tube model and their coefficients are known, it is possible to calculate the three differential parameters *E*, *C*, *T* and corresponding growth stage *s*. Thirdly, there is trial and error, using computer graphics after making rough estimates of *E*, *C*, and *T*; by comparing the result with actual specimens, the pattern of these differential parameters can be precisely determined.

In practice I employed all three methods until I obtained a satisfactory approximation to the actual fossils. Some of the results are shown in text-figs. 10 and 11, together with graphs of *E*, *C*, and *T*. The following specimens were used for the comparisons:

Eubostrychoceras japonicum (Yabe, 1904). KPMG 6373, text-fig. 11B; Pl. 7, fig. 9.
E. muramotoi Matsumoto, 1967. WEA 003T-1, text-fig. 10C; Pl. 7, figs. 3 and 4.
Nipponites mirabilis Yabe, 1904. UMUT MM17738, text-fig. 11D; Pl. 7, fig. 10.
Muramotoceras yezoense Matsumoto, 1977. WEA 001Y, text-fig. 10B; Pl. 7, fig. 2.
Hyphantoceras orientale (Yabe, 1904). WEA 002K, UMUT MM17741, text-fig. 11A; Pl. 7, figs. 7 and 8.
Ainoceras kamuy Matsumoto and Kanie, 1967. GK H5575, text-fig. 10D; Pl. 7, fig. 5.
Scalarites scalaris (Yabe, 1904). UMUT MM17739, 17740, text-fig. 10A; Pl. 7, fig. 1.
Polyptychoceras sp. KPMG 6374, text-fig. 11C; Pl. 7, fig. 6.

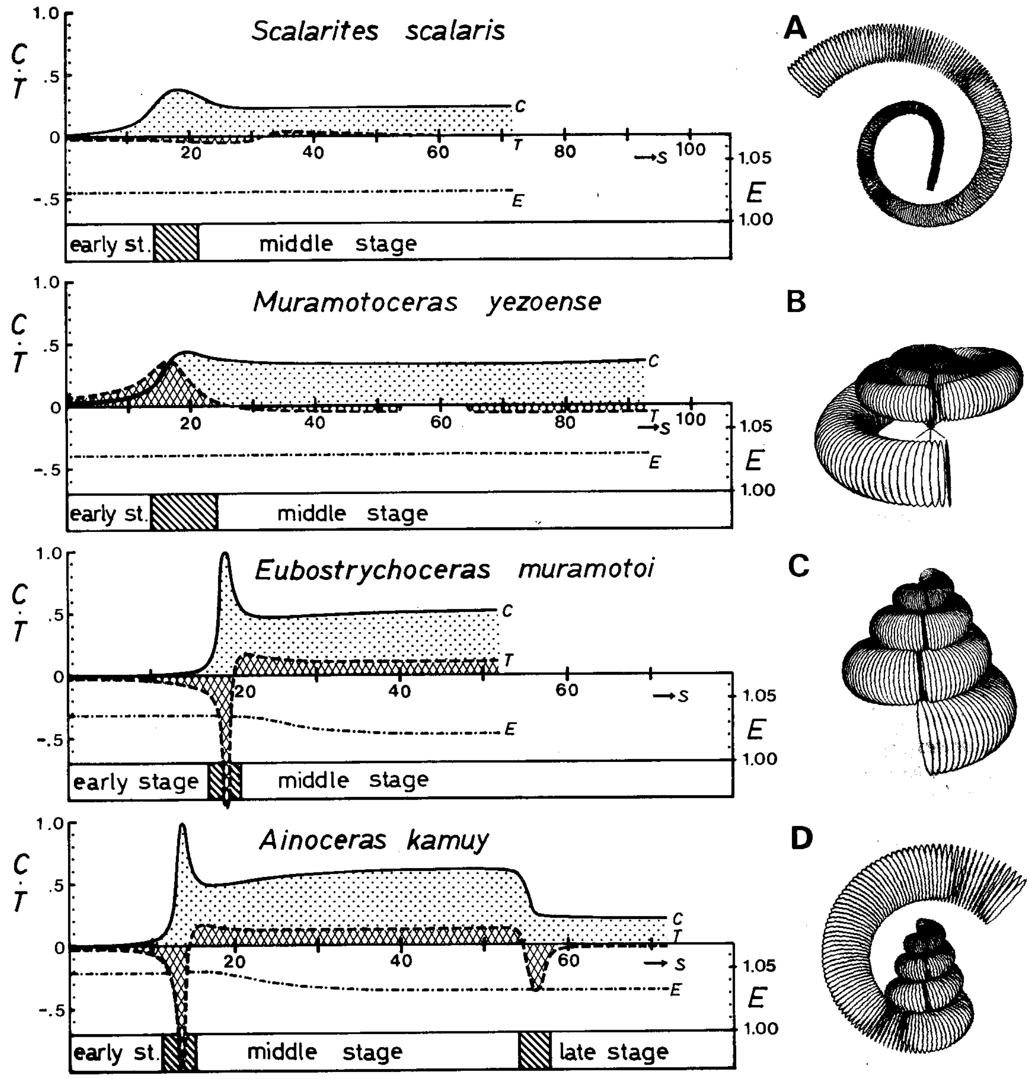
The computer-produced figures represent well the fundamental coiling properties of real specimens (text-figs. 10 and 11).

DISCUSSION

Ontogenetic change

The shell growth of heteromorph ammonoids often consists of a few stable stages divided by abrupt changes of coiling pattern. For example, *M. yezoense* and *E. muramotoi* show a transitional interval between two stable stages (early orthoconic stage and helicoid stage; text-fig. 10B, C). In each stable stage, the three differential parameters maintain nearly constant values, but in the transitional interval standardized curvature *C* and torsion *T* change abruptly. *A. kamuy* shows essentially the same coiling pattern (text-fig. 10D) in its early-middle growth, but then goes through a short transitional interval and finally forms a retroversal hook, which also has comparatively stable differential parameters. In *N. mirabilis* (text-fig. 11D), two stages are clearly discriminated. Early on, the whorl forms a loose open helix with constant differential parameters; later, however, the whorl meanders intensely around the earlier helicoid. *C* and *T* oscillate regularly during this meandering, but the stage should still be regarded as stable because the variation is regular.

Changes of coiling pattern during ontogeny can be understood clearly using moving frame analysis. Rapid change of *C* indicates rapid change of the whorl's direction of growth. Provided the ventral margin of the organism roughly coincides with the whorl maximum growth point (*MGP*), a rapid change of *T* suggests a rapid twist of the ventral side of the living chamber. In a transitional interval

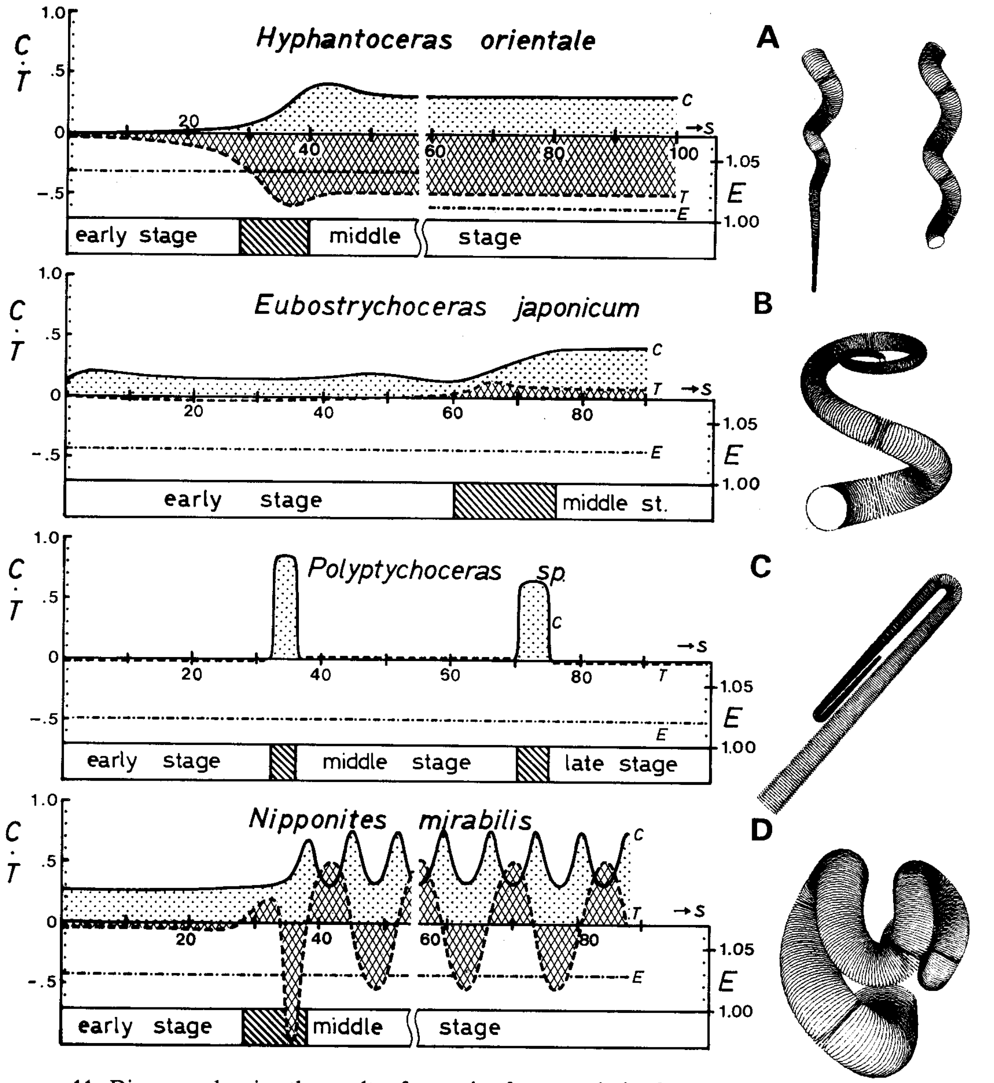


TEXT-FIG. 10. Diagrams showing the results of a moving frame analysis of some actual specimens. Right-hand figures are computer-produced profiles corresponding to the diagrams. A, *Scalarites scalaris*, UMUT MM17739, 17740. B, *Muramotoceras yezoense*, WEA 001Y. C, *Eubostrychoceras muramotoi*, WEA 003T-1. D, *Ainoceras kamuy*, GK H5575.

between stable growth stages, *C* and *T* often change simultaneously. Such abrupt changes of coiling mode between stable stages suggest changes in mode of life.

Interspecific comparison

In early growth, many heteromorph species possess a nearly orthoconic shell, with very small values of *C* and *T*. After the first transitional interval, shell forms become variously diversified. Similar



TEXT-FIG. 11. Diagrams showing the results of a moving frame analysis of some actual specimens. Right-hand figures are computer-produced profiles corresponding to the diagrams. A, *Hyphantoceras orientale*, WEA 002K, UMUT MM17741. B, *Eubostrychoceras japonicum*, KPMG 6373. C, *Polyptychoceras* sp., KPMG 6374. D, *Nipponites mirabilis*, UMUT MM17738.

coiling patterns may occur in different lineages. For example, a similar change of coiling pattern is found in *M. yezoense*, *E. muramotoi*, and *A. kamuy*. These ammonoids have orthoconic shafts in early growth; after the quick turn up, a helical whorl forms and coils around the earlier orthocone. *N. mirabilis* and *Madagascarites ryu* have a similar meandering coiling pattern in their middle growth stage (Matsumoto and Muramoto 1967), yet the former belongs to Nostoceratinae and the latter to

Hyphantoceratinae (Matsumoto 1967); this morphological convergence suggests a similar mode of life.

On the other hand, some heteromorph ammonoids show quite different coiling patterns in spite of a close phylogenetic relationship. For instance, *N. mirabilis* and *E. japonicum* share similar surface ornamentation and loose helical coiling in early growth. Matsumoto (1977) suggested that *Nipponites* was derived from *Eubostrychoceras*. During their middle growth stages, however, the two species are quite different in coiling pattern, and no transitional form has been found. Also, in the differential parameters, a transition between the two species is difficult to envisage; some saltation of coiling geometry must have occurred, if this phylogenetic relationship is true.

Hypothetical shell coiling

Analysis using these differential parameters appears to elucidate the mechanism of shell coiling. Nostoceratid and diplomoceratid ammonoids show considerable intraspecific variation and coiling diversity. If the three parameters were freely variable, a tremendous range of shell form would result. An analysis of the coiling of actual specimens, however, shows that changes in these parameters are closely related to one another and, consequently, produce well-regulated shell forms. For example, I have successfully reconstructed the trombone-like profile of *Polyptychoceras* sp. mainly using a trial and error method of computer graphics (text-fig. 11c), and values 10% larger or smaller than the best fit values of C and T produce biologically impossible shell shapes (text-fig. 12). This result strongly suggests that some regulatory mechanism affects the pattern of shell growth, so as to produce 'well-proportioned' coiling, which occupies only a very narrow band within the imaginable spectrum; this probably has high adaptability to the environment.

CONCLUSIONS

The shells of many invertebrates are formed by accretionary growth. Therefore, if growth at the aperture is exactly described, shell form can be determined absolutely. The growing tube model was derived from such a recognition, and is applicable to any pattern of shell coiling as a first approximation. One of the most practical merits of the model is that perfect similitude is kept at any growth stage because growth patterns are described relative to tube radius. This model is probably the most appropriate one available for the recognition of the actual growing process of tubular shells. Moving frame analysis enables the highly allometric and complicated coiling patterns of tubular

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EXPLANATION OF PLATE 7

Fig. 1. *Scalarites scalaris* (Yabe). UMUT MM17739, Middle Yezo Group, Turonian; Tappu area, central Hokkaido. Lateral view, ×1·5.

Fig. 2. *Muramotoceras yezoense* Matsumoto. WEA 001Y, Middle Yezo Group, Turonian; Oyubari area, central Hokkaido. Upper view, ×1.

Figs. 3 and 4. *Eubostrychoceras muramotoi* Matsumoto. WEA 003T-1, Upper Yezo Group, Coniacian; Tappu area, central Hokkaido. 3, lateral and 4, apical views, ×1·5.

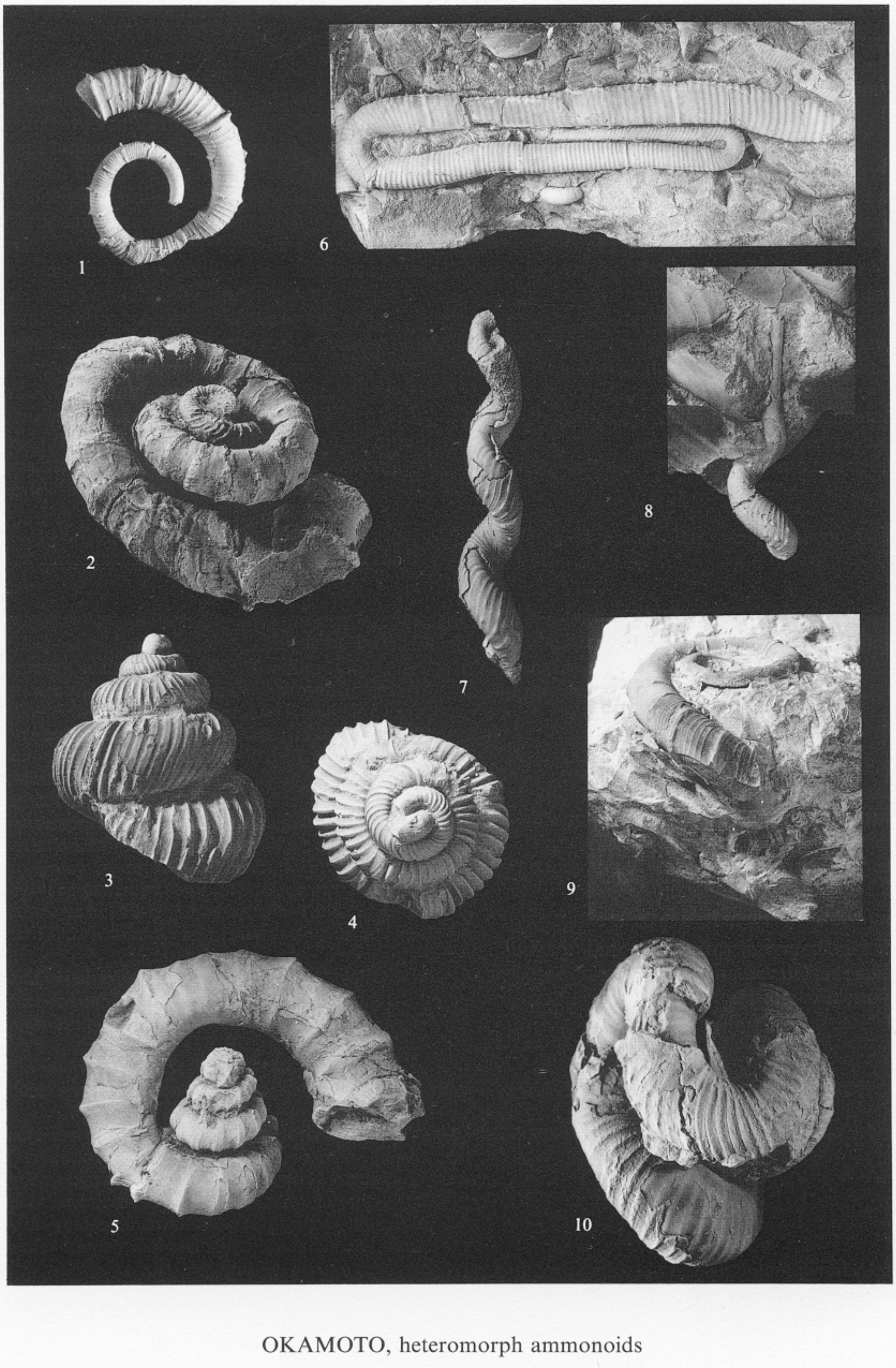
Fig. 5. *Ainoceras kamuy* Matsumoto and Kanie. GK H5575, Upper Yezo Group, Campanian; Saku area, north Hokkaido. Lateral view of retroversal hook, ×1.

Fig. 6. *Polyptychoceras* sp. KPMG 6374, Upper Yezo Group, Santanian–Campanian; Saku area, north Hokkaido. Lateral view, ×0·67.

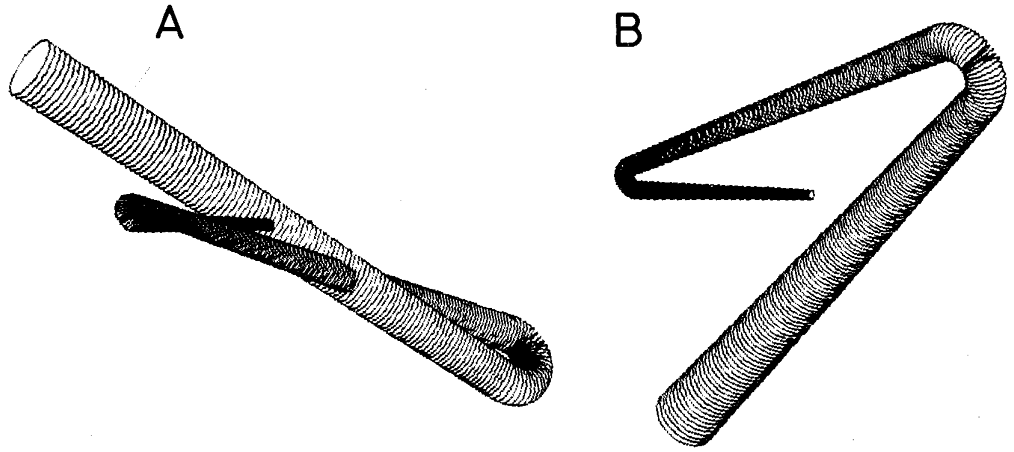
Figs. 7 and 8. *Hyphantoceras orientale* (Yabe). Upper Yezo Group, Santonian; Kotambetsu area, central Hokkaido. 7, UMUT MM17742, lateral view of middle helicoid stage, ×1. 8, WEA 002K, lateral view of early stage, ×1·5.

Fig. 9. *Eubostrychoceras japonicum* (Yabe). KPMG 6373, Middle Yezo Group, Turonian; Kiritachi area, central Hokkaido. Ventral view of early stage, ×1.

Fig. 10. *Nipponites mirabilis* Yabe. UMUT MM17738, Middle Yezo Group, Turonian; Oyubari area, central Hokkaido. Lateral view, ×1.



OKAMOTO, heteromorph ammonoids



TEXT-FIG. 12. Two hypothetical but unlikely shell forms of *Polyptychoceras* sp. A, differential parameters C and T 10% larger than actual values of text-fig. 11C. B, 10% smaller.

shells to be described, analysed, and compared. If ontogenetic similarity indicates close phylogenetic relationship, moving frame analysis may be useful for the classification of heteromorph ammonoids and the reconstruction of evolutionary lineages.

The growing tube model has other possible applications. If the growth of a whorl is successfully reproduced, the volume or capacity of the shell, its surface area, centre of gravity (or buoyancy), and many other physical quantities can be easily computed by integrating the differential parameters. Trueman (1941) made some qualitative inferences about the living position of some heteromorph ammonoids by considering the relationship of centre of gravity to centre of buoyancy. Klinger (1981) discussed qualitatively the mode of life of some heteromorph ammonoids from the standpoint of possible buoyancy control. By combining his concept of life orientation with the growing tube model, any changes in life position during ontogeny can be predicted for various heteromorph ammonoids (Okamoto, in press).

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APPENDIX

The SNAKY program was written in N-88 BASIC for a 16-bit personal computer NEC PC-9801 series, interfaced with PC-8853n CRT and PC-PR101F (for hard copy production). The abridged version for *Palaeontology* does not provide some supplementary functions (e.g. elimination of back lines and calculation of physical quantities), and requires the input of sequential data for parameters *E*, *C*, *T*, and *s* before running.

```
1 '****************************************************************
2 '*  label : SNAKY.abg                                            *
3 '*          programmed by T. Okamoto                1985/2/12    *
4 '*          abridged version for 'Palaeontology'   1987/5/24    *
5 '****************************************************************
6 CONSOLE 0,25,0,0: SCREEN 3: CLS 3
1000 '*********************************** Data Input ******* 1000
1010 INPUT "Label of data ";LBL$
1020 OPEN "2:"+LBL$ FOR INPUT AS #1
1030 INPUT #1,COMENT$,NUM
1040 DIM S(NUM),E(NUM),C(NUM),T(NUM)
1050 FOR I=1 TO NUM
1060 INPUT #1,DAM,S(I),E(I),C(I),T(I)
1070 NEXT I: CLOSE #1
1080 XO=300: YO=200:   XS=5: YS=5:  PI=3.14159
1090 INPUT "VIEW ANGLE   [p,q,r]";P1,Q1,R1
2000 '*********************************** First Setting **** 2000
2010 IF P1=0 AND Q1=0 THEN COC=1: SIC=0: GOTO 2040
2020 COC=Q1/SQR(P1^2+Q1^2)
2030 SIC=P1/SQR(P1^2+Q1^2)
2040 COD=SQR(P1^2+Q1^2)/SQR(P1^2+Q1^2+R1^2)
2050 SID=R1/SQR(P1^2+Q1^2+R1^2)
2060 '                              [ coordinates ]
2070 P0=40: Q0=0: R0=0: GOSUB *ANGLE   ' X-axis
2080 LINE (XO-XS*S,YO+YS*U)-(XO+XS*S,YO-YS*U),1
2090 P0=0: Q0=40: R0=0: GOSUB *ANGLE   ' Y-axis
2100 LINE (XO-XS*S,YO+YS*U)-(XO+XS*S,YO-YS*U),1
2110 P0=0: Q0=0: R0=40: GOSUB *ANGLE   ' Z-axis
2120 LINE (XO-XS*S,YO+YS*U)-(XO+XS*S,YO-YS*U),1
2130 '                              [ starting condition ]
2140 X=0   : Y=0   : Z=0                ' origin
2150 P=0   : Q=0   : R=1                ' growth direction
2160 RA=2                               ' radius
2170 MGX=RA   : MGY=0   : MGZ=0         ' maximum growth point
3000 '*********************************** Growing Process ** 3000
3010 FOR I=1 TO NUM-1
3020 IF I<>1 THEN GOSUB *MOVEMENT
3030 '                              [ view angle ]
3040 P0=P: Q0=Q: R0=R                   ' growth direction
3050 GOSUB *ANGLE
3060 PP=S: QQ=T: RR=U
3070 P0=X: Q0=Y: R0=Z                   ' centre of tube
3080 GOSUB *ANGLE
3090 XX=S: YY=T: ZZ=U
3100 P0=MGX: P0=MGY: R0=MGZ             ' maximum growth point
3110 GOSUB *ANGLE
3120 MGX1=S: MGY1=T: MGZ1=U
3130 GOSUB *GRAPHICS
3140 NEXT I: END
4000 *MOVEMENT '-------------------------------------------- 4000
4010 EPSILON=S(I+1)-S(I)
4020 RA=RA*E(I)^EPSILON
4030 CUR=C(I)*EPSILON
4040 TOR=T(I)*EPSILON
4050 '                              [ next condition ]
4060 GOSUB *ROTATION1                   ' maximum growth point
4070 FX4=RA: FY4=0: FZ4=0
4080 GOSUB *ROTATION2
4090 FZ5=FZ5+RA*EPSILON
4100 GOSUB *ROTATION3
4110 GOSUB *ROTATION4
4120 MGX=FX8: MGY=FY8: MGZ=FZ8
4130 FX4=0: FY4=0: FZ4=0                ' centre of tube
4140 GOSUB *ROTATION2
4150 FZ5=FZ5+RA*EPSILON
4160 GOSUB *ROTATION3
4170 GOSUB *ROTATION4
4180 X=FX8: Y=FY8: Z=FZ8
4190 FX4=0: FY4=0: FZ4=1                ' growth direction
4200 GOSUB *ROTATION2
4210 GOSUB *ROTATION3
4220 P=FX7: Q=FY7: R=FZ7
4230 RETURN
4240 '                                     [ revolutionary subroutines ]
4250 *ROTATION1                                             ' *** R1 ***
4260 '..........  F:(1) ...................................
4270 FX1=MGX-X
4280 FY1=MGY-Y
4290 FZ1=MGZ-Z
4300 '..........  F:(2) ...................................
4310 IF P^2+Q^2=0 THEN CO1=1 ELSE CO1=P/SQR(P^2+Q^2)
4320 IF P^2+Q^2=0 THEN SI1=0 ELSE SI1=Q/SQR(P^2+Q^2)
4330 CO2=R/SQR(P^2+Q^2+R^2)
4340 SI2=SQR(P^2+Q^2)/SQR(P^2+Q^2+R^2)
4350 FX2=FX1*CO1*CO2+FY1*SI1*CO2-FZ1*SI2
4360 FY2=-FX1*SI1+FY1*CO1
4370 FZ2=FX1*CO1*SI2+FY1*SI1*SI2+FZ1*CO2
4380 '..........  F:(3) ...................................
4390 CO3=COS(TOR)
4400 SI3=SIN(TOR)
4410 FX3=FX2*CO3-FY2*SI3
4420 FY3=FX2*SI3+FY2*CO3
4430 FZ3=FZ2
4440 '..........  F:(4) ...................................
4450 IF FX3^2+FY3^2=0 THEN CO4=1 ELSE CO4=FX3/SQR(FX3^2+FY3^2)
4460 IF FX3^2+FY3^2=0 THEN SI4=0 ELSE SI4=FY3/SQR(FX3^2+FY3^2)
4470 FX4=FX3*CO4+FY3*SI4
4480 FY4=-FX3*SI4+FY3*CO4
4490 FZ4=FZ3                      : RETURN
4510 *ROTATION2                                             ' *** R2 ***
4520 '..........  F:(5) ...................................
4530 GR1=RA*(EPSILON+CUR)
4540 GR2=RA*(EPSILON-CUR)
4550 CO5=2*RA/SQR((GR1-GR2)^2+(2*RA)^2)
4560 SI5=(GR1-GR2)/SQR((GR1-GR2)^2+(2*RA)^2)
4570 FX5=FX4*CO5-FZ4*SI5
4580 FY5=FY4
4590 FZ5=FX4*SI5+FZ4*CO5          : RETURN
4610 *ROTATION3                                             ' *** R3 ***
4620 '..........  F:(6) ................. rev. of F(4)....
4630 FX6=FX5*CO4-FY5*SI4
4640 FY6=FX5*SI4+FY5*CO4
4650 FZ6=FZ5
4660 '..........  F:(7) ................. rev. of F(2)....
4670 FX7=FX6*CO1*CO2-FY6*SI1+FZ6*CO1*SI2
4680 FY7=FX6*SI1*CO2+FY6*CO1+FZ6*SI1*SI2
4690 FZ7=-FX6*SI2+FZ6*CO2         : RETURN
4710 *ROTATION4                                             ' *** R4 ***
4720 '..........  F:(8) ................. rev. of F(1)....
4730 FX8=FX7+X
4740 FY8=FY7+Y
4750 FZ8=FZ7+Z                    : RETURN
5000 *ANGLE '---------------------------------------------------- 5000
5010 S=P0*COC-Q0*SIC
5020 T=P0*SIC*COD+Q0*COC*COD+R0*SID
5030 U=-P0*SIC*SID-Q0*COC*SID+R0*COD
5040 RETURN
6000 *GRAPHICS '------------------------------------------------- 6000
6020 IF PP^2+QQ^2=0 THEN COA=1 ELSE COA=PP/SQR(PP^2+QQ^2)
6030 IF PP^2+QQ^2=0 THEN SIA=0 ELSE SIA=QQ/SQR(PP^2+QQ^2)
6040 COB=RR/SQR(PP^2+QQ^2+RR^2)
6050 SIB=SQR(PP^2+QQ^2)/SQR(PP^2+QQ^2+RR^2)
6060 FOR J=0 TO 360 STEP 9
6070 X2=X1: Y2=Y1: Z2=Z1
6080 X0=RA*COS(J*PI/180)
6090 Y0=RA*SIN(J*PI/180)
6100 Z0=0
6110 X1=X0*COA*COB-Y0*SIA+Z0*COA*SIB
6120 Y1=X0*SIA*COB+Y0*COA+Z0*SIA*SIB
6130 Z1=-X0*SIB+Z0*COB
6140 IF J=0 THEN 6160
6150 LINE (XO+XS*(X1+XX),YO-YS*(Z1+ZZ))-
          (XO+XS*(X2+XX),YO-YS*(Z2+ZZ)),6
6160 NEXT J                      : RETURN
```