Computer simulation of some ammonoid suture lines

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1 author:

Giuseppe Damiani
Italian National Research Council

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GIUSEPPE DAMIANI

c/o Dipartimento di Genetica e Microbiologia - Via S. Epifanio 14, 27100 Pavia

RIASSUNTO

Algoritmi che si basano su semplici istruzioni ricorsive sono in grado di generare al computer delle linee suturali di ammonoidi. Queste simulazioni al computer mostrano alcune caratteristiche comuni alle linee suturali e alla loro evoluzione. Tali linee sono frattali, vascolari, peaniane e presentano una tendenza all'aumento del grado di complessità e della dimensione frattale durante l'ontogenesi e lafilogenesi. Quindi l'evoluzione delle linee suturali ha rappresentato un miglioramento nella raccolta e nella distribuzione uniforme degli sforzi di trazione e compressione sulla conchiglia degli ammonoidi rendendola più resistente alla pressione idrostatica.

ABSTRACT

In computer simulations algorithms based on simple recursive rules can generate different ammonoid suture lines revealing some common characteristics of the suture lines and their evolution. These lines are fractal, vascular, peanian and both their complexity and fractal dimension have had the tendency to increase during ontogenetic and phylogenetic development. Therefore the evolution of suture and septa morphology has improved the gathering of the traction and compression stresses and their uniform distribution on the ammonoid shell making it more resistant to hydrostatic pressure.

KEY WORDS
Septal morphology, fractal, shell strength

INTRODUCTION

The evolution of ammonoid septum and their associated suture line has been intensively studied due to its great importance in the determination of ammonoid classification and phylogeny (Arkell, Kummel & Wright, 1957; Wiedmann R.L. & Kullman, 1981). There is a general trend of suture ontogenetic and phylogenetic evolution leading to a continuous increase in their complexity due chiefly to the increase in sutural lobe number and frilling. A variety of opinions exist regarding the reasons for this evolution. Many important questions are open. What has caused this evolution? What is the functional significance of the septal morphology? What mechanism underlies septum and suture line formation?

The non-adaptionists, as Gould (Gould, 1982), claim that the septum evolution has no functional meaning but many Authors disagree with this opinion.

A variety of adaptive explanations have been proposed, among which the oldest (Owen 1843, fide Spath, 1919), the most reasonable and backed by data proposes that the complex septal morphology increases the strength of the shell. This implies that the ammonoid phragmocone was a rigid floating structure tending to have maximum volume with minimum weight. In a recent paper, Hewitt &

Westermann review and discuss the different hypotheses and functional models concerning complexly fluted ammonoid septa evolution (Hewitt & Westermann, 1986; Hewitt & Westermann, 1987). The analysis of the mechanical principles involved in the static of ammonoid shell leads to the conclusion that septal evolution serves to increase shell resistance to hydrostatic pressure applied via the shell wall ("Westermann model") (Westermann, 1971; Westermann, 1975) and the body chamber ("Pfaff model") (Pfaff, 1911).

This agrees with my conclusions presented in previous works (Damiani, 1978; Damiani, 1984; Damiani, 1986). Using some principles of the construction theory, it is possible to analyse the processes and the structural constraints that have determined septa and suture line evolution. A. Seilacher has also demonstrated using mechanical simulations, that when an elastic membrane is pressed into a rigid cylinder with an elliptical cross section, the frontal pressure induces the septum to assume a hemispherical shape and the lateral pressure produces the anticlastic folding of the septum which in turn attaches itself to the wall along a ring shaped suture line (Seilacher, 1975).

This is due to the fact that in a homogeneous and elastic material the deformation energy is spread in the most homogeneous of all possible ways in every element: therefore, every fixed long axial element subjected to a load (like septa and shell walls) which tends to compensate some of the compression stresses transforming them into traction stresses by means of Eulerian arch bulking. For this reason an arch is more resistant to a uniform load than a lintel and a fixed long rod, or a thin panel, subjected to a load bend itself in an arch shape. In these structures, the stresses are discharged and compensated for better along the fixing points while the value of the bending stresses in points distant from the fixing points is higher. Therefore these central points are the weakest points, so that a rupture is more probable. In a rigid cylinder with a non-circular cross section the distribution of bending stresses is asymmetric. It is possible to derive this distribution by drawing one or more circles most closely approximate the cylinder section. A graphical representation of these bending stresses along the section corresponds well with the general aspect of the simplest suture line. An experimental demonstration of this theoretical consideration can be obtained using a polariscopy which permits visualisation of the stresses distributions in a thin sheet of fotoelastic material, whose shape is analogous to that of an ammonoid septum, subjected to a uniform pressure on the perimeter.

The presumed orientation of the septum making structure along these main bending stress lines results in the production of the most ancestral and simple septa of nautiloids and Paleozoic ammonoids with a sinuous and goniatitic type suture.

The genesis of the more complex septa and sutures is not well understood. Westermann suggests that the septum making structure was an aponeurosis-like structure reattached sequentially from the extremities of the lobes anterior to those of the saddles at fixed tie-points during the construction of the saddles at fixed tie-points during the construction of each septum (Westermann, 1975). But little has been said regarding the localisation of these tie-points: whether this has been genetically determined or influenced by the bending stress on the shell walls and septum still remains an open question. In this article I will try to provide a possible answer to this question.

COMPUTER SIMULATION OF STRUCTURES ANALOGOUS TO THE SUTURE LINES

Scientists describe unifying analogies and common aspects of different natural phenomena by means of mathematical relations. The standard way of modelling the laws of physics is through analytical calculus, typically in the form of differential equations. With the advent of computers a new kind of mathematics was developed, which deals with functions defined on a discrete rather than continuos set of points. Recently, in particular, the French researcher Mandelbrot has developed the discrete mathematics of irregular structures called fractals (Mandelbrot, 1975; Mandelbrot, 1982). A fractal structure is endowed with scale-invariance: it reveals the same pattern, more or less ordered, at different scales when examined with magnifying lenses of different strengths. Many objects in nature are fractal structures, such as trees, cumulus clouds, coastlines, mountains, lungs and many others. As written in a recent article: “The mathematical concept of fractal scaling brings an elegant new logic to the irregular structure, growth and function of complex biological forms”. (West & Goldberger, 1987).

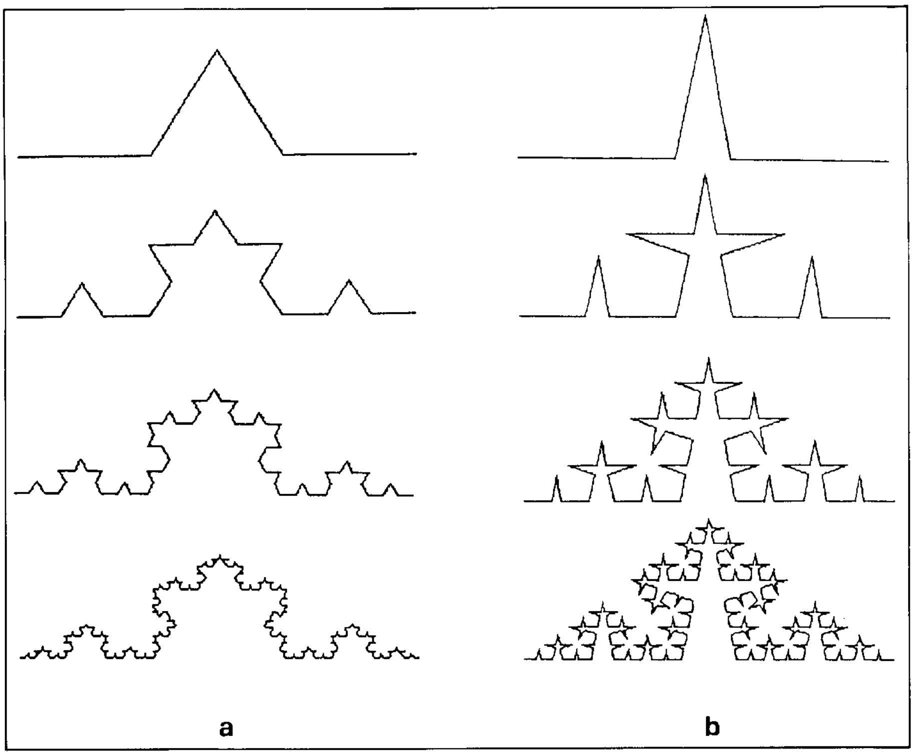
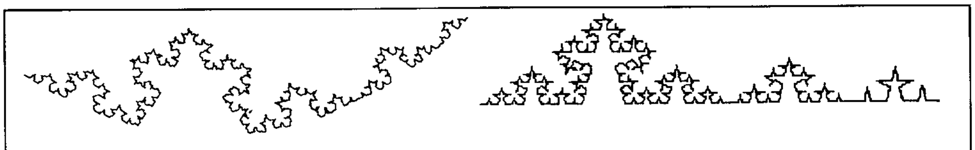


Fig. 1 - The first four stages in the growth of Koch lines. The recursive rules for the generation of the two lines are the same except for the angle of the new growing tips.

Everybody can observe the morphological analogy between complex suture lines and the tree-like fractal structures. In particular, I was interested in the analogy between the ammonitina suture line and a line discovered in the 1904 by the mathematician Koch (fig. la) (Koch, 1904). It is possible to write simple computer programs in Basic or in Logo language for the generation of this line. A Koch line is produced by the repetition of a set of simple rules which is called a generator: a straight line segment of N length is divided into three equal parts and then the central part 1/3 N long is displaced with two sides of an equilateral triangle which make an angle A of 60 degrees with the starting segment of length N (fig. la). The result is a broken line 4/3 N long composed by four segments 1/3 N long.

Another way of producing the Koch lines by means of the Logo “turtle geometry” is to follow these generator rules: forward 1/3 N, turn left A, forward 1/3 N, turn right 2 x A, forward 1/3 N, turn left A and forward 1/3 N (fig. 2). Repetition of these recursion generation rules on each new line segments K times produces a line (4/3) K long. K is called recursion level or



FR 280 70 4

```
TO F :N :A :L
IF :L = 0 [FD :N STOP]
F :N / 3 :A :L - 1
LT :A
F :N / 3 :A :L - 1
RT :A * 1.99
F :N / 3 :A :L - 1
LT :A
F :N / 3 :A :L - 1
END

TO FR :N :A :L
HT
PU
SETPOS [-100 -50]
SETH 90
PD
F :N :A :L
F :N - 200 :A :L - 1
F :N - 250 :A :L - 2
END
```

FR 330 78 4

```
TO F :N :A :L
IF :L = 0 [FD :N STOP]
F :N / 3 :A :L - 1
LT :A
F :N / 3 :A :L - 1
RT :A * 2
F :N / 3 :A :L - 1
LT :A
F :N / 3 :A :L - 1
END

TO FR :N :A :L
HT
PU
SETPOS [-100 -50]
SETH 90
PD
F :N :A :L
F :N - 200 :A :L - 1
F :N - 250 :A :L - 2
END
```

Fig. 2 - Programs generating Koch-like line analogous to the suture line. The programs are written in Logo language. F and FR are the names of the procedures. The variables :N, :A and :L are respectively the length of the starting segment, the value of the growing tips angle and the degree of complexity. The Logo rules abbreviations are: FD = forward, LT = left, RT = right, HT = makes cursor invisible, PU = pen up, SETPOS = moves cursor to specified coordinates, SETH = sets cursor direction to specified degree and PD = pen down.

degree of complexity.

Another important entity, called fractal dimension D, is a value that indicates how the Koch line fills in the plane: for each scale change by three, we need four such parts, thus according to the equations D = log4/log3 = 1.26. Therefore the Koch line is more "dense" than a monodimensional line (D = 1) and less "dense" than a bidimensional plane (D = 2). The increasing values of the angle results in an increasing D value (fig. lb) and in particular for A = 90 degrees a special line with D = 2 is obtained (fig. 3a). This line, discovered in the 1903 by Cesaro (Cesaro E., 1903), fills the entire plane and is therefore a "peanian line": a monodimensional entity, which fills in a bidimensional entity. An interesting fractal line, discovered by Mandelbrot (Mandelbrot 1973), is produced by a generator similar to that of the Koch line and is shown in fig. 3b.

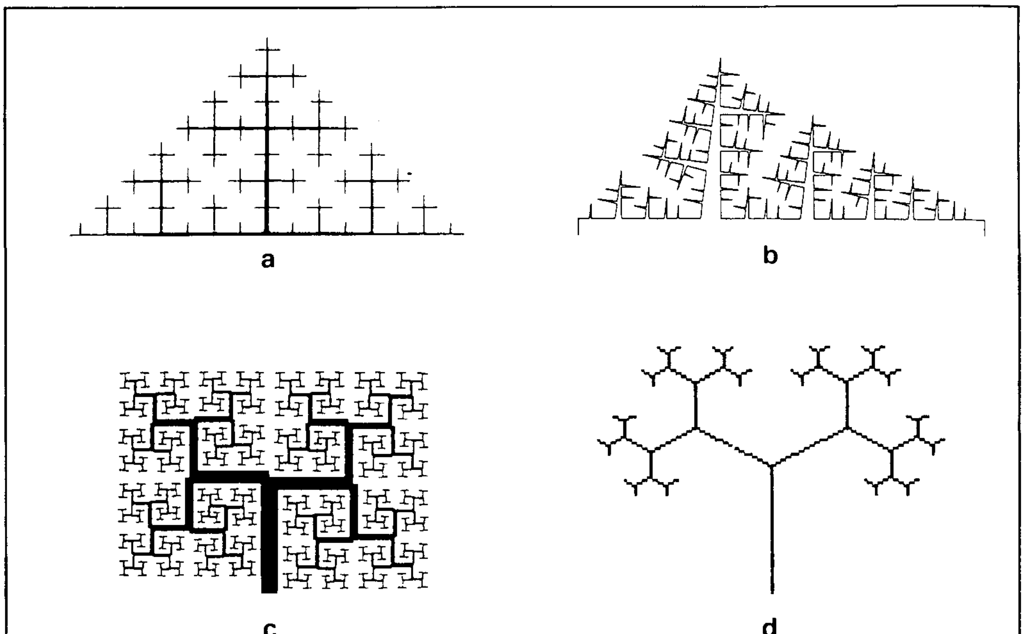


Fig. 3 - Comparasion among Koch-like lines and tree-like lines. These lines, whose fractal dimension is equal or close to two, are generated by recursive rules: at each growth stage each tip develops two new tips located at the middle of the old tip in the Cesaro line (a) (and also in most of the other Koch-like lines), at an asymmetric position in the Mandelbrot line (b) and at the free extremity of the old tip in the tree-like lines (c, d).

Other generators producing tree-like structures (fig. 3c, d) (Mandelbrot, 1973; Mandelbrot, 1982; MacDonald, 1983) have some characteristics in common with the generators producing the Koch, Cesaro and Mandelbrot lines: in these structures the number of the tips increases in each generation cycle because every tip splits in two other tips in each generation. The new tips are located at the middle of the old tip in the Cesaro line (and also in most of the other Koch-like lines), at an asymmetric position in the Mandelbrot line and at the free extremity of the old tip in the tree-like lines.

Other types of programs producing structures analogous to the suture line are the so-called "cellular automata" (Hayes, 1984; Wolfran, 1984). A cellular automaton is a set of many cells having only a few possible states and interacting among themselves. The evolution of a cellular automaton depends on the initial configuration of the cells and on the rules for the calculation of the next state of each cell in each generation. An important program of this type is the diffusion limited aggregation (DLA) model developed by Witten & Sander in the 1981 (Witten & Sander, 1981; Sander, 1986; Sander, 1987). This computer simulation starts with a single seed particle in a limited space. Then the particles are introduced into the space one at a time and move randomly until they approach another particle getting dose enough to stick. Fractal vascular patterns are produced in this way. A program similar to the DLA is the dielectric breakdown model (DBM) by Niemeyer, Pietronero and Wiesmann in which the tip splitting and growth are regulated by different parameters (Niemeyer, Pietronero & Wiesmann, 1984). This model produces patterns similar to the "viscous finger" formed by a fluid when it is forced under pressure into another immiscible fluid of higher viscosity (fig. 4) (Nittmann, Daccord & Stanley, 1985; Sander, 1986; Sander, 1987).

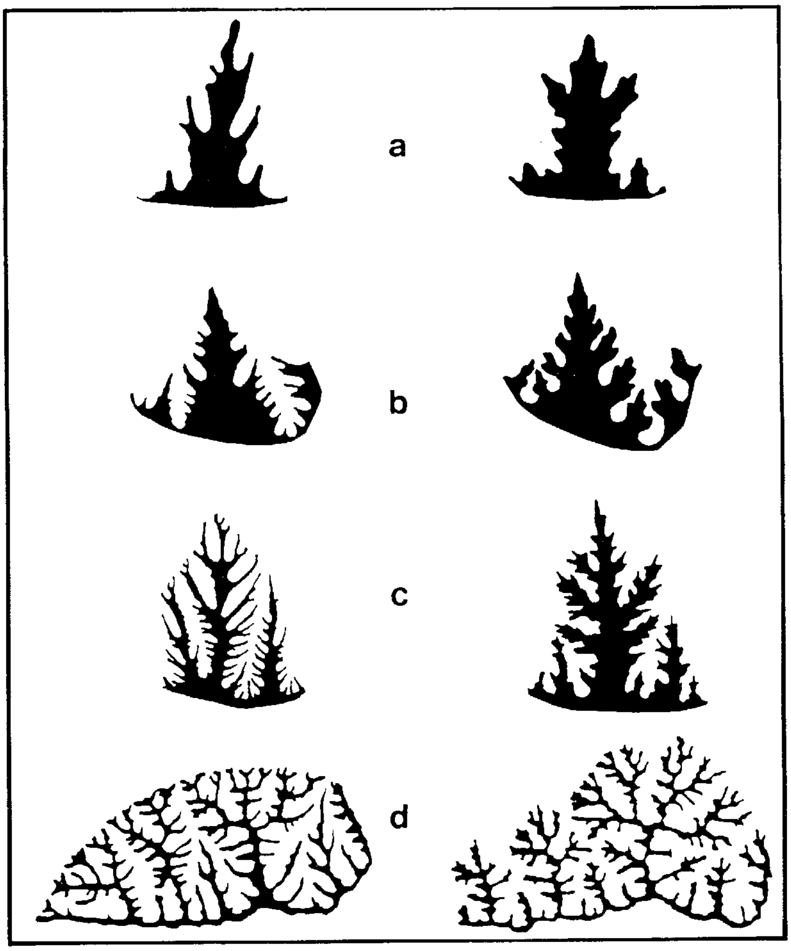


Fig. 4 - Analogy between viscous fingers and suture lines. The viscous fingers (on the left) with (b, c) or without (a, d) molecular anisotropy were obtained in an Hele-Shaw cell (a,b,c) (Buka, Kertesz & Vicsek, 1986) or by squeezing a drop of a viscous substance between two glasses which are then pulled off (d) (Damiani, 1984 - Damiani, 1986). The suture lines (on the right) of *Silesites seranonis* (D'Orbigny) (a), *Perrinites hilli* (Smith) (b), *Kosmaticeras theobaldianum* (Stol.) (c) and *Streblites adolphi* (Uhlig) (d) were redrawn (Eliane, 1952). Computer simulations reproducing this kind of patterns were developed (Nittmann & Stanley, 1986 - Damiani, 1984 - Damiani, 1986).

The experimental study of these phenomena involves an apparatus called the Hele-Shaw cell, which consists of viscous fluid confined between two parallel plates. When a less viscous fluid is injected into the middle of the cell, it breaks hp into many branched fractal structures displacing the higher viscous fluid. A morphological transition between random patterns (tips splitting) and quasi-regular dentritic growth patterns (stable tips) is observed if one of the fluids possesses a molecular anisotropy, which happens when nematic liquid crystals are used as the high viscous fluid (Buka, Kertesz & Vicsek, 1986). A DBM, simulation is able to reproduce both these patterns (Nittman & Stanley, 1986).

Another experimental apparatus for studying the viscous finger patterns is obtained by squeezing a drop of a viscous substance between two glasses which are then pulled off slowly (fig. 4d) (Damiani, 1984 - Damiani, 1986). The attractive force among the molecules of the viscous substance and the tendency to go toward the point of separation between the two glasses, located near the centre of the drop, produce a convergent vascular structure. Many separation points originate between the glasses and the viscous substance when the speed with which the glasses are lifted is increased causing the vascular structure to be gradually transformed into an irregular hexagonal lattice: therefore the collapse of the viscous substance is not only along the front of the drop, but it also begins at these detachment points, which are almost uniformly distributed inside the drop.

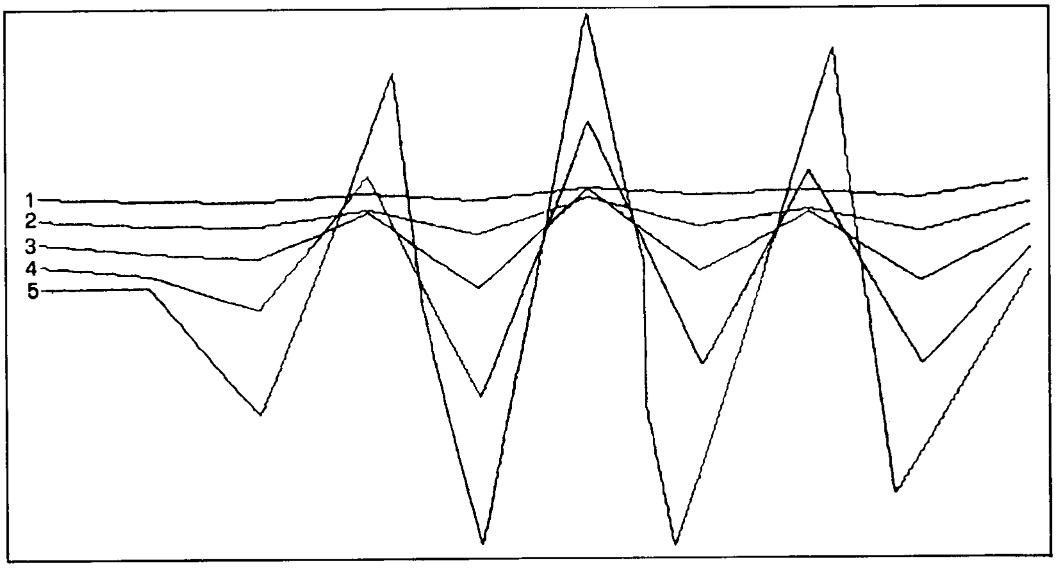


Fig. 5 - Computer simulations of the development of a structure analogous to the Goniatitic-Z type of suture line. The small anisotropies present in the starting line grow at each step.

I have developed and studied many computer programmes based on recursive rules producing different kinds of divergent or contracting many-branched, fractal and vascular structures. A general characteristic of these programs is that when uniformly distributed entities are diffused or concentrated by a repulsive or attractive force, they respectively produce divergent or contracting fractal and vascular structures. In the cellular automaton simulations the repulsive or attractive force may be transmitted by means of the emission and absorption of vector entities. A very important aspect in these simulated processes is that recursion of few rules produce complex multidimensional lattices beginning with simple monodimensional entities or viceversa.

CHARACTERISTICS OF ONTOGENETIC AND PHYLOGENETIC SUTURE LINES EVOLUTION

In the introduction we explained that the evolution of the simplest sinuous suture lines was an adaptation for the reduction of bending stresses due to the non-circular shape of the whorl section. In fact, as many Authors have reported, the distribution and relative size of ammonoid lobes closely correspond to the shape and dimension of the whorl section (Seilacher, 1973; Westermann, 1973). The successive evolution of suture and septa further reduces the bending stress on shell wall and septa.

Since the bending stresses in a lintel (and therefore in a section of the ammonoid shell) increase with the square of the distance from the fixed points, reduction of spacing among the suture, and in particular within the same suture, aids the septa in their function of supporting the hydrostatic pressure on the shell wall.

Subdivision of lobes and saddles increases their number and height which either reduces or maintains suture spacing during shell growth. In the sutural type named Goniatitic-Z, lobes and saddles assume a V-shape while a U-shape is assumed in the Goniatitic-M type. Computer simulations producing these kinds of patterns and their ontogenetic development are very simple. In the computer simulation of fig. 3 the small anisotropies present in the starting line grow at each step. If the extremity of a lobe or a saddle is unstable a new anisotropy is developed in a new lobe or saddle. If this instability appears late during septum development, the new anisotropies give rise to “lobes” and “saddles” of smaller scale producing the second order marginal frilled common in the suture of Ceratitic type. A second order marginal frilled ammonitic suture is produced if the instability of the suture line appears late during the septum development and is located in the middle of the saddles and of the segments connecting the saddles and lobes extremities (fig. 6a). In a later step the new segments can give rise to tips in their central part generating once again a third order frilled ammonitic suture.

This kind of recursive rules is exactly the same as that generating the Kock-like lines. Therefore in the morphological and constructional processes there is a strong relation between the ammonitic suture lines and the Kock-like lines. The main differences are the “stretching”, some asymmetries and the tendency to form a hexagonal lattice. The “stretching” of a suture is sometimes only an anamorphic transformation of a Koch line (fig. 6b,c). More than one secondary unstable region appears on the stretched segments connecting the extremities of lobes and saddles, and the number of growing lateral secondary lobules and folioles increases proportionally with the length of the segments. The faster rate of growth in the adoral direction rather than in the lateral direction is probably due to the pressure difference between the cameral fluid and body (or also higher viscous fluid located between the last septa and the body) and perhaps also to muscular pull. These two elements are also responsible for the inflation of saddles, folioles, lobes and lobules which results in average convexity of the septum. A continuous change in the direction of the suture curvature increases the spread of stresses in every direction causing the suture line, as well as the Koch line, to become a non-derivable line. Moreover, the extremities of each lobule and foliole with opposite orientation tend to meet, in order to permit arch formation from their corresponding flutes on septa. Another tendency of the most complex suture line is to produce a hexagonal doweling of the plane which represents the most uniformly distributed dowel as demonstrated by experiments with viscous substance squeezed between two glasses which are then pulled off quickly. A simple way to obtain an approximate hexagonal doweling is to produce two fused Koch-like line, one in front of the other: the instability points in the starting simple sinuous suture lines are located not only in the middle points of the saddles and of the segments connecting the saddle and lobe extremities, but also in the middle points of the lobes (fig. 6d).

The successive recursive rules are the same as those generating the Kock-like lines. An important result of the increase in the degree of complexity, stretching and hexagonal doweling is the increase in the fractal dimension of the suture lines, which usually is about 2 in most complex patterns. Another general tendency in ontogenetic and phylogenetic evolution of suture lines is to achieve reduction of suture spacing maintaining the septum surface to its minimum.

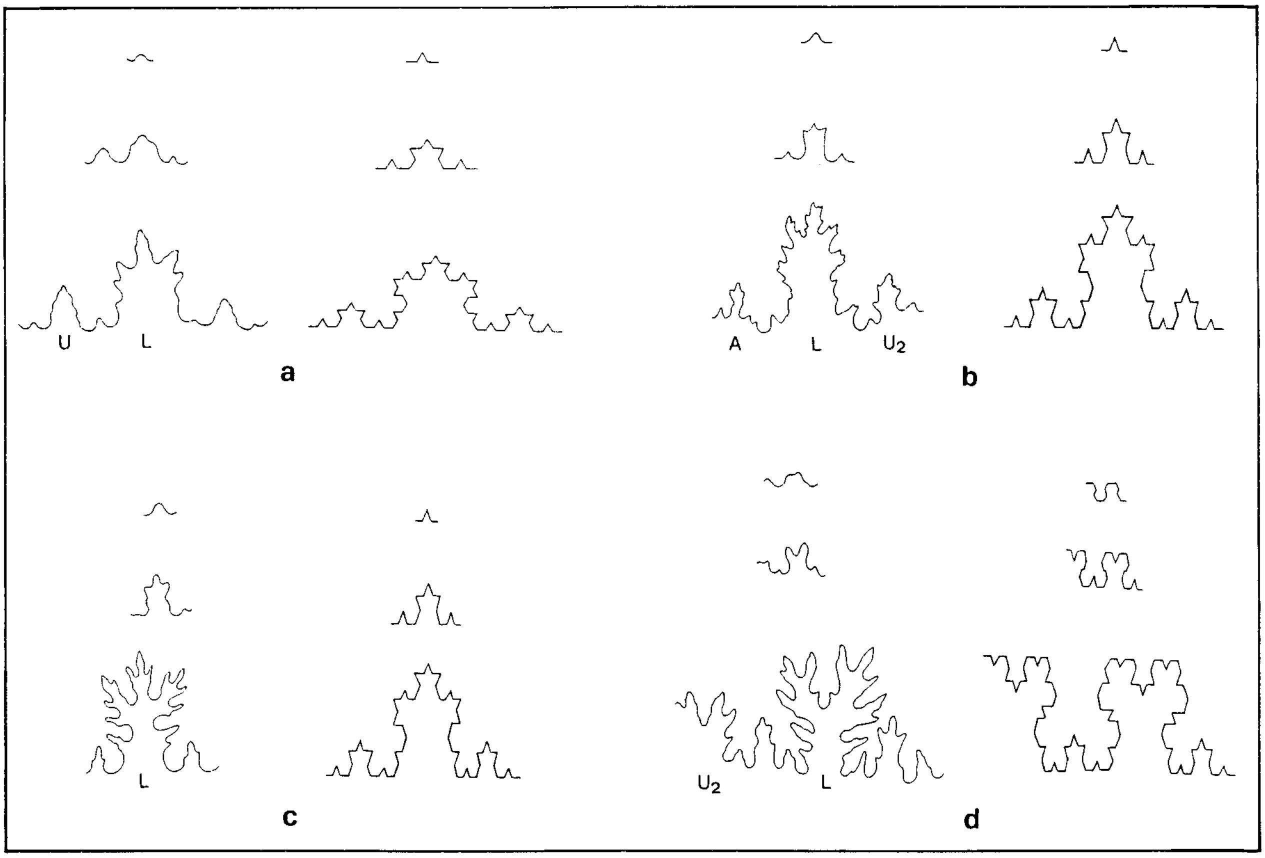


Fig. 6 - Developmental analogies between the Mesozoic ammonoid suture lines and the Koch-like line. Suture ontogeny of the Ammonitina type *Leptoceras studeri* (Ooster) (a) and *Hildoceras lusitanicum* (Meister) (b), of the Phylloceratina type *Sowerbyceras (Holcophylloceras) calypso* (D'Orbigny) (c) and of the Lytoceratina type *Lytoceras juilleti* (D'Orbigny) (d) are compared respectively with the first three stages in the growth of a Koch line (a), of a stretched anamorphic transformation of the Koch line (b, c) and of two fused Koch-lines one in front of the other (d). The suture lines were redrawn (Eliane, 1952 - Venturi, 1982). The Koch lines were generated by simple computer programs.

In conclusion the evolution of suture lines produced fractal, vascular and peanian Koch-like line. Examples of analogies between computer generated Koch-like lines and some suture lines typical of the three main suborder of the Mesozoic ammonoids (Phylloceratina, Ammonitina and Lytoceratina) are shown in fig. 6. Convexity, stretching and growth of secondary lateral branches are characteristics of the Phylloceratina suture lines. Instead both hexagonal doweling and symmetry with respect to the latitudinal axis suture lines are typical of the Lytoceratina. The patterns of these complex ammonoid suture lines are very similar to the real or computer simulated viscous fingers (fig. 4).

CONCLUSION

The analysis of suture line evolution by means of fractal geometry and computer simulation agrees with the "Westermann-Pfaff model" proposed to explain the origin, functions and construction of fluted ammonoid septa. Moreover, this analysis reveals new aspects of the most complex suture genesis, resulting from the interaction between genetic and environmental elements. The shell shape, the viscosity of the biological fluids and tissues present on both sides of the rising septum, the sensitivity and responsiveness to stresses of the sensory cells and their localisation in the aponeurosis-like mantle structure were chiefly predetermined genetic elements. Stresses due to hydrostatic pressure applied via the shell wall and the body were chiefly environmental depending elements. In general, the septum shape seems to have been determined by responsiveness of sensory cells to stress and pressure differences and by their alignment along stress lines.

The sensory cells were probably not located only along the aponeurosis-like mantle structure but also along the shell walls of the last camera. This hypothesis explains the strong relation between the septum morphology and the shell shape and dimension.

The stress gradients were transformed into chemical gradients of diffusible substance secreted by sensory cells. In a few cases the production of chemical gradients may have been exclusively determined by genetic elements and therefore independently from the environmental stress gradients. In every case, the mantle cells arranged themselves along these chemical gradients and secreted the septum. Generally, in a lobe, in a saddle and in a suture segment connecting the extremity of a lobe and a saddle, the central part has the highest values of the bending stress and corresponding chemical gradients: therefore this unstable region developed a growing tip. Increase in the sensitivity of sensory cells led to the growth of second order tips at a smaller scale and so on. I suggest that the final patterns of the most complex septa were achieved in many of these sequential steps. This type of recursive rules is the same which generates the Koch-like lines analogous to the suture lines and viscous fingers: therefore analogous rules produce analogous patterns. The relation with the diffusion of viscous substance is revealed by the analogy between the viscous finger and the suture line convexity and also by the analogy between same suture lines and the patterns produced by diffusion of lower viscous fluid in a higher one composed by nematic liquid crystals (fig. 4). These suture lines were probably produced when an anisotropic fluid was in the apical region of the body chamber during septum fabrication. The existence of suture lines with inverted convexity of lobules and folioles or with no convexity at all indicates that in these rare cases the viscosity of the cameral fluid could be superior or equal to that of the fluid (or tissues) in the apical region of the body chamber near the new septum.

There is no doubt that the complex septa morphology has made the shell structure more resistant to hydrostatic pressure, by collecting the stresses of traction and compression and uniformly distributing them in every point of the shell. This explains why most evolved suture lines are branching, fractal, vascular, peanian and non-derivable structures with a hexagonal doweling of plane.

Many other structures with analogous characteristics are very common in nature: trees, venation of leaves, lungs and in general most circulatory and transport systems in living organisms, aggregation structures produced by myxobacteria and myxomyceta, cromatophores of some animals, nervous cells, some minerals and crystals, dentritic snowflakes, electric discharges, course of river beds and large scale clusters of matter in the universe (Maddox, 1987).

A single optimisation principle leads to the formation of these branching, fractal and vascular structures: to distribute or to concentrate something in the most economic and uniform (scale-invariant) connected pattern produced by recursive rules.

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