A Simple Mathematical Model for Chamber Arrangement
of Planktic Foraminifera

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We propose a simple mathematical model for chamber arrangement of planktic foraminifera. The arrangement is approximated using connection of spheres. It is represented by combination of four sequences: they correspond to radius of chamber, horizontal/vertical distance of connected chambers, and angle of horizontally projected two lines constructed by connection of centers of adjacent spheres. We assumed that the sequences of the radius and horizontal/vertical distances are geometric series and that of the angle is constant. We succeeded in reproducing the chamber configuration of all recent planktic foraminifera at the level of family in taxonomy. We also point out that some other parameters are required in order to classify the chamber arrangement in detail. The model enables us to consider an optimization problem of the volume-surface area ratio which corresponds to the cost of chamber forming materials. Using the simplest case of our models, we obtain an optimized radius-distance relation.
Key words: Planktic Foraminifera, Chamber Arrangement, Mathematical Model

1. Introduction

Foraminifers, a kind of single-celled marine Protista, live in the sea all over the world. At present, the number of species of foraminifers is known up to a few thousands including fossils in the geologic ages. Foraminifers have two prominent types of lifestyles: one is planktic, which lives in surface water through the life, and the other is benthic, that lives in surface sediments on the sea floor. They grow up by preying small marine zooplankton, phytoplankton, and/or organic detritus in the seawater and sediments, and build calcareous ($CaCO_3$; carbonate) skeleton to protect their cells. Since most of foraminifers are less than 1 mm in size, we cannot recognize their detailed forms by naked eyes. Observations by optical microscopes have revealed numerous polymorphic variations in the calcareous skeletons, which are called "chambers". Classification schemes of foraminifers have been constructed based on their microscopic morphological features.

In general, the skeletons of modern planktic foraminifers are simplified coils. Figures 1a–d show their representative shapes. Each chamber is spherical or ovoid, and is inflated and porous. Most of planktic foraminifers have trochoid-spires (named "trochospire") and their coiling heights are one of the important criteria for classification.

Benthic foraminifera exhibit larger variations in their coiling morphology than planktic ones as shown in Figs. 1e–g. On the other hand, the variation of benthic foraminifer's morphology and coiling variations are huge and complicated compared with planktic ones. Benthic foraminifers have large, rigid and thicker skeletons. The shape of chambers and its arrangement are also variable: low and high trocospire (Figs. 1e and 1f), and biloculais (Fig. 1g) forms are popular in benthic foraminifers. Other different morphotypes are also frequently observed; e.g. uniserial (adding chambers to one direction without coiling), plano-spire (ammonoid-like coiling named "planispire").

It has been believed that benthic foraminifera has existed since 0.5 billion years ago (Cambrian Period) on the earth according to some evidences of fossil records. On the contrary, planktic foraminifera appeared on 0.17 billion years ago (middle Jurassic Period). It is believed that they had evolved from one and/or some benthic foraminiferal lineages by the results of morphological analysis (e.g. Pessagno, 1967). Planktic foraminifera adapted to all ocean environments from surface to deeper (ca. ~1,000 m) water depths throughout the geological time. Throughout such an adaptation, they achieved some morphological variations accompanying adaptations (Fig. 2). It seems that these variations are considered tightly related to the ambient environments including their mechanical properties and their ecological functions in evolutionary histories. However, their functional meaning of morphology has not been considered until today. From the taxonomic standpoint, the classifications of lives are generally based only on their morphological features. Therefore it is also important to de-
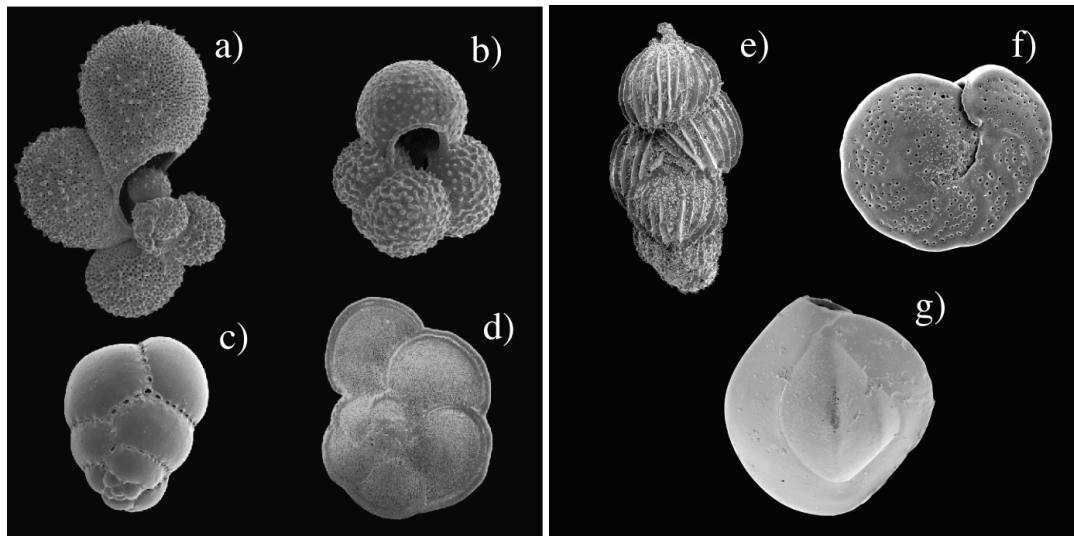
Fig. 1. Representative morphologic variations of planktic and benthic foraminifera. Samples from a to b correspond to planktic foraminifera and others correspond to benthic one. a) *Globigerinella*, b) *Globigerina*, c) *Candeina*, d) *Globorotalia*, e) *Uvigerina*, f) *Cibicidoides*, and g) *Quinqueloculina*.

scribe quantitatively their morphologies quantitatively using mathematical expression. If their morphological features are described mathematically, we can test their mechanical properties with their boundary conditions using numerical analysis. Furthermore it might be understood their morphological meanings in terms of mechanical functions through evolutionary processes over the earth history. In this study, we investigate a simple mathematical model for chamber arrangement of planktic foraminifera in order to consider the parametric description of their forms systematically.

Here, we construct a discrete growth model for foraminifera and examine the reproducibility of their forms. The arrangement of foraminifera chamber can also be related to shells of snails and ammonoids. Thompson (1942) insisted that the chamber arrangement of foraminifera was qualitatively approximated to logarithmic spirals. Okamoto (1988) proposed a differential geometrical model of ammonoids called growing tube model. His model described many types of ammonoids and reproduced the formation of an irregularly arranged coiling of *Eubostrychoceras japonicum*. Both of Thompson's and Okamoto's models are based on continuous function. Their methods are not directly applicable to chamber formation of foraminifera since foraminifers have discrete chambers. We also discuss the optimization of simple chamber arrangement which for maximizing the ratio of volume to surface area as an application of the mathematical model of the chamber arrangement.

Fig. 2. Classification of modern planktic foraminifera. Right side photographs correspond to typical morphospecies of each family.

2. Model
2.1 Chamber arrangement

We choose a sphere as a representative shape of a chamber for simplicity and applicability to analyses such as optimization problem described below. Construction of sphere arrangement is successive addition of given radii of spheres. So there is an initial sphere at the beginning of construction. The 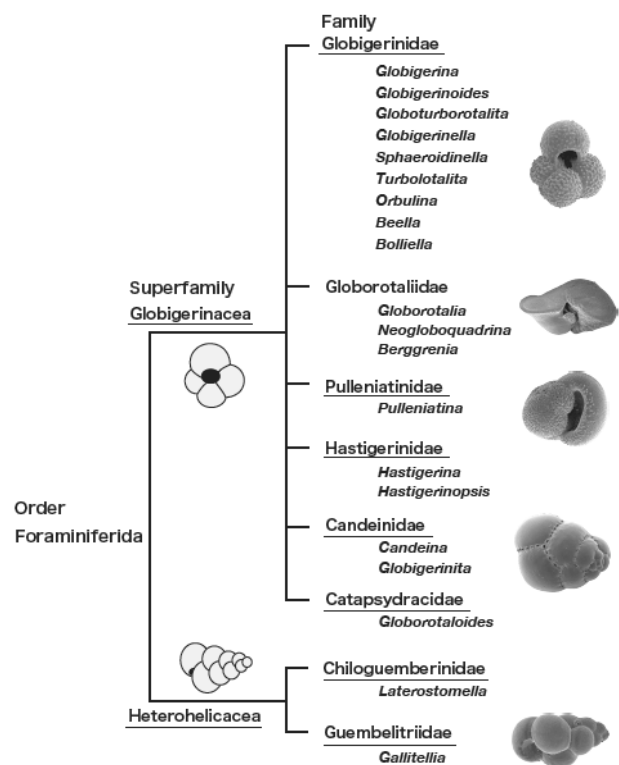radius of the initial sphere is set to be unity and the radii of other spheres are given by the relative lengths to the initial one. We allocate the initial sphere at the origin of coordinate. The locations of the other spheres are determined by relative vectors with the center of the initial sphere. Locations of the other spheres are determined by relative vectors with their beginning points at the center of the initial sphere. Because we focused on chamber arrangement, not formation process, the radii are kept constant once
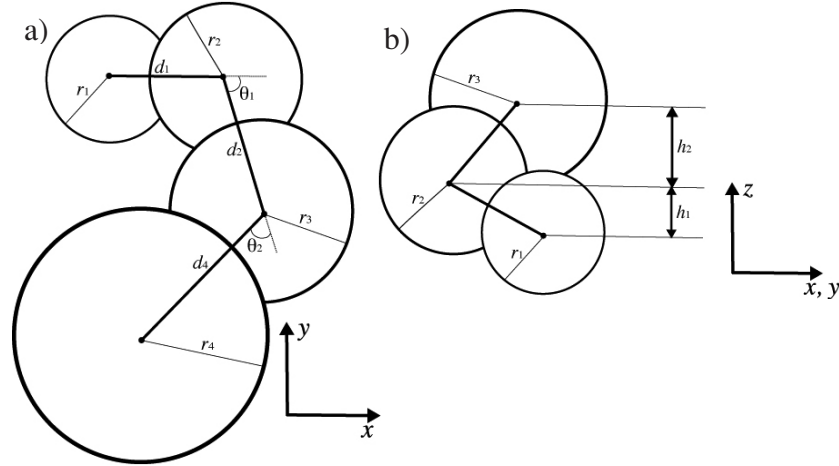
Fig. 3. Schematic sketches of chamber arrangement model. a) Vertical view. b) Horizontal view.

they added to previous sphere.

The configuration sequence of chamber spheres, which corresponds to the temporal chamber formation as well, is described by the series of four variables: radius of chamber, horizontal and vertical distances of connected chambers, and angle of two lines connecting the centers of adjacent spheres on horizontal projection. Figure 3a shows a vertical view of the model with the chamber radius r_i, the horizontal distance d_i, and the angle of centerlines θ_i. Figure 3b shows a horizontal view with the vertical distance h_i. In addition to these variables, the total number of chambers, i.e. the total growth steps of chamber generation, is denoted by n. A chamber arrangement of planktic foraminifer is determined by these five variables. We choose the z-axis as the axis of rotation called pivot since we defined the angle of centerlines on the horizontal x-y plane. Note that any coordinate axis does not specify the direction of gravity.

There is another selection of three variables concerning with location of sphere such as distance between centers of neighboring spheres and two angles which denote the direction of relative vectors of neighboring centers. Although such a selection is better than ours from a viewpoint of intuitive understanding of foraminifera's morphogenesis, we preferred our definition from a viewpoint of descriptive language.

We assume that the configuration of a chamber is a function of that of the previous chamber, what is called recurrence formula, throughout the sequence of chamber formation. Therefore, arrangement of chambers can be described by,

$$r_i = f_r(r_{i-1}), \quad d_i = f_d(d_{i-1}),$$
$$h_i = f_h(h_{i-1}), \quad \theta_i = f_\theta(\theta_{i-1}). \tag{1}$$

Furthermore, we assume that the variables r_i, d_i, and h_i are geometric series and θ_i is constant such that,

$$r_i = r^{i-1}, \quad d_i = dr^{i-1}, \quad h_i = hr^{i-1}, \quad \theta_i = \theta, \tag{2}$$

where r, d, h, and θ are parameters which determine the chamber arrangement of a foraminifer. We call these parameters radius ratio, initial horizontal/vertical distance,
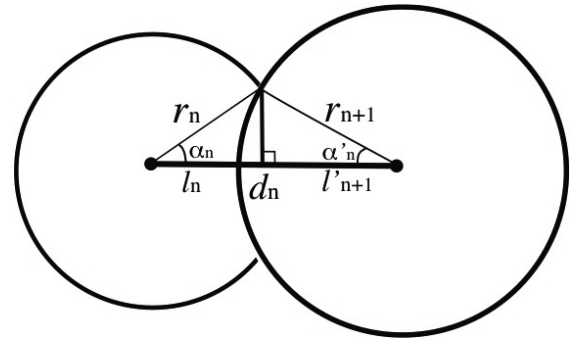

Fig. 4. Definition of variables for chamber connection.

and initial angle, respectively. These geometric series of variables provide a discrete version of Thompson's logarithmic spiral model, which we can extend by changing the functions in Eq. (1) if necessary.

Due to the geometrical restriction, the following relationships fold for the above four parameters: radius ratio $r > 0$, initial horizontal distance $0 < d < 1 + r$, initial vertical distance $0 < h < d$, and initial angle $-\pi < \theta \leq \pi$. The ranges $-\pi < \theta < 0$ and $0 < \theta < \pi$ correspond to right and left of foraminifeal coiling directions, respectively.

Real growth of foraminifers is initiated with a pair of chambers. Observational studies revealed that the first chamber, called proloculus, was so special in its features that it is not consistent with its following arrangement sequence described by Eqs. (1) and (2). For example, chamber radius of proloculus is about 5 percent larger than the other chambers. Therefore, we omit proloculus from our model and construct the arrangement from the second chamber.

2.2 Optimization analysis

We apply our mathematical model of chamber arrangement to an optimization problem of the initial horizontal distance d to make the volume-surface area ratios maximized. This optimizes the cost of chamber forming material (carbonate). As described above, the value of initial distance d is restricted between 1 and $1 + r$ because of the triangle inequality. As the simplest but not trivial case, we
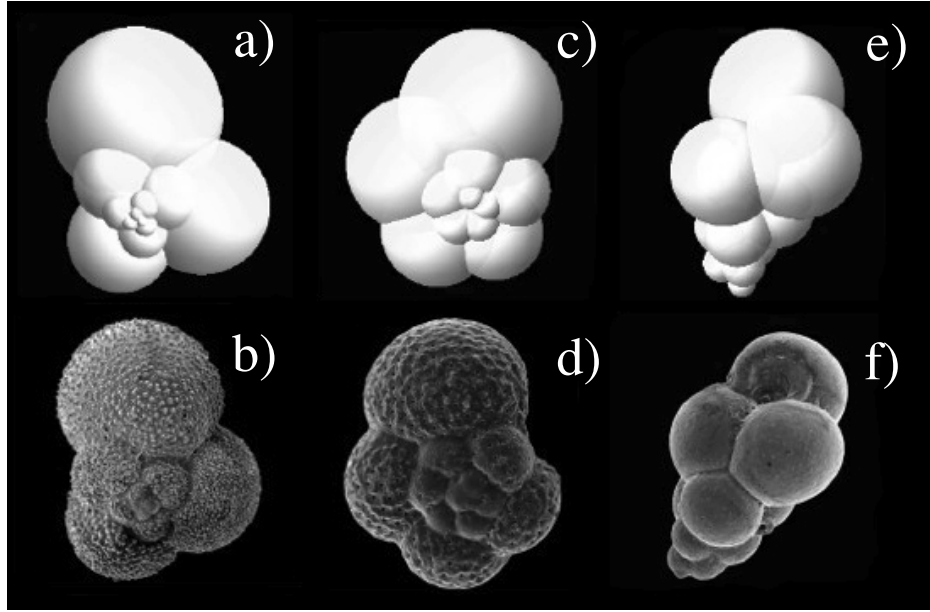
Fig. 5. Comparison of real species and results of our model. Upper parts (a, c, and e) are simulated forms by our model. Lower parts are Scanning Electron MIcroscopes (SEM) images of real species. b) *Globigerinita glutinata*, d) *Neogloboquadrina incompta*, and f) *Gallitellia vivans*.
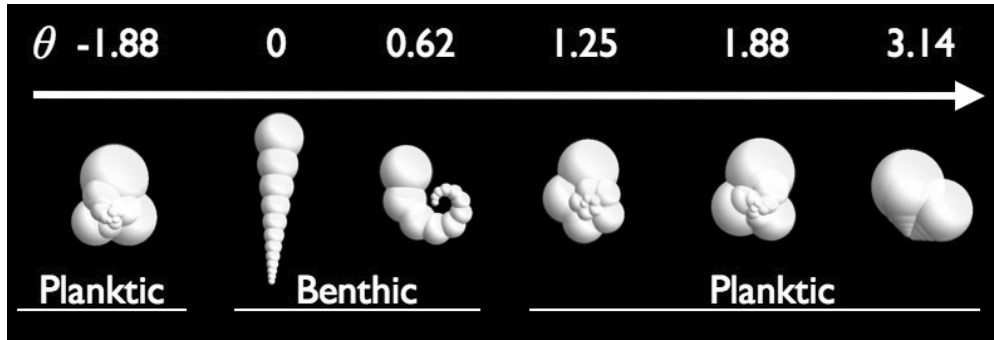

Fig. 6. Initial angle dependence of foraminiferal models. Other parameters are fixed.

consider the case of $\theta = 0$ at which the chambers are connected on a straight line. Results of this linear connection condition can be applied to the cases of other θ values as far as the chambers overlap only with neighboring ones. This type of sequential form corresponds to an uniserial form of benthic foraminifers.

The objective function can be expressed as,

$$p(d|r, n)$$
$$= \frac{\frac{4}{3}\pi r_1^3 - v(l_1', r_1) + \sum_{i=2}^{n}\left(\frac{4}{3}\pi r_i^3 - v(l_i, r_i) - v(l_i', r_i)\right)}{4\pi r_1^2 - s(l_1', r_1) + \sum_{i=2}^{n}\left(4\pi r_i^2 - s(l_i, r_i) - s(l_i', r_i)\right)},$$

(3)

where l_n and l_n' are

$$l_n = r_n \cos \alpha_n = \frac{r_n^2 + d_n^2 - r_{n+1}^2}{2d_n},$$
$$l_n' = r_n \cos \alpha_{n-1}' = \frac{r_n^2 + d_{n-1}^2 - r_{n-1}^2}{2d_n}.$$

(4)

Figure 4 shows the definitions of these variables. The functions $v(x, r)$ and $s(x, r)$ correspond to volume and surface area of spherical cap of a sphere whose radius and radius of cross section are x and r, respectively. These functions are written as,

$$v(x, r) = \pi \left(\frac{2}{3}r^3 - r^2 x + \frac{1}{3}x^3\right),$$

(5)

and,

$$s(x, r) = 2\pi x (r - x).$$

(6)

The optimized value of d with fixed r and n can be found numerically using the steepest descend method (e.g. Press *et al.*, 2002).

3. Results

Using some parameter set, the model realized the chamber forms that are nearly identical to the real foraminifera. Figure 5 shows the comparison of model results and the SEM images of real foraminifers. The form of Fig. 5a was obtained by the parameter set of $r = 1.3$, $d = 1.4$, $\theta = -1.26$, and $h = 0.3$ at $n = 12$, which was identical to
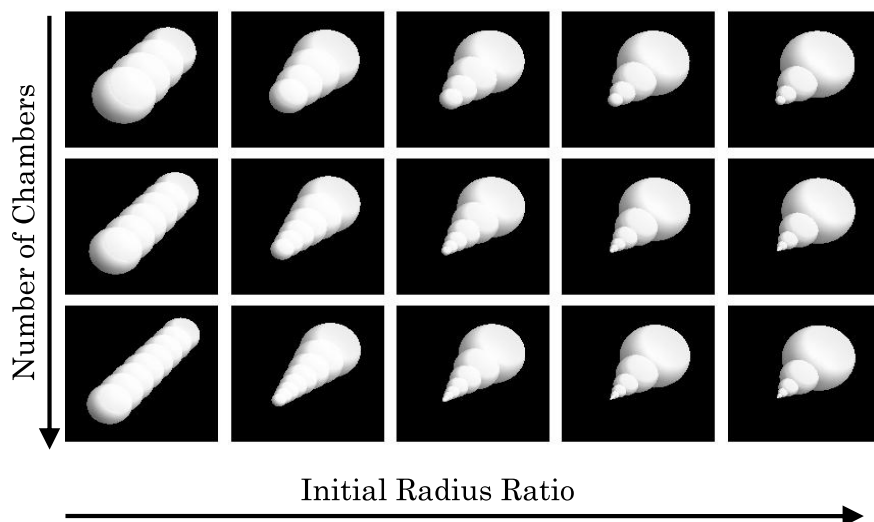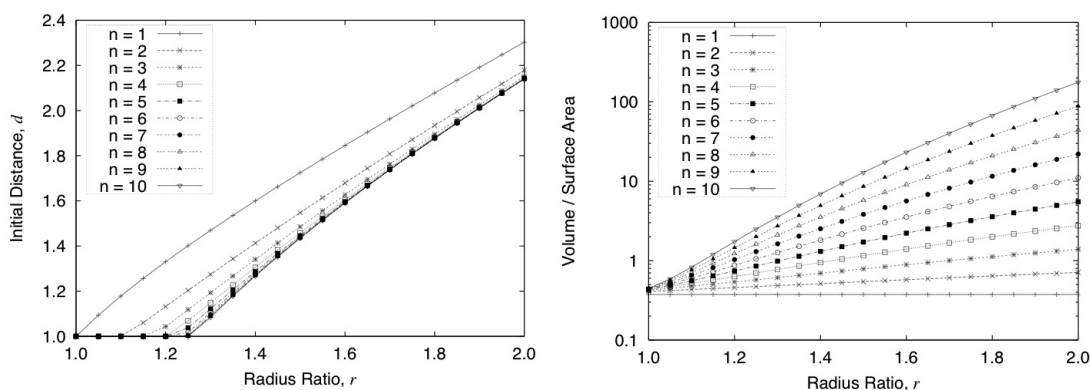
Fig. 7. Examples of optimized form.

Fig. 8. Radius ratio dependence of the maximized volume surface area ratio (left). Radius ratio dependence of optimized initial distance (right).

the form of *Globigerinita glutinata* shown in Fig. 5b. Furthermore, the conditions $r = 1.2$, $d = 1.3$, $\theta = -1.28$, $h = 0.25$ and $n = 11$ in Fig. 5c well reproduced the form of *Neogloboquadrina incompta* shown in Fig. 5d. Figure 5e was obtained using $r = 1.15$, $d = 1.3$, $\theta = -1.88$, $h = 0.4$ and $n = 12$, and corresponded to *Gallitellia vivans* shown in Fig. 5f. Changing the parameters adequately, we also acquired other types of chamber configurations.

Figure 6 shows an example of θ dependence of the form with other parameters fixed. Chamber arrangement of all recent planktic foraminifera can be produced using our model at the level of family in taxonomy. Ranges of parameter values for present planktic foraminifera are compiled as follows: $1.2 \leq r \leq 1.3$, $d \leq 1.9$, $1.0 \leq |\theta| \leq \pi$, $0 \leq h \leq 0.5$, and $n \leq 20$.

We also found out several types of forms that are similar to some kinds of benthic foraminifers. They were obtained using $|\theta|$ values out of the above range of actual planktic foraminifera. Particularly, simulated forms with $0 \leq |\theta| \leq 0.62$ indicate uniserial and relatively looser coiling (i.e. large number of chambers in outermost or final whorl, see Fig. 6). Actually, these forms are frequently observed in present benthic foraminifers. The uniserial arrangements of chambers are common in modern benthic foraminiferal morphologies. Such uniserial form had never appeared in the past planktic foraminifers in the geologic history. In other words, chamber arrangements of planktic foraminifers are certainly composed of at least 3 chambers which are connected each other in nature. For this reason, it can be considered that parameter θ provides morphological and ecological "boundary" between planktic and benthic foraminifers.

Figure 7 shows the examples of the optimized chamber arrangements, and Fig. 8 shows the numerical results of the optimization problem. The examples in Fig. 7 indicate that the optimal shapes are not similar to real chambers. As shown in Fig. 8, the solution d is a monotonic increase function of r for each n. This function converges with an increase of n. Because the adult foraminifera consist of more than 10 chambers, the solution for foraminifera can be regarded as almost the same function. The obtained volume/surface area ratio is also monotonic increase function of r. Radial dependence of the ratio becomes sensitive with an increase of n. We can conclude that there exists the optimized solution of d for all r and n for our simple case and that the solution converges when n goes to infinity.

4. Discussions

Although we have not yet examined that our mathematical model reproduced all kind of shapes of foraminifers, as seen in right hand side of Fig. 1, θ is considered to be one of the most sensitive parameters for classification of form between planktic and benthic foraminifers. At this moment, it is not clear why the separation occurs sensitively by changing θ. However, θ seems to be the universal parameter for considering foraminiferal morphologic variability.

To give a possible answer for this question, we consider a proposition about the phylogeny of planktic foraminifera. Based on the morphologic analysis, the early planktic foraminifers are thought to have possibly evolved from a group of benthic foraminifer (Tappan and Loeblich, 1988). Recent phylogenetic techniques using small subunit of ribosomal DNA gene (SSU rDNA) of foraminifera revealed that almost recent planktic foraminifera are the polyphyletic in origin, and derived at least three ancestral benthic lineages (Darling *et al.*, 1999). It is possible that planktic foraminifer had been changed above five parameters to adapt their lifestyles from benthic to planktic in the geological history. In other words, morphologic changes should be tightly connected to their surrounding environments. We infer that these five parameters, especially parameter θ, are the key to interpret functional, morphologic variations and evolutions of foraminifers.

Overlapping of chambers of not-successive generation is also an important factor for chamber arrangement from a viewpoint of the optimization problem of chamber forming material. It may cause the difference of d value between observation and numerical solution. In order to argue the meaning of the extra overlapping further, we have to develop a method for considering mechanical aspect of the chamber structure: location of centroid and strength of the chamber structure, for example.

We have other problems left unsolved, relating to complete description of foraminifera. The first one is the treatment of proloculus. As described above, proloculus is not consistent with the sequence of chamber arrangement so that we have to describe the location of the special chamber apart from the following chambers. The second one is that the locations and directions of their aperture (opening of chambers). Although we do not discuss them in this article, they are also critical factors for classification because they are conservative traits in the evolution of foraminifera. The last one is that the descriptions of species whose growth cannot be described by our geometrical series model and/or spherical chambers. Further improvement of the model is required for reconstructing unconventional species of planktic foraminifera.

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