

A new approach to modeling of foraminiferal shells

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Abstract.—The emergence of shell forms in the growth of foraminifera is an essential problem in the morphogenesis of these microorganisms. We present a model of foraminiferal shells that applies a moving-reference system. Previous models have referred to fixed-reference axes and have neglected apertures. Our model focuses on real morphologic characteristics and follows stepwise natural biological processes. It introduces apertures based on minimization of the local communication path and applies three parameters, which are either predetermined or selected at random from given ranges. Expression of stochastic parameters mimics phenotypic variability of a shell. We also present a detailed description of the method with examples of simulated shells and the first step toward analyses of the theoretical morphospace. The morphospace is divided into certain regions (phases) separated by transitional planes (phase transitions). Further prospects for foraminiferal modeling, which should focus on more in-depth models based on realistic intracellular dynamics, are also presented.

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Introduction

Foraminifera, like many organisms, grow by a process of discrete, stepwise additions of elements to an already existing morphology. Although there has been spectacular progress in defining molecular relationships between different foraminiferal taxa, and our knowledge of morphology of recent and fossil foraminifera is substantial, we still do not know how genetic codes are translated into actual chamber shapes and overall shell patterns. To understand this better, we need to construct more realistic models of morphogenetic processes.

The emergence of shell patterns during the growth of foraminifera is an essential problem in the morphogenesis of these microorganisms. A majority of foraminifers are built of chambers (Fig. 1), which are cavities containing the protoplasm and surrounded (enveloped) by a firm wall (Hottinger 1986, 2000; Lipps 1993). This firm, easily fossilizable wall (shell) and the widespread occurrence of foraminifera within marine deposits make them an extremely useful group of microfossils for biostratigraphic and paleoecologic studies. Depending on the group, a foraminiferal shell may be made of organic compounds, sand

grains and other particles cemented (agglutinated) together, or secreted crystalline calcium carbonates. Foraminiferal shells occur in an enormous variety of shapes (see Loeblich and Tappan 1987). The shape of a shell results from growth processes and mostly depends on chamber form, location of chambers, and type of aperture (primary opening within the shell).

Foraminifera can be divided into three informal groups corresponding to the trend of increasing shell complexity: (1) unilocular shells; (2) simple multilocular (polythalamous) shells (Fig. 1); and (3) complex (polythalamous) shells with chambers divided into smaller chamberlets and/or having complex wall structure (see Hottinger 1978, 1986, 2000; Lipps 1993; Hohenegger 1999). Multilocular foraminifera enlarge in a discrete process of serial chamber additions (Fig. 1).

Theoretical morphology is an important tool in morphodynamics (Seilacher 1991). Modeling of foraminifers started very early with the classical work of Berger (1969), which appeared just a few years after the first publication on theoretical morphology of accretive coiled shells (Raup and Michelson 1965) and the first mathematical models of plant de-

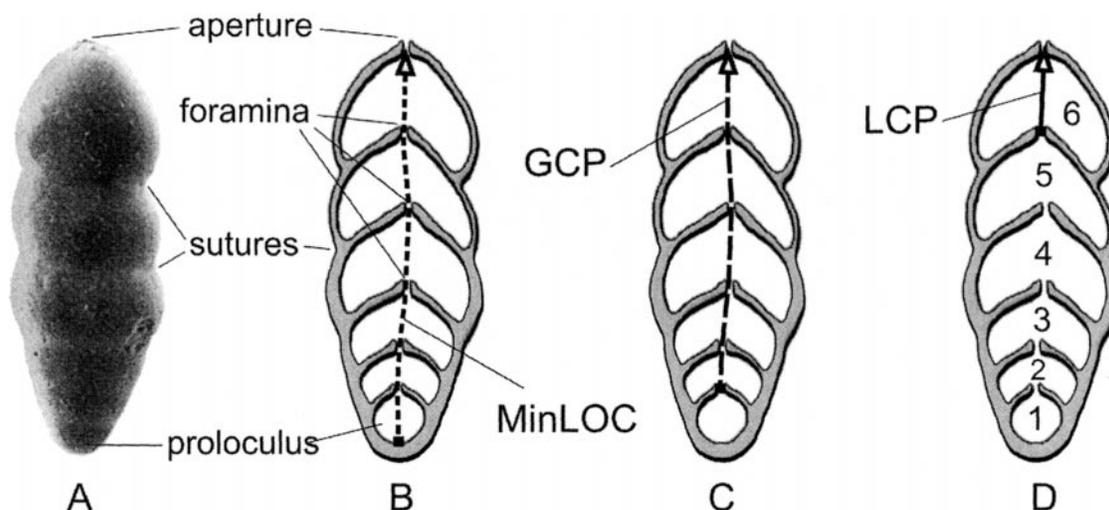


FIGURE 1. External (A) and internal (B–D) views of the multilocular uniserial foraminifer *Pseudonodosaria humilis* with basic terminology used in the text. B, MinLOC—minimum line of communication (after Brasier 1982). C, GCP—global communication path. D, LCP—local communication path; ascending order of chamber numbering represents succession from the oldest to the youngest final chamber. Shell length = 0.44 mm. See text for further explanation.

velopment (Lindenmayer 1968). Nonetheless, so far only simple regular morphologies (e.g. planispiral, helicoidal, uncoiled) have been simulated, and these do not express the complexity of foraminiferal shell patterns (see Signes et al. 1993; McGhee 1999). Thus, it is worthwhile to find an alternative approach for constructing a theoretical morphospace of these organisms (Topa and Tyszka 2002). The general aim is to find essential growth rules and to gain a better understanding of the processes responsible for the creation of shell patterns and their incredible variability. This knowledge should help explain the functionality of various shell characters and verify evolutionary relationships among foraminifera. The systematics of foraminifera is based on shell morphology (e.g., shell composition and microstructure, chamber form and arrangement, aperture type). Therefore, theoretical shell morphology can help verify selected taxonomic rules. This paper summarizes previous foraminiferal models using a fixed-reference frame and presents in detail a new approach based on a moving-reference frame.

Fixed-Reference Models of Foraminiferal Shells

Research on the morphogenesis of foraminiferal shells started with the seminal mono-

graph of Thomson (1919), "On Growth and Form," but the first formal model was presented just over three decades ago by Berger (1969), who created the first theoretical morphospace of foraminifera. This morphospace was based on three parameters (Fig. 2):

1. [q-ratio]—the ratio between successive chamber radii (R_i);
2. [a-angle]—"angle of advance," which is the angle between the lines connecting the center of the shell with two successive chamber midpoints;
3. [o-lap]—"amount of overlap" between two successive chambers, which is used to calculate a distance between centers of these two chambers, i.e., $d = R_i/[o-lap]$.

In the model, the shell is fixed to a point that defines the center of the shell. The model represents a simple step-by-step rotation of a circle with a certain amount of overlap and expansion of circle radius (R_i). This model simulates isometric growth (all three parameters are held constant through ontogeny) and is confined to planispiral shells composed of circular chambers (Fig. 2) (see Scott 1974).

Signes et al. (1993) designed a four-dimensional theoretical morphogenetic model based on two basic assumptions: the shape of chambers in the shell remains constant with

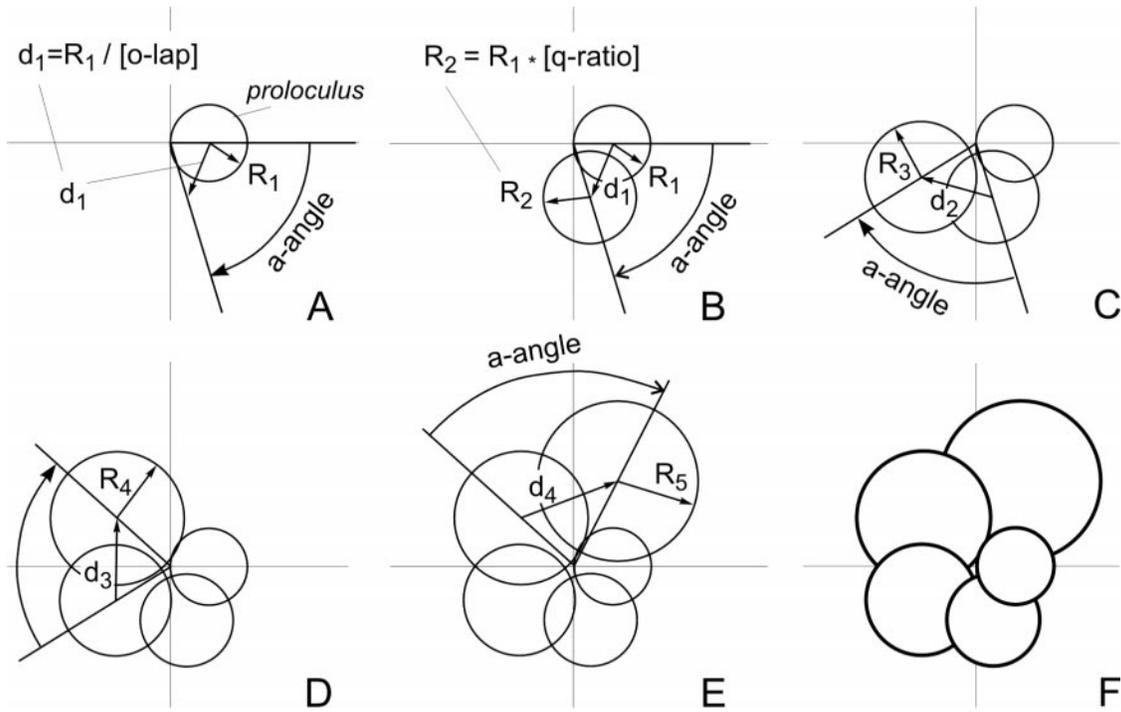


FIGURE 2. Construction of a planispiral foraminiferal shell based on Berger's model (after Berger 1969, modified).

growth, and the volume of each new chamber increases in constant proportion to that of the preexisting chamber. This model produces isometric growth with coiling in a fixed-reference frame, which is very similar to Raup's (1966) model and does not differ substantially from Berger's model. For example, Berger's (1969) "center of the shell" is replaced by the axis that is necessary to define a three-dimensional relationship. An extra parameter (Ky), characterizes the displacement of the chambers along the coiling axis of the shell.

Other authors have tried to simulate allometry of foraminiferal shells. Brasier (1980) produced a morphospace model using four parameters, which correspond to Berger's parameters, expanded by the degree of growth extension along the coiling axis and the degree of chamber compression. The latter parameter introduces allometry into the system and mimics the changing proportions of chambers during ontogeny of real foraminifera. Another important aspect of this model is that chambers are not rotated but translated. Although this approach was not developed

further, it did stimulate the modeling of foraminifera (Brasier 1980; McGhee 1999).

Another significant contribution to fixed-reference models was the logistic approach introduced by De Renzi (1988, 1995), who simulated allometric growth of some larger planispiral foraminifera.

Moving-Reference Model

The above models rely on an abstract coordinate, which is arbitrarily defined and has no morphogenetic or physiological meaning. Chambers (circles or spheres) are rotated and translated along these artificial axes, which are fixed and serve as a reference line for the growth process. Therefore, although these models can simulate simple planispiral, trochospiral, or uniserial chamber arrangement, they cannot simulate more complex patterns found in foraminifera. For instance, they cannot model gradual or abrupt changes of growth modes that cause different chamber arrangements during ontogeny, such as planispiral and switching to biserial or streptospiral to uniserial.

These constraints can be overcome by abandoning a fixed-reference frame in favor of a moving-reference system. In general, the moving-reference model is based on simple principles of motion and stepwise growth. At each growth step, the aperture migrates to a new position, according to locally defined rules (Ackerly 1989). Such models have been used in simulating ammonite growth. Okamoto (1988) proposed a tube model for all types of shell coiling, including heteromorph forms with abrupt changes of coiling patterns. His approach integrates accretional growth of the aperture (opening of the shell) without defining any fixed coordinate system. A similar moving-reference frame has been used in simulating radiate accretive growth of marine sessile organisms, such as corals and sponges, where the growth axis is associated with the local maximum of growth (e.g., Kaandorp 1994; Hammer 1998; Kaandorp and Kuebler 2001). A comparable approach was used in simulating plant growth (Lindenmayer 1968; Prusinkiewicz and Lindenmayer 1990).

Signes et al. (1993: p. 72) were aware of the moving-reference models and recognized that the foraminiferal "axis of coiling may not be stable and often lacks a physical representation on shells" and "the advantage of these [above mentioned] local-coordinate models is that they describe growth from an organismal vantage point, that is from the aperture"; nonetheless, they concluded that "it is difficult to estimate the orientations of apertural planes" and chose "to use a fixed coiling axis as a landmark."

Webb and Swan (1996) took the first step towards application of the moving-reference frame in modeling of foraminifera (see Fig. 3). Their 3-D theoretical morphospace has three parameters: (α) angle between coiling axis and the line connecting centers of consecutive chambers; (β) angle between lines connecting centers of two consecutive pairs of consecutive chambers; and (W) chamber expansion rate. Just one of their parameters, α , is related to the fixed coiling axis. This parameter is necessary to move chambers along the fixed axis of coiling. The parameter β refers to the line that moves together with created chambers (Fig. 3). This line is actually a part of the mov-

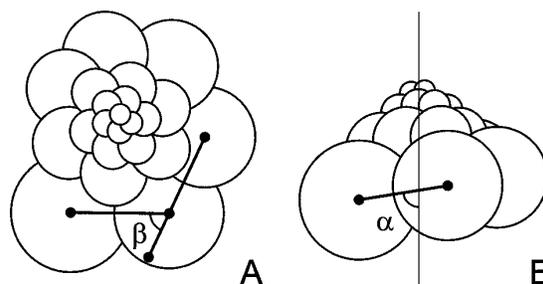


FIGURE 3. Definitions of two parameters in the model of Webb and Swan. A, Spiral view; β is defined by the centers of three consecutive chambers (from Webb and Swan 1996, modified). B, Peripheral view of trochospiral foraminifer; α refers to the fixed axis of coiling.

ing-reference system. The morphospace based on this model includes a variety of forms from planispiral through trochospiral, biserial to uncoiled uniserial, yet it does not introduce considerable changes into the range of morphologies produced by other models, such as that of Signes et al. (1993).

To go beyond the above models in modeling foraminifers, we need to define a moving-reference system using apertures; this is essential for locating the new growing chamber. Analysis of different modes of chamber growth in foraminifera suggests that the position of the aperture controls local chamber position and its final arrangement. The problem is that although stages of chamber formation are relatively well recorded, we still know very little about how foraminiferal apertures actually form. This is in contrast to "apertures" created by accretionary growth of "open-end shells," such as those in gastropods, bivalves, ammonites, tubular foraminifera, etc. In those cases, a shell opening (aperture) is self-defined by the growing accretive margin of the shell (Fig. 4A,B). This open end is therefore modeled by the so-called generating curve, which simulates formation of the shell margin.

Such a pattern of chamber formation cannot be applied in modeling of polythalamous foraminifera because the chamber itself does not define an aperture. Thus, it is necessary to search for information concerning formation of apertures in such foraminifera. Hottinger (1978) noted that foraminifers tend to shorten distances between the first and last compart-

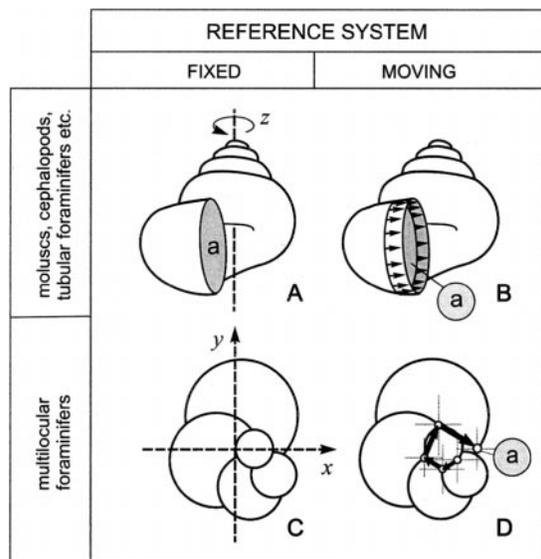


FIGURE 4. Comparison of the fixed (A, C) and moving (B, D) reference systems in modeling of shells; z is the axis of coiling and the x - and y -axes represent fixed-reference systems; a denotes apertures; vectors (see B, D) depict steps of the moving-reference frames during growth of shells. Based on Raup 1961 (A); Okamoto 1988 and Ackerley 1989 (B); Berger 1969 (C); and Topa and Tyszká 2002 and Łabaj et al. 2003 (D).

ments of their shell. Brasier (1982) analyzed the energetics of protoplasmic pathways through the organism and concluded that foraminifers show a trend toward minimizing the distance between the back of the first chamber (proloculus) and the most proximal aperture in the final chamber (Fig. 5B). He standardized this cumulative distance and called it the MinLOC—the minimum line of communication (Fig. 1B).

Brasier's "rule" seems to be valid for many foraminiferal architectures, but not for all of them. *Lenticulina* and other coiled lagenids are curious exceptions because their foramina are located at the outer margin of the shell (Hottinger 1978), creating the longest possible global line of communication, termed here the "global communication path" (GCP) (Fig. 5B). This morphotype has a very different type of aperture, referred to as "terminal" (a kind of areal aperture in the face of a final chamber). One could speculate that foraminifers with such chambers and apertures are governed by another morphogenetic rule that has priority over the local minimization principle. The re-

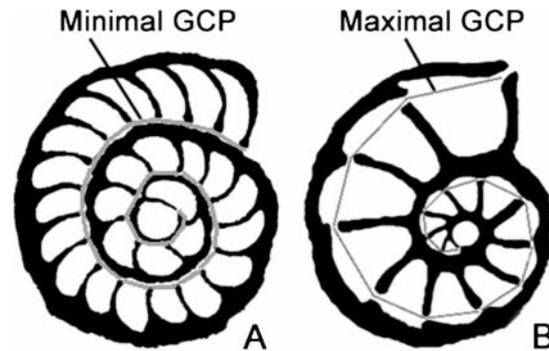


FIGURE 5. A, *Miscellanea*, planispiral with the shortest global communication path (GCP) via foramina. B, *Lenticulina*, planispiral shell with the longest GCP. Maximal size of foraminifers: (A) 2.4 mm, (B) 0.5 mm.

sulting chambers must create chambers at the pointed end, which by definition cannot be located at basal parts of chambers. In this way both local and global communication paths (LCP and GCP) cannot be the shortest. The conclusion is that the "growth program" that controls formation of every chamber is itself based on various "rules." The optimization (minimization) of the local distance is probably just one of the rules that directly control chamber shapes, location of apertures, and, ultimately, the cumulative arrangements of chambers.

The Algorithm

The model presented in this paper does not capture the whole complexity of morphogenesis in foraminifera. We have limited our study to the 2-D case only. The shells generated by our model are composed of circular chambers, whereas real chambers can have many different shapes. Our model incorporates two concepts: the moving-reference system and the minimization of local communication path (LCP). Unlike fixed-reference models, in our model the location of aperture is critical. Together with the reference growth axis, the aperture constitutes the reference system in which a new chamber is constructed.

The reference growth axis describes the current direction of growth of the shell. Actually, the reference growth axis has no direct morphogenetic representation during formation of a chamber. This axis resembles the fixed "axis of coiling" in the sense of Raup (1966) or

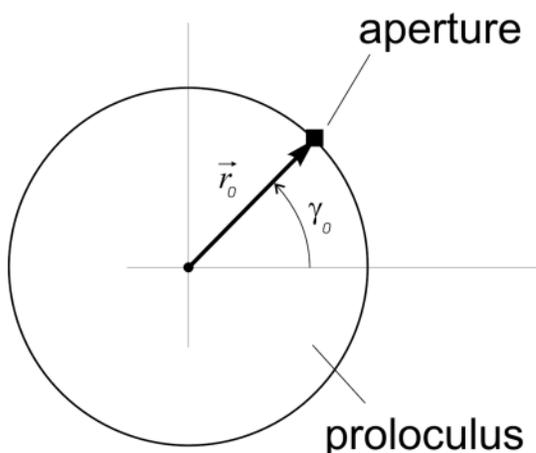


FIGURE 6. Initial chamber (proloculus) with an aperture defined by \vec{r}_0 .

Signes et al. (1993). In both cases it serves as a reference line for certain transformations. The difference is that our growth axis is not fixed but instead moves with the formation of successive chambers.

The modeling of development of a foraminiferal shell consists of discrete steps in which successive chambers are added to the forming shell. The location of a new chamber is calculated by displacement of its center with respect to the aperture of the previous chamber. The range and direction of this displacement is determined by a "growth vector." The growth vector is calculated on the basis of the reference growth axis and indicates the local growth direction for the newly created chamber.

The aperture of the new chamber is calculated according to the local minimization

principle. The distance between the apertures of two successive chambers must be as short as possible. The apertures cannot be enclosed inside any other already existing chamber. The last aperture must be connected to the first chamber by a line of communication running through all previous apertures (Topa and Tyszka 2002). To add a new chamber to the shell, the algorithm performs a sequence of geometrical transformations. Because we consider only circular chambers, polar rather than Cartesian coordinates are more convenient to use in constructing the new chamber.

The simulation starts with the initial chamber (proloculus). Its radius and the location of the first aperture are described by an arbitrarily defined vector $\vec{r}_0 = [r_0, \gamma_0]$ (in polar coordinates; see Fig. 6). The procedure, which adds a new chamber to the growing form, consists of two parts:

1. Positioning of the new chamber. The following calculations are made:
 - a. The radius of the new chamber, r_i , is calculated by using the following rule: $r_i = GF r_{i-1}$, (GF stands for chamber expansion ratio, $GF \geq 1.0$).
 - b. Next, the reference growth axis is calculated. Its direction (denoted as Φ_i angle) is determined by the center and aperture of previously added chamber (see Fig. 7A), in this case $\Phi_i = \gamma_{i-1}$.
 - c. The growth vector, \vec{v}_i , indicates the center of the new chamber. Its polar coordinates $[v_i, \phi_i]$ are calculated as follows:
 - i. Two successive chambers must overlap; therefore, the length of the

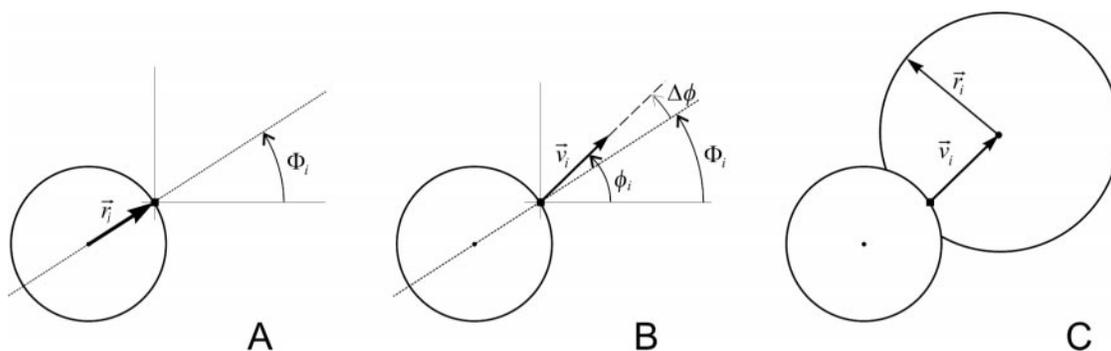


FIGURE 7. Formation of a new chamber. A, Determination of the reference axis. B, Deviation from the reference axis. C, Emplacement of the chamber (see text for details).

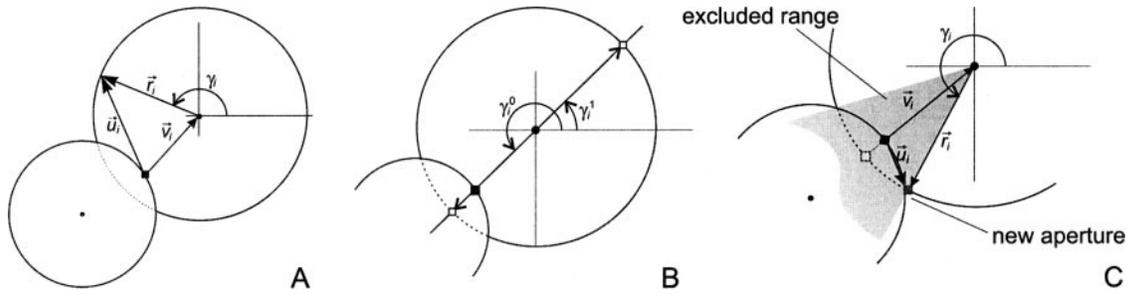


FIGURE 8. Calculating the aperture location. A, Definition of vector \tilde{u}_i . B, Searching for the shortest distance. C, Relocation of the new aperture, outside the excluded range.

growth vector cannot exceed the radius of the new chamber. We use the following formula: $v_i = TFr_i$ (TF stands for chamber translation ratio, $0 \leq TF < 1.0$).

- ii. The direction of the vector (described by ϕ_i angle) is calculated by deviation with respect to the reference growth axis by angle $\Delta\phi$: $\phi_i = \Phi_i + \Delta\phi$ ($\Delta\phi$ stands for the deviation growth vector parameter, $-180 \leq \Delta\phi \leq 180$; see Fig. 7B).
2. Finding a new aperture:
 - a. Vector $\tilde{r}_i = [r_i, \gamma_i]$ points to the location of the new aperture. We already know r_i from 1a (see above). To find γ_i , we define vector $\tilde{u}_i = \tilde{v}_i + \tilde{r}_i$ (see Fig. 8A). It connects two successive apertures and represents a Local Communication Path (LCP). We are looking for such a γ_i value for which the length of the vector \tilde{u}_i is the shortest. The shortest distance from a point located inside the circle to the circle border lies along a line passing through this point and the center of the circle. The direction of this line is described by the previously calculated ϕ angle (see 1cii above). Thus we examine two values, $\gamma_i^0 = \phi_i + \pi$ and $\gamma_i^1 = \phi_i + \pi$ (see Fig. 8B), and select the value for whichever distance is shorter.
 - b. The new aperture cannot be located inside any previously created chamber. For each previously created chamber we check whether it overlaps the new chamber and if so we calculate the range of γ_i values for which the new aperture could be placed inside this chamber (see sup-

plementary materials online at <http://dx.doi.org/10.1666/04062.S1> for details). The individually calculated ranges are combined into one global excluded range of γ_i . If necessary the new aperture is relocated to one of the boundary points of the excluded range (see Fig. 8C). The boundary point for which the length of \tilde{u}_i is the shortest is finally taken as the new aperture. If there are two such points, either can be chosen.

Figure 9 presents a few successive steps of the simulation.

Parameters.—The development of the shell in 2-D is controlled by three parameters:

GF —the chamber expansion ratio. In our model GF is equal to the ratio between the radius of two successive chambers: $GF = r_i/r_{i-1}$; $GF \geq 1.0$ —a new chamber is not smaller than its predecessor.

TF —chamber translation ratio (overlap) is equal to the ratio of the length of the growth vector to the radius of the chamber: $TF = v_i/r_i$; $0 \leq TF < 1.0$ It cannot exceed 1.0, otherwise a new chamber will be detached from the shell.

$\Delta\phi$ —deviation of the growth vector from the reference growth axis, $-180 \leq \Delta\phi \leq 180$ (see Fig. 7B). Negative and positive values of $\Delta\phi$ mean that the growth vector is deviated in clockwise or anticlockwise direction respectively.

These parameters can be used in the model in two different ways:

1. parameters are constant at each step of simulation;

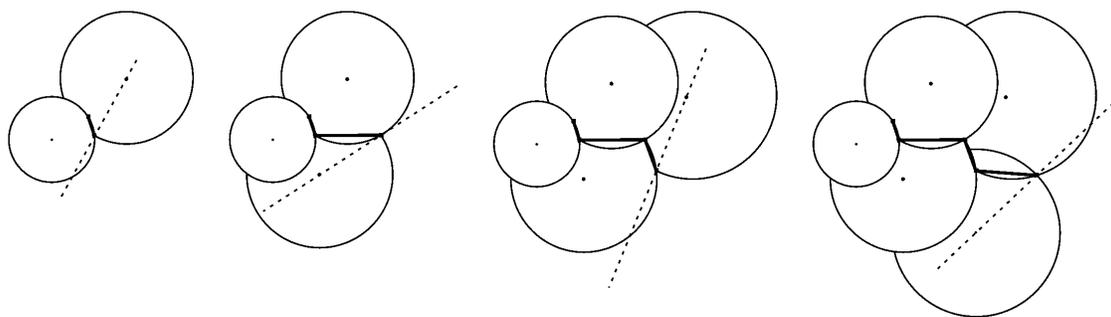


FIGURE 9. Successive steps in the creation of a biserial foraminiferal shell. Dotted line represents current reference growth axis. Successive apertures were connected to the communication path.

2. parameters are generated at random at each step of simulation.

The combinations of both approaches (e.g., one parameter is constant, the rest are generated at random) are also considered.

The first approach assumes that the set of parameters (GF , TF , and $\Delta\phi$) is established at the start and the same values are applied at each step of the simulation. This method mimics to some extent the influence of a genetic code on generated foraminiferal shells. The same set of parameter values produces an identical shell form.

In the second approach, we define the ranges of fluctuations of the parameters instead of exact values. At each step of the simulation a new set of parameters (in this case denominated as GF_i , TF_i , and $\Delta\phi_i$) is generated at random (from the specified ranges) and applied to the algorithm. Distribution of the probabilities in these ranges is monotonic. This method assumes that environmental factors can influence the growing form during the ontogeny and randomly deform the shell.

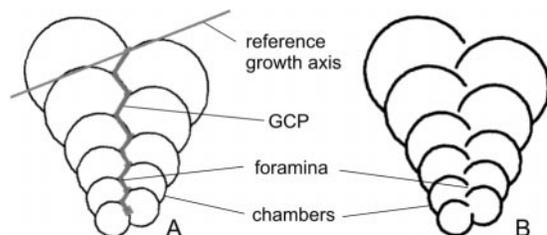


FIGURE 10. Foraminiferal shell generated by using the presented model. A, The shell with global communication path (GCP) and latest reference growth axis marked. B, Cleared image to mimic cross-sections of real foraminifera. Not to scale.

Results

The model was implemented in C++ language using the OpenGL/GLUT graphics libraries (Stroustrup 1997; Woo et al. 1997). This approach enables easy porting of the model to different platforms, which support these libraries. All the simulated foraminiferal shells shown in Figures 10–14 were generated by this program. Each presented form is supplemented by a set of parameters, which was applied to the program in order to model this form.

Figure 10A depicts basic terms used in describing simulated foraminiferal shells, including accessory points and lines, such as apertures, GCP and the latest reference growth axis for a new chamber. Figure 10B presents the same form with the skeletal pattern only. Apertures (including foramina) are represented by white gaps within black shell elements. This pattern resembles cross-sections of real foraminifera (Fig. 1)

Figure 11 shows the forms generated mostly with random parameters (Table 1). The first two uniserial forms are partly defined by non-random parameters to show an ideal rectilinear growth pattern ($\Delta\phi_i$ is fixed at 180°). A wide range of this parameter, $144^\circ \leq \Delta\phi_i \leq 216^\circ$, creates random changes of growth direction (Fig. 11C). The last fully uniserial form (Fig. 11D) is constructed with a relatively narrow range of $\Delta\phi_i$ ($174.6^\circ \leq \Delta\phi_i \leq 177.3^\circ$), which is slightly asymmetric to all local reference axes. The resulting form is gently curved (Fig. 11D).

Spiral morphotypes show an incredible variety of shapes. Nonetheless, general growth

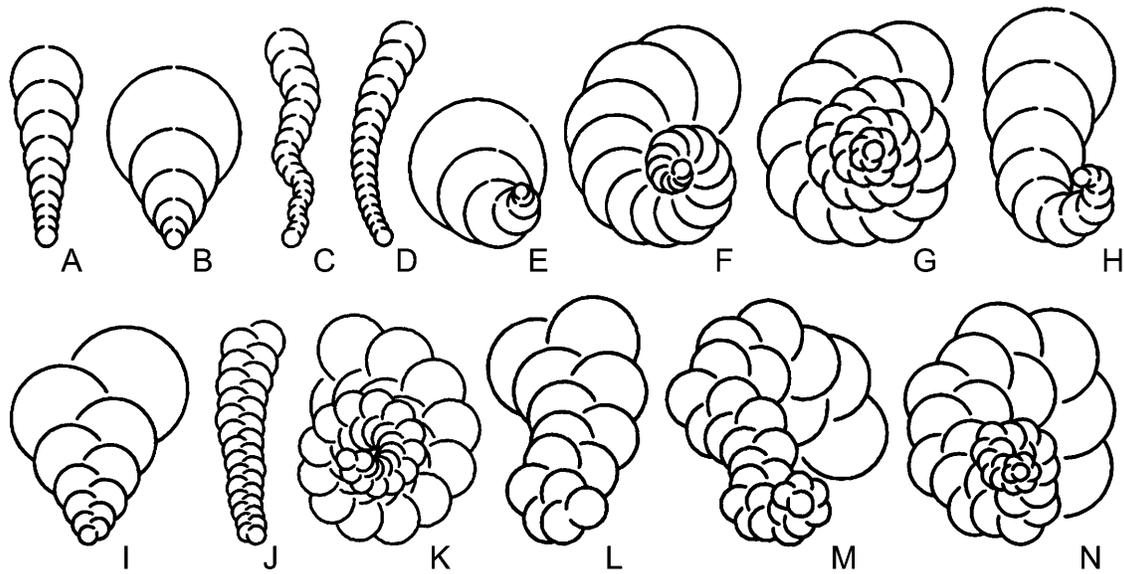


FIGURE 11. Variability of simulated foraminiferal shells. A–D, Uniserial morphotypes. E–G, Different spiral forms. H, Coiled to uncoiling uniserial form. I, J, Biserial forms. K, Biserial-spiral form. L–N, Mixed chaotic forms switching from biserial to spiral patterns. Random (A–N) and nonrandom (TF and $\Delta\phi$ only in A, B) parameters of simulations are shown in Table 1.

patterns are very stable, even with relatively wide ranges of parameters (Fig. 11E–G). Chamber overlaps and global proportions of shells depend on different configurations of expansion ratios (GF_i) and translation ratios (TF_i). The main difference is the localization of apertures. Most of the forms reveal basal apertures, which are located at the base of created chambers (Fig. 11F,G). Areal apertures (enclosed by the same chamber, as opposed to a basal one) also occur and tend to characterize uncoiling morphotypes (Fig. 11E,H). Form H gives an example of such a shell with quite

a drastic changeover from coiled pattern to uncoiled, rectilinear growth. The existence of two such different aperture types is typical for real foraminifers.

Biserial morphotypes are represented by elongated shells, mostly a function of the chamber expansion rate (GF_i) (Fig. 11I,J). High GF_i results in quickly expanding chambers and diverging peripheries (margins) of the shell (Fig. 11I). Low GF_i creates long and slender forms with nearly parallel peripheries (Fig. 11J). Another biserial morphotype with a coiled pattern is produced by relatively nar-

TABLE 1. Parameters of simulated shells from Figure 11.

Fig. 11	GF	TF	$\Delta\phi$ [°]
A	(1.05, 1.25)	0.1	180.0
B	(1.4, 1.8)	(0.01, 0.1)	180.0
C	(0.96, 1.15)	(0.03, 0.08)	(144.0, 216.0)
D	(1.0, 1.11)	(0.01, 0.05)	(174.6, 177.3)
E	(1.4, 1.5)	(0.3, 0.4)	(126.0, 153.0)
F	(1.05, 1.18)	(0.65, 0.75)	(129.6, 142.2)
G	(0.95, 1.15)	(0.13, 0.18)	(84.6, 106.2)
H	(1.15, 1.25)	(0.1, 0.2)	(120.6, 189.0)
I	(1.15, 1.25)	(0.25, 0.35)	(-18.0, 18.0)
J	(1.01, 1.05)	(0.03, 0.28)	(-27.0, 27.0)
K	(1.01, 1.05)	(0.63, 0.68)	(30.6, 41.4)
L	(1.05, 1.1)	(0.35, 0.45)	(18.0, 54.0)
M	(1.01, 1.09)	(0.33, 0.48)	(34.2, 63.0)
N	(1.01, 1.09)	(0.23, 0.28)	(34.2, 63.0)

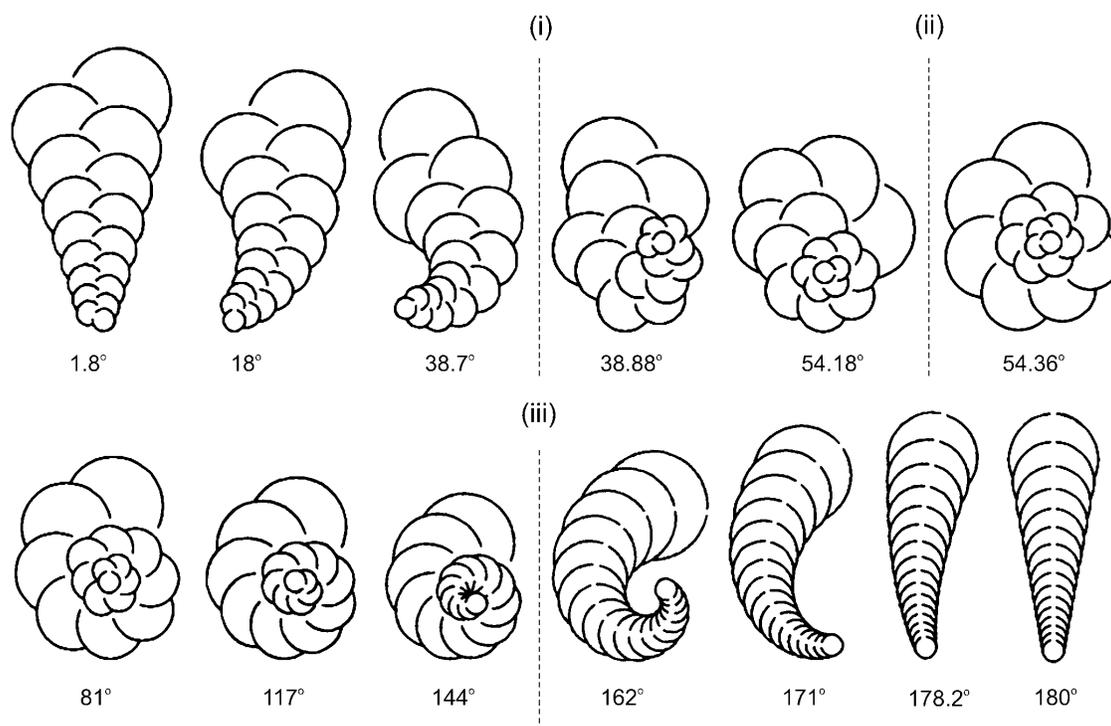


FIGURE 12. Fragment of foraminiferal shell morphospace generated by using nonrandom parameters. The chamber expansion rate and the chamber translation are fixed at constant values: $GF = 1.1$, $TF = 0.4$. The deviation angle of the growth vector $\Delta\phi$ is changing from 1.8° to 180° .

row ranges of all parameters and resembles simple spiral morphotypes with two series of chambers (Fig. 11K). It is worth noting that all of the above morphotypes (A–K) resemble 2-D cross-sections of real foraminifera.

The last three morphotypes show strongly unpredictable growth patterns, switching from biserial to spiral (Fig. 11L–N). They are defined by relatively wide ranges of the deviation angles $\Delta\phi_i$. These chaotic forms are rare in nature, but some of them mimic abnormal shells usually related to environmental stress (Fig. 11L,M). Others may be similar to real attached (adherent) foraminifera, as well as some irregular (in 3-D) agglutinated foraminifera (Fig. 11N).

Although detailed morphospace analysis is beyond the scope of this paper, it is reasonable to test how the model reacts to changing parameters. To understand general behavior in morphospace, it is best to focus on a deterministic model based on nonrandom parameters. It seems clear that simulated shell morphology is very sensitive to changes of the de-

viation angle $\Delta\phi_i$ parameter. Therefore, discrete steps of $\Delta\phi_i$ from 0° to 180° were chosen to test the response of morphotypes to different values of this parameter. Two other two parameters are set constant (i.e., $GF_i = 1.1$; $TF_i = 0.4$) for all simulated forms and for all time steps. The resulting variability of shell patterns reveals four areas (phases) of characteristic morphologies (Fig. 12):

- biserial forms ($\Delta\phi_i$ varies from 0° to 38.844°),
- mixed forms ($\Delta\phi_i$ from 38.862° to 54.324°),
- trochospiral forms ($\Delta\phi_i$ from 54.342° to 158.814°),
- uniserial forms ($\Delta\phi_i$ from 158.832° to 180.0°).

These four areas are separated by three phase transitions (the term introduced in the context of morphospaces by M. Paszkowski (personal communication 2003): (i) from biserial to mixed forms; (ii) from mixed to trochospiral forms; and (iii) from trochospiral to uniserial forms. The first two (i and ii) transitions are abrupt because the morphology rapidly changes its patterns. The last transi-

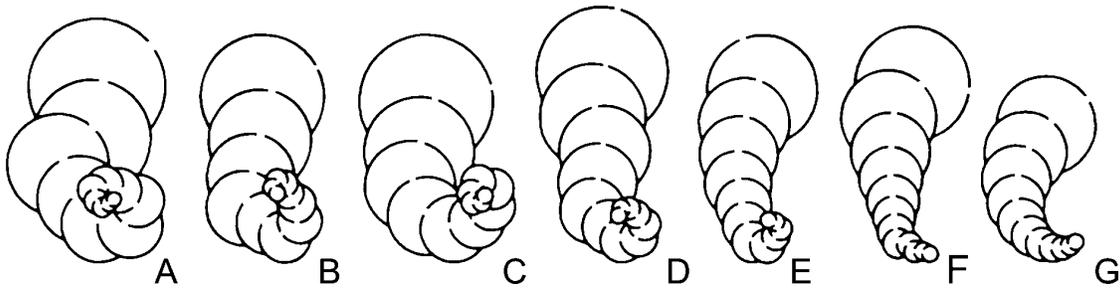


FIGURE 13. Simulations of spiral to uncoiling (A–E) and purely uniserial (F, G) foraminiferal morphotypes with random parameters (A–F) compared with the nonrandom (G); (A–F) $1.15 \leq GF \leq 1.25$ and $0.1 \leq TF \leq 0.2$; (A) $90^\circ \leq \Delta\phi \leq 216^\circ$; (B) $90^\circ \leq \Delta\phi \leq 198^\circ$; (C) $90^\circ \leq \Delta\phi \leq 180^\circ$; (D–F) $108^\circ \leq \Delta\phi \leq 216^\circ$; (G) $GF = 1.2$; $TF = 0.15$; $\Delta\phi = 90.0^\circ$.

tion (iii) is gradual from strictly trochospiral, through to coiled uniserial forms, to uniserial forms. It is important to note that shells with $\Delta\phi_i > 117^\circ$ for all i reveal a tendency towards development of an areal aperture, in contrast to the basal aperture generated at smaller $\Delta\phi_i$ values.

In general, such a set of morphotypes can be treated as a traverse through the three-dimensional morphospace of all possible morphologies. However, this traverse does not include forms that are initially spiral and switch during ontogeny to the stable biserial mode of growth. Furthermore, initially spiral forms switching to uniserial are also missing. On the other hand, they can be simulated by using random parameters (Figs 13, 14).

Figure 13A–E presents examples of such spiral morphotypes changing to uniserial pattern with very wide ranges of the $\Delta\phi_i$ angle.

The model simulates such morphologies, nevertheless, they are completely random and nonrecurring. A similar set of stochastic parameters also creates uniserial forms (Fig. 13F). By comparison, Figure 13G shows the simulated uniserial arched shell defined by averaged nonrandom parameters.

Figure 14A depicts a form that is initially spiral, then switching to a biserial growth pattern. Such forms can only be modeled with random deviation angles ranging around 37.8° – 42.48° . This biserial mode of growth is broken after the addition of the twelfth chamber (Fig. 14B). The averaged value of $\Delta\phi_i$ defines a nonrandom morphotype with mixed spiral and biserial growth patterns (Fig. 14C). This form comes from the same area of the morphospace where mixed morphologies are created (Fig. 12).

Discussion and Future Prospects

A comparison of our moving-reference model with selected fixed models and their parameters is presented in Table 2. An overview of simulated forms based on the moving-reference model indicates that its theoretical morphospace strongly overlaps those developed by fixed-reference models. Elimination of the fixed references reveals a much wider variety of chamber arrangements, which are especially well expressed in simulations of gradual and abrupt ontogenetic changes in chamber arrangements. Such changes also characterize morphotypes of some real foraminiferal shells.

It was arbitrarily decided that the model would select just a single aperture per cham-

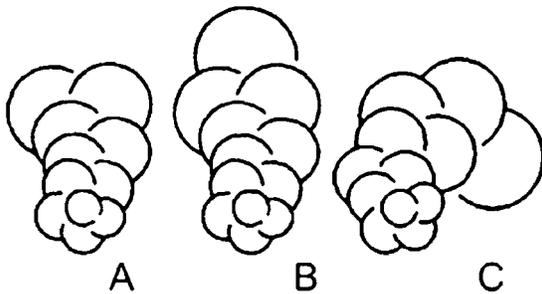


FIGURE 14. Foraminiferal shells generated with random (A, B) and nonrandom parameters with constant values of $GF = 1.1$ and $TF = 0.4$. A, Spiral form (first five chambers) changing to biserial (last six chambers). B, The same form with additional chamber breaking the biserial growth pattern (deviation angle $\Delta\phi$ varies from 37.08° to 42.48°). C, Alternating spiral and biserial form with the constant deviation angle $\Delta\phi = 39.78^\circ$.

TABLE 2. Tentative relationships between reference systems and the parameters of discussed models of foraminiferal shell growth. The parameters are defined either in the fixed-coordinate system (*) or in the moving-reference system (**).

	Berger 1969	Signes et al. 1993	This model
Reference system	Fixed-coordinate system*	Fixed cylindrical coordinates system*	Moving-reference system**
Apertures	None	None	Calculated as a result of LCP minimization
Size of chambers	"q-ratio" between successive chamber radii	Kt parameter (chamber vs. shell volume ratio)	GF -chamber expansion ratio between successive chamber radii
Angle between successive chambers (centers)	'a-angle' of advance	ϕ	None
Local growth angle**	None	None	$\Delta\phi$ -angle of deviation from the reference growth axis**
Amount of chamber overlap	"o-lap"-amount of overlap	None	TF -chamber translation ratio
Distance from the axis*	None	D^*	None
Translation along the coiling axis (in 3-D)*	None	Ky parameter	None
Selection of parameters	Nonrandom	Nonrandom	Random or nonrandom

ber. This is the case for most small foraminifera. Multiple apertures were not taken into account at this stage to keep the model as simple as possible. Including such apertural variability will be essential in future attempts to simulate complex foraminiferal shells.

In order to avoid "forbidden morphospace regions" sensu Berger (1969), i.e., detachment of chambers, the translation ratio parameter (length of the growth vector) is defined in such a way that it cannot be longer than the radius of a new chamber. Foraminifera with chambers that do not touch one another cannot exist as integral individuals. Future studies should focus on the mapping out of geometric constraint boundaries, the parameter coordinates that represent possible versus impossible geometries (G. McGhee written communication 2004). We believe this is an essential analytic technique of theoretical morphology (see Berger 1969; McGhee 1999).

Our model is not able to simulate forms, such as *Lenticulina*, with a maximal global communication path (Fig. 5B). This is due to the assumptions that chambers are isometric with constant circular shapes and that the position of an aperture does not shape the chamber. On the other hand, our empirical observations have shown that apertures often have

a strong impact on the shape of a chamber; e.g., chambers tend to show specific apertural structures, such as necks (tubiform extensions of ultimate chambers), radial structures (e.g., in *Lenticulina*), depressions around apertures, etc. Future studies ought to include this aspect into the theoretical morphology of foraminifera.

The reference growth axis used in our model has a vague morphogenetic representation during the formation of a chamber (see Figs. 7, 9, 10). This growth axis is defined by the center of the last chamber and the final aperture. It moves with the formation of successive chambers. It should be noted that this line describes growth from an essential morphogenetic point, i.e., from the aperture. Another option would be to define the reference growth line as connecting the last two adjacent apertures. Its physical representation would be clear because it would follow the local communication path (LCP). An important analog of our hypothetical reference growth axis can be found in large complex foraminifera, which often show intercameral foramina situated along straight lines, facilitating the protoplasmic streaming between chambers or chamberlets (see Hohenegger 1999; Hottinger 2000). This means that when a new chamber

is formed, its new aperture or apertures tend to follow the same foraminal line (created by the former apertures). The protoplasmic streaming may also play a role in small foraminifera. Coiled forms with uncoiled final stages, as well as fully uniserial morphotypes, show a tendency to stabilize their uniserial pattern as soon as they reach it. Therefore, our reference growth axis may have a true morphogenetic meaning; i.e., the protoplasmic streaming and/or cytoskeletal structures may force a new aperture to locate *vis-à-vis* the former opening. Empirical examples should be used to investigate this point further and the results should be incorporated into the model.

The previous models used a nonrandom selection of parameters, which were kept constant throughout the ontogenesis. Our first method also applies this approach in order to test the response of the model to fixed parameters. Simulations with such parameters reveal very regular patterns with gradually changing forms of chambers (Fig. 11G,H). However, this does not match reality because foraminiferal shells never show ideal chambers that follow strict geometric rules. Some chambers are larger or smaller than average; others are more or less twisted from general growth directions or overlapped in different manners. Extremely regular forms are unrealistic in nature but may resemble individuals of certain species developed under very stable environmental conditions. Therefore, this fixed-parameter approach represents the end-member of the continuum covering the whole spectrum of susceptibility of chambers to flexible ontogenetic variability.

Our second approach incorporates this ontogenetic variability into the model. In this stochastic approach, selected parameters are allowed to fluctuate within given ranges. These ranges correspond to the physiological response of the cell to different environmental conditions during the formation of chambers. Therefore, variability of chambers within the same individual defined by the specific genotype is limited by intrinsic morphogenetic constraints. These constraints are indirectly defined by the genotype itself through complex self-organization of coded molecular processes. Actually, the best term for such varia-

tions is a "reaction norm," which is the set of phenotypes produced by a single genotype across a range of environmental conditions (Stearns 1992).

Our simulations mimic real morphogenetic processes, which are always strongly affected by external factors, such as nutrition availability, temperature, salinity, and pH level. Some foraminiferal species show very stable shell morphologies, others change strongly within a certain range. For instance, adherent (attached) foraminifers sometimes have an irregular morphology, which seems to have strong functional value controlled by a substrate, competition for space, and food availability. These irregularities, directly controlled by environmental factors, must be tolerated by genetic control.

An instructive example refers to fluctuations of chamber volumes, which are most likely to be related to food availability during different phases of ontogeny. Larger chambers are probably formed during high food availability; relatively smaller chambers may be linked to periods with distinctly lower access to nutrition (see Rhumbler 1909; Holbourn et al. 2001; Tyszka 2004).

In conclusion, modeling the influence of external factors on morphogenesis of foraminifers based on simple randomization of parameters. This stochastic approach, introducing random fluctuations of parameters within a given range, mimics reality much better than fixed parameters. This approach should be further investigated, even if morphogenesis of foraminiferal shells seems to be strongly genetically controlled, in contrast to an accretive growth of marine sessile organisms, such as corals, sponges, coralline algae, which often grow under strong and continuous influence of the environment (e.g., Kaandorp 1994; Kaandorp and Kuebler 2001).

Comparison of simulated morphotypes with real foraminiferal shells indicates that the model with nonrandom parameters (deterministic) is not able to simulate some important morphotypes, e.g., the forms that are initially spiral but finish either with biserial or uniserial patterns. Such forms are modeled only with random parameters (Figs. 13, 14). Real foraminifers do reveal such recurrent

and relatively stable morphologies, which seem to be indirectly controlled by their "genetic programs." If such stable, repeatable morphologies are missing in the nonrandom model, then the model should be further verified and/or extended by using additional rules or parameters. In the future, we would like to focus on the definition of $\Delta\phi$ and introduce certain additional rules controlling placement of apertures. Although the local minimization principle appears to be one of the basic rules, it is very likely that other rules take part in the morphogenetic processes of shell formation.

The model presented herein is size-independent, which may be considered as a limitation. We are aware that real foraminifera are size-dependent, as has been suggested by several authors (e.g., Brummer et al. 1986; Hemleben et al. 1989; Signes et al. 1993; Tyszka 2004). Size-dependency was analyzed and extensively discussed by Signes et al. (1993). This approach, including isometry or allometry of chambers and shells, will be incorporated and extended in further studies. Our present focus is on development and optimization of the model before application of additional relationships.

Spherical shapes of simulated chambers do not reflect the tremendous variability of chamber shapes in nature. Furthermore, foraminiferal growth is often strongly allometric, and in many foraminifers the shape of the chamber changes during ontogeny. All these ontogenetic changes influence the overall form of the whole specimen, which directly depends on cumulative succession of chambers. It is clear that we have to test other methods (under study) to incorporate chamber shape into the model. A first approximation could be an introduction of implicit surfaces (blobs, metaballs) (Opalach and Gascuel 1995) to model chambers with irregular shapes. The best method would be to model intrinsic morphogenetic processes, which directly control the shape and size of chambers, including the localization of apertures. These processes are just roughly understood and should be addressed in future investigations.

All former and recent models of foraminiferal theoretical morphology are purely geo-

metric in nature. Although the most recent model introduces apertures as local and moving reference points, it still uses artificial parameters, such as angles and ratios. Another model based on simulation of real processes is necessary. Such a model should still act locally; thus, apertures should represent local reference centers for the formation of successive chambers. The model should further introduce intracellular dynamics during the formation of chambers, including, among others, cytoskeletal dynamics with the formation of microtubular networks, internal signaling, formation of primary organic membrane, "Anlage," processes of the test secretion, formation of aperture/s, pores, external structures, and secondary laminae. The model should mimic biochemical reactions and biophysical processes rather than geometric transformations. Theoretical foraminiferal morphogenesis may then emerge spontaneously from simple rules and parameters, instead of being predefined in the form of geometric figures and their transformations. Constructing such an emergent model is a challenging prospect for the future (see Tyszka et al. 2005).

Conclusions

Previous models of foraminiferal shells (e.g., Berger 1969; Signes et al. 1993) referred to fixed axes and neglected apertures (see Figs. 2, 3). Our simple 2-D model applies a moving-reference system, an idea that comes from simulations of heteromorphic shells of ammonites (Okamoto 1988; Ackerly 1989). This system is based on introducing apertures as reference points, which in reality and in our model are responsible for emplacement of every new chamber (Figs. 1, 6–9). A minimization paradigm of the local communication path (LCP) helps to define an aperture in every newly added chamber. The LCP rule derived from previous studies (Hottinger 1978; Brasier 1982) suggests global shortening of the distance between the first and the last chamber via internal foramina and an external aperture. This rule is based on local optimization during formation of a new chamber. Even if it does not explain all cases (Fig. 5B), it is a close approximation of actual morphogenetic relationships during the stepwise growth of fo-

raminiferal shells. The model also introduces three parameters, i.e., chamber expansion rate, chamber translation ratio (overlap), and deviation angle. This model tries to use real morphologic characters and to follow basic biological processes, which usually act step-by-step. In order to imitate reality, some elements of randomness, another novelty in foraminiferal modeling, are applied in selection of parameters. This approach seems to be very promising for future studies. It mimics random genetic variability (mutations) and the influence of external (environmental) factors. Comparison of the moving-reference model presented herein with selected fixed models is shown in Table 2.

Simulated foraminiferal shells based on the moving-reference model indicate that their variety is much wider than for morphotypes developed by fixed-reference models. The moving-reference model is especially well suited for simulating gradual and abrupt changes in growth patterns as features characteristic of real foraminiferal shells (Figs. 1, 11–14).

We are aware of numerous oversimplifications in the model. Some of them can be overcome by further updating this model. To move further toward reality, the model should be verified and extended by applying additional rules as well as parameters. Two-dimensional simulations have only limited value, because foraminifera grow in three dimensions and some of the growth patterns cannot be reduced to two dimensions (see Łabaj et al. 2003). Furthermore, we want to test other methods to incorporate variability of chamber shapes into the model. Ideally we would like to construct an emergent model that simulates intrinsic morphogenetic processes and emergent shell patterns (see Tyszka et al. 2005).

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