Morphospace of foraminiferal shells: results from the moving reference model

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The moving reference model of foraminiferal tests (shells) is based on principal morphogenetic rules revealed from real foraminifera. The model has introduced apertures as moving reference points based on minimization of the distance between them. These modifications greatly enhanced variability of simulated shells closely resembling actual complexity of small polythalamous foraminifers. The resulted theoretical morphospace of all simulated forms is far more extensive than any produced before. The fragments of the multidimensional theoretical morphospace are presented in two forms, i.e. a (classical) box model and a *morphotree*. The theoretical morphospace of foraminifera reveals regions of the morphospace that include similar forms. These specific fields in the morphospace, called *morphophases*, are separated from each other by either sharp or gradual *morphophase transitions*, which involve sharp or gradual changes in morphology controlled by changes of the model parameters. Optimized emplacement of foraminiferal apertures is responsible for these *morphophase transitions*. The overall morphospace splits into the 'possible range' and the 'forbidden range'. The 'possible range' includes existent and nonexistent foraminiferal forms, which are further separated into 'vacant', 'dysfunctional', and 'deficient' ranges. All the ranges provide additional knowledge on theoretical foraminiferal morphology. The 'vacant range' of possible, although nonexistent, morphologies is limited and that may suggest that the real evolution of foraminifera has discovered most of the morphologic possibilities. It is suggested that the 'forbidden' and 'deficient' ranges present model constraints useful for understanding morphogenesis, which may be tested by further modifications of the model. The analysed theoretical morphospace verifies the moving reference model, indicating the fundamental role of apertures in the morphogenesis of foraminifera. □ *Foraminiferida, modelling, morphogenesis, morphophase transition, theoretical morphology.*

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Theoretical morphology covers two different conceptual areas focused on the morphology of organisms, including: (1) the simulation of organic morphogenesis, and (2) the analysis of the possible spectrum of organic form via hypothetical morphospace construction (McGhee 1999). Both areas are essential for understanding the broad spectrum of fossil and living organisms. The first area models the actual process of biological morphogenesis itself. The second area explores the possible range of morphologic variability produced by constructing *n*-dimensional geometric spaces called 'theoretical morphospaces', which are created by systematically varying parameter values of a modelled form (McGhee 1999). In contrast to theoretical morphospaces, we can also construct 'empirical morphospaces' (*sensu* McGhee 1999) based on real measurements of morphologies and applying different ordination techniques. Nevertheless, analyses of 'empirical morphospaces' use completely different approach focused on biometrics and quantifi-

cation in contrast to theoretical morphology's interested in simulation, not quantification (McGhee 1999). McGhee's definition (1999, p. 289) stresses that empirical morphospaces "have no existence in the absence of actual measurement data." Therefore, in order to avoid confusion in this paper, all existing real morphotypes are called 'empirical morphologies'.

This discipline of theoretical morphology was inspired from early monographs of E. S. Russell (1916) and D'Arcy W. Thomson (1919) on the 'form, shape, and function' of animal morphologies. Nonetheless, D. M. Raup is the founder of modern theoretical morphology. His early fundamental works described the theoretical morphology of coiled shells (Raup 1961, 1962; Raup & Michelson 1965). The first theoretical morphospace of foraminiferal tests (shells) was created by W. Berger in 1969. His geometric model focused on spiral planktonic foraminifera and is based on the x-y origin as a fixed reference frame and three parameters.

Berger (1969) constructed two dimensional sections of a three-dimensional morphospace, identifying regions of possible forms and impossible forms. The latter forms were defined by the 'forbidden range' because it produced impossible forms of successive foraminiferal chambers that did not touch one another. In contrast to Berger's isometric model, Brasier (1980), Signes *et al.* (1993), and De Renzi (1995) constructed allometric theoretical models of foraminifera. Brasier (1980) presented a generalized theoretical morphospace defined by four parameters and including a high variety of forms.

A new generation of foraminiferal models based on the moving reference approach was introduced by Topa & Tyszka (2002). The model follows Raup's (1962) and Berger's (1969) idea of geometric transformations, but introduces basic modifications, i.e. foraminiferal apertures as moving reference frames and minimization of the distance between apertures. The moving reference models have been used in early models of plant growth (Lindenmayer 1968) and ammonite shells (Okamoto 1988; Ackerly 1989). So far, previous papers have focused on the description of successive models (Topa & Tyszka 2002; Łabaj *et al.* 2003; Tyszka & Topa 2005). The aim of this paper is to present and analyse the theoretical morphospace of foraminiferal shells based on the moving reference model.

It should be stressed that foraminifera (Order Foraminiferida Eichwald 1830; Loeblich & Tappan 1988) are an important group of fossil and living organisms used for geological and environmental bio-monitoring studies. It is therefore essential to analyse and verify factors controlling their endless morphologic variability. This new theoretical approach is focused on real morphogenetic process and is tested by realistic simulations of shell forms, and may shed new light on foraminiferal architecture and taxonomy of this group. There is also a great chance that the combination of *in silico* and *in fossilio* experiments complemented by biological *in vivo* and *in vitro* methods may further contribute to a better understanding of foraminiferal morphogenesis and evolution.

Methods

The moving reference model of foraminiferal shells has been described separately (Topa & Tyszka 2002; Łabaj *et al.* 2003; Tyszka & Topa 2005). This morphospace analysis is based on the model presented by Łabaj *et al.* (2003) simulating theoretical foraminiferal shells in 3-dimensional space. Simulations have been performed using an implementation of the model as a Java applet with the Java3D library for

visualisation purposes (Łabaj *et al.* 2003). The applet, further modified and upgraded by P. Topa, is available at: http:// www.icsr.agh.edu.pl/foraminifera/index_ en. html or http://www.icsr.agh.edu.pl/ ∼otwornic/ index_en.html

Parameters of the model

Parameters of the model are used to represent a number of morphospace dimensions. This means that morphospace dimensions are defined by changing parameters: the moving reference model includes four parameters in isometric growth and six parameters in allometric growth.

Chamber scaling rates are defined in 3-dimensional space by three parameters (Fig. 1): k_y – chamber height ratio; k_x – chamber width ratio; k_z – chamber depth ratio. If all chamber expansion ratios equal each other ($k_x = k_y = k_z = GF$), a new chamber is isometric to the previous one. Any differences in chamber scaling ratios cause allometric growth of successive chambers. These parameters correspond to the parameter GF (growth factor), i.e. the chamber expansion ratio *sensu* Topa & Tyszka (2002) and Tyszka & Topa (2005) described for isometric growth of chambers. Chamber scaling rates of real foraminifera usually range from 1.1 to 1.5 and may change during ontogenesis (see Gradstein 1974; Hemleben *et al.* 1989; Tyszka 2004). In order to simplify our results, the studied model keeps these ratios constant throughout morphogenesis.

TF (*translation factor*) shifts the centre of a new chamber outside (positive values) or inside (negative values) the last chamber (Fig. 1). TF represents the length of the growth vector (see Łabaj *et al.* 2003). The 0 value places the centre of a new chamber directly at the aperture of the last chamber. This parameter ranges from -1 to $+1$ values, i.e. $\langle -1; 1 \rangle$. Higher values detach a new chamber from the existing shell. $TF < -1$ may disconnect a new chamber from the preceding chamber, and thus, from the whole shell. These out of range values represent a 'forbidden range' *sensu* Berger (1969).

$\Delta\phi$ is the *deviation angle* (deflection) and is an angle between the local growth line and the line defining the centre of a new chamber (Fig. 1). This angle ranges $\langle -180°; 180° \rangle$. Higher or lower out of range values can be recalculated to the values from the given range.

β represents the *rotation* angle along the local growth line, which is defined by the preceding two apertures (Fig. 1). This parameter is necessary in 3-dimensional space. It ranges from $-180°$ to $180°$, i.e. $\langle -180°; 180° \rangle$. Higher or lower values can be recalculated like deflection angles to the values from the given range.
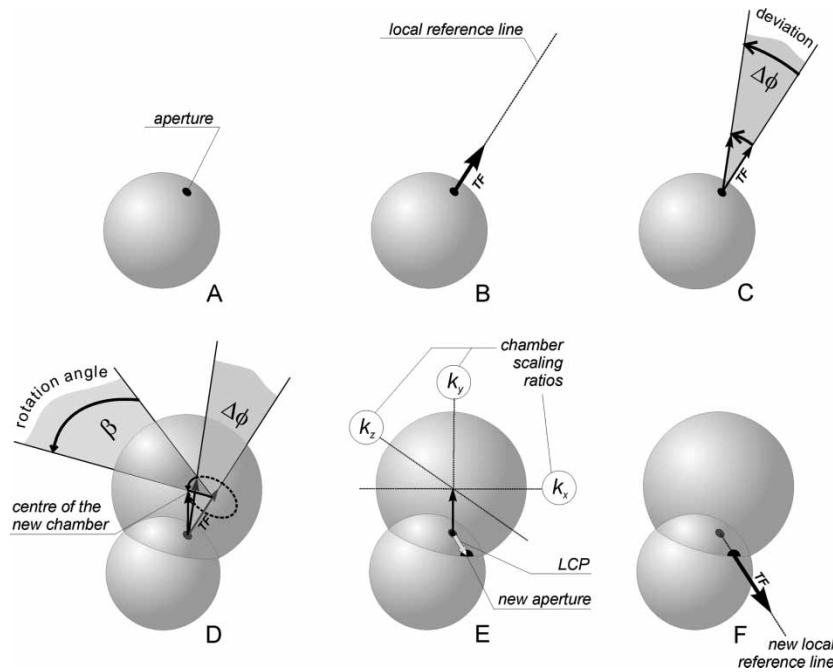
Fig. 1. Basic stages, rules and parameters of the moving reference model of foraminiferal shell morphogenesis (Łabaj *et al.* 2003). □A. First chamber (proloculus) with its aperture. □B. Defining a local reference line and the growth vector; parameter *TF* (translation factor) defines the length of the growth vector. □C. Deviation (*Δφ*, deflection) of the growth vector. □D. Rotation (*β*) of the growth vector, which finally defines the centre of a next chamber; constructing a new chamber according to chamber scaling ratios (k_x; k_y; k_z – see E). □E. Searching for the LCP (local communication path) as the shortest line connecting the last aperture with the surface of the new chamber. □F. Constructing a new local reference line with a new growth vector defined by *TF*.

Morphospace visualization

Presentation of any morphospace with three or more dimensions is strongly limited on 2D surfaces. A classical option of morphospace visualization applies 2-dimensional cross-sections through a 3- or more dimensional morphospace. Such foraminiferal morphospaces have already been presented before (see Berger 1969; Webb & Swan 1996; Tyszka & Topa 2005; Tyszka *et al.* 2005). Although this method has limitations, this (classical) box model is still applied herein (Fig. 2). Nonetheless, other alternative techniques of morphospace visualization have been tested, focusing on a *theoretical morphospace tree* (also called here a *morphotree*) as another method of visualization and exploration of multidimensional morphospaces. It resembles the 4-dimensional foraminiferal morphospace illustrated by Brasier (1980). The construction of the *morphotree* starts from any basic morphologic form defined by selected parameters, where their number equals the number dimensions in a model one deals with. The basic form is modified along selected dimensions, presenting successive morphologies on the same line that depicts increasing or decreasing values of parameters. The same procedure can follow along other dimensions, represented by other lines or branches, radially spreading out from the centre, i.e. the basic

form. This method can also be modified, allowing new branches to begin from any successive form.

Theoretical morphospace

Classical box model

A three-dimensional visualization of the foraminiferal morphospace is presented on Figure 2. The morphospace is described by: the deviation angle (deflection) angle (*Δφ*), translation factor (*TF*), and growth factor (*GF*) where all chamber scaling rates are the same (i.e. $GF = k_x = k_y = k_z$) and the rotation angle (*β*) is set constant at 0°. Deviation angles (*Δφ*) are changed at 30° increments except for the 179.99° value which replaces the 180°-angle. This value creates zigzag chamber arrangements presented in Figure 4 at the end of the Δφ-branch. Such forms are possible and actually known from nature, but represent artefacts of virtual measurements of local communication paths (LCPs) because these measurements depend on the mesh of the network used to visualize spherical shapes (Łabaj *et al.* 2003; P. Topa, 2005 personal communication).

The translation factor (*TF*) is plotted in 0.3 increments, except for the 0 value, which seems to be a critical level and needs further explanation. This value represents a sharp and distinct transition between very different
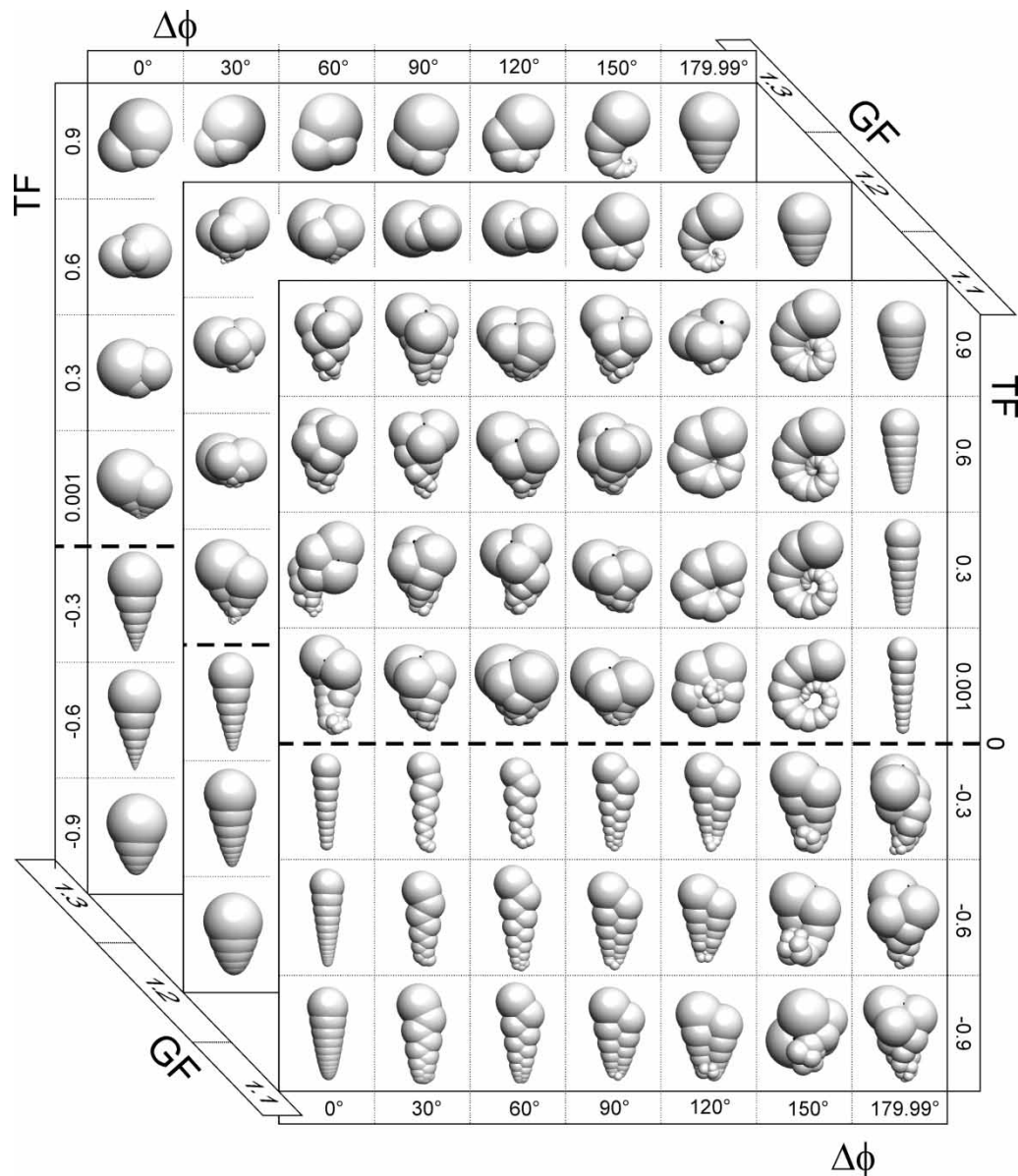
Fig. 2. Three-dimensional fragment of the theoretical foraminiferal morphospace based on the moving reference model (compare Fig. 3 and the text for further explanations). $\Delta\phi$ – deviation angle (deflection); *TF* – translation factor; *GF* – growth factor that equals ($GF = k_x = k_y = k_z$).

theoretical morphologies. This is related to setting the centre of every chamber exactly in the aperture of the preceding chamber (see Fig. 4 – 0.0-case). Such a particular case causes an ambiguous state when all possible distances (LCP's) between the aperture and the surface of a new chamber are identical. Although it could be possible to introduce random choice of the next aperture, nonetheless, Figure 2 avoids this case by using a slightly positive TF-value that equals 0.001.

Morphophases and morphophase transitions

It is important that the zero-TF-value defines a line (in 2D) or a plane (in 3D) that separates areas with

positive and negative TF-values. This transitional plane represents a *phase transition* between two states (phases). The term *phase transition* has already been introduced in the context of the theoretical morphology (M. Paszkowski, personal communication 2004; Tyszka & Topa 2005). This term is adopted here as a *morphophase transition*, defined as a distinct change from one morphologic state (morphophase) to another with changing model parameters, but without changing the rules of a model. This new term is unrelated to the term morphocline restricted to transitions of morphologic characters within a species along an environmental factor (Yordanova & Hohenegger 2004). There are other *morphophase transitions* and areas with distinctly

different theoretical morphologies in the morphospace (see Figs 2, 3). These areas represent *morphophases* that group similar theoretical morphologies in terms of uniform geometrical properties. Therefore, we can distinguish a morphophase as a 'uniserial morphophase' or 'biserial', 'coiled biserial', 'trochospiral', 'planispiral', 'planispiral-to-biserial', 'irregular' and other *morphophases* (Fig. 3).

A gradual change of a model parameter usually causes a gradual change in resultant morphology. This means that if we are inside a certain morphophase, there are no abrupt changes in morphology of simulated forms. If we cross a sharp *morphophase transition*, even a small parameter change results in drastic morphologic changes that are analogous to physical phase transitions. It should be stressed that such a drastic change (sharp *morphophase transition*) takes place during an infinitesimally small change of a controlling parameter. The transition TF = 0 is the best example of a sharp *morphophase transition*. There are also gradual *morphospace transitions*, such as those between planispiral and trochospiral *morphophases* or uniserial and planispiral *morphophases* (see Figs 2, 3).

It is not surprising that similar morphologies are created in different parts of the morphospace as similar configurations of chambers can be formed based on very different parameters. For instance, a morphophase of
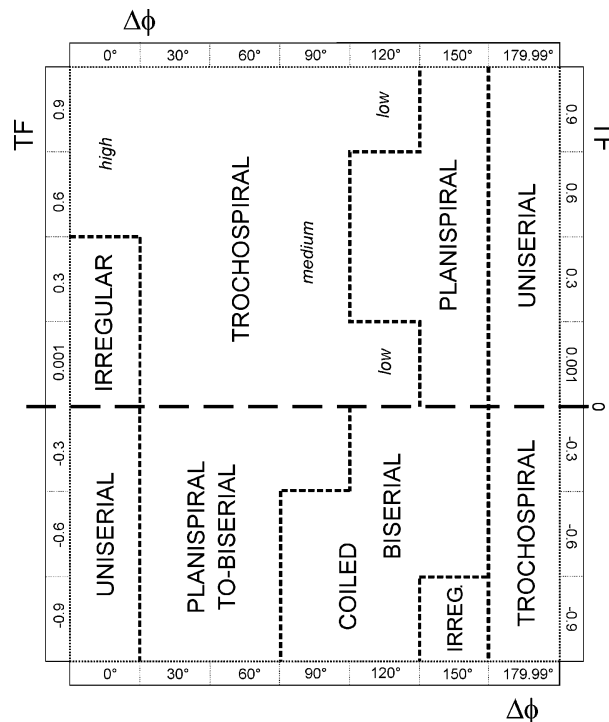

Fig. 3. Various *morphophases* distinguished within the 2-dimensional morphospace presented in front layer of 3-dimensional morphospace from Fig. 2. *Morphophases* including similar chamber arrangements (shell morphologies) are separated by *morphophase transitions* (dashed lines).

trochospiral or uniserial shells can be generated with very different parameters (Figs 2, 3). This means that similar morphologic forms can either be closely related or nearly unrelated phylogenetically. Closely related morphotypes would have similar geometric parameters, in contrast to distantly related forms.

Morphotrees

Our results can also be presented on a *theoretical morphospace tree* (*morphotree*). Figure 4 shows such a *morphotree*, which is just a single example of an unlimited number of morphotrees. In order to construct such a tree, we simulate a basic shell form defined by any combination of selected parameters. This form is placed in the centre from which other dimensions spread out. Then this original form can be modified along any dimension, presenting the succeeding morphologies on the same line depicting changing, i.e. increasing or decreasing, parameters. In order to keep the morphotree simple, just a single parameter is changed along the same line (Fig. 4). The same procedure can be applied to other parameters/dimensions represented by additional lines spreading out from the centre. An example of such a morphospace tree simulates a simple biserial morphotype as a central form (Fig. 4). Such forms are well known from calcareous (*Bolivina*, *Brizalina*, *Gabonita*, *Bolivinella*) and agglutinated foraminifera (*Textularia*, *Textulariopsis*) (Loeblich & Tappan 1988).

The *morphotree* illustrates (Fig. 4) that changes of the parameter *TF* (translation factor) modify test arrangements from biserial, through streptospiral-biserial forms, then triserial-biserial forms to highly trochospiral in the positive values of the parameter up to 0.99. Values higher than 1.0 cause separation of the chambers and represents the forbidden range of Berger (1969). This transition, indicated by a thick dashed line between the possible and impossible forms (Fig. 4) can be treated as a morphophase transition. Lower or negative *TF*-values produce uniserial or biserial rectilinear forms with strongly overlapping chambers in the most negative values.

If we switch from the '*TF*-branch' to 'Δφ-branch' and go from 5° to 180° Δφ-angles, we can see relatively strong changes in foraminiferal patterns from biserial, through streptospiral-biserial, then streptospiral, streptospiral-to-tetra-serial, highly trochospiral, low trochospiral, planispiral, curved uniserial, rectilinear uniserial to zigzag-like uniserial forms. As mentioned above, the zigzag-like uniserial form is an artefact of the model implementation. This morphology is still possible, and actually, such patterns are known from agglutinated foraminifers (a rare species of *Subreophax*).

Parameter β (rotation angle) gradually modifies morphotypes via spiral twisting of biserial forms, which
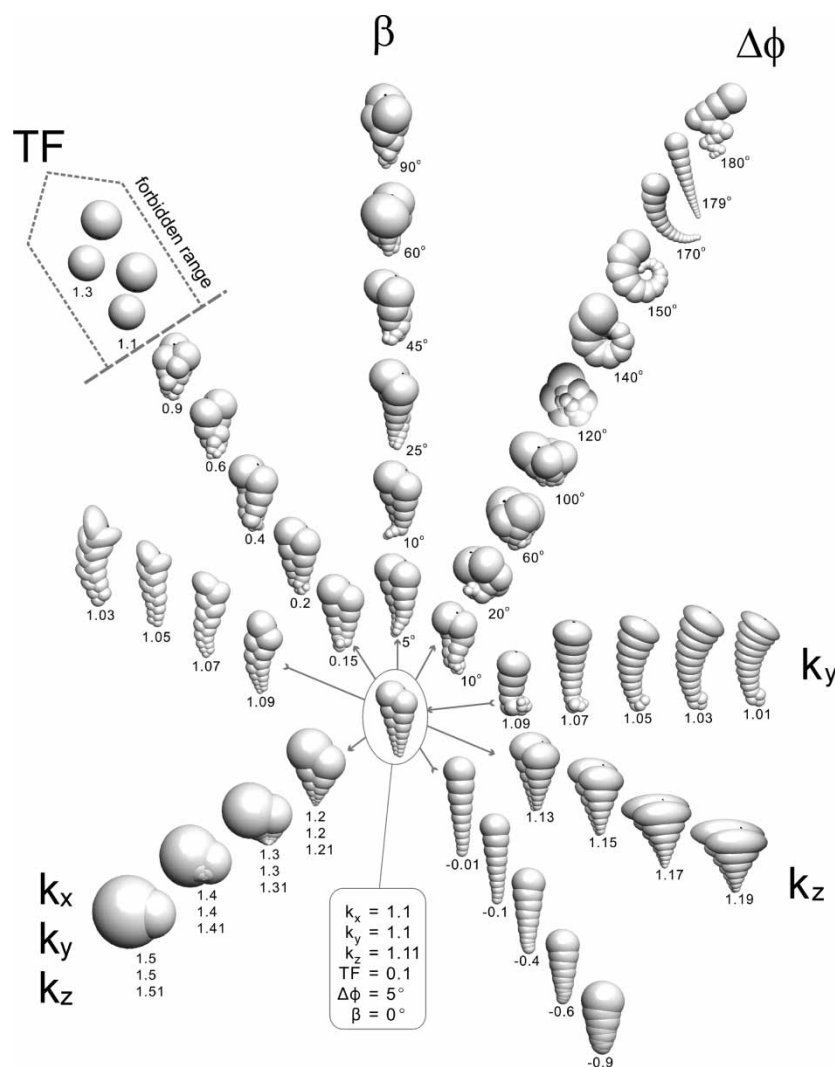
Fig. 4. Six-dimensional *morphotree* of foraminiferal shells (after Tyszka 2005, extended and modified). Arrows, pointing to increasing values of parameters, indicate directions of dimensions (branches). Numbers depict changing values of parameters.

resemble *Fursenkoina*- or *Cassidella*-like forms. Rotation angles above c. 60° give twisted biserial form, which are hardly recognizable from similar highly trochospiral forms. Such morphotypes resemble agglutinated *Arenobulimina*-like tests (see Loeblich & Tappan 1988).

Possible vs. impossible morphologies

The complete theoretical foraminiferal morphospace covers all possible and impossible morphologies. Theoretically possible morphologies include all forms constructed from attached chambers with their internal parts connected via apertures (foramina). These theoretical-form assumptions derive directly from empirical morphologies of multilocular foraminiferal shells. In contrast, impossible morphologies represent the forbidden range (*sensu* Berger 1969) and incorporate two

types of impossible forms at least, i.e. (1) those with detached chambers and (2) the others with disconnected foraminal paths. The model can, for instance, simulate such forms when the *TF*-value is (1) higher than 1.0 or (2) lower than −1.0, respectively (Figs 4, 5).

Finding the specific *morphophase transitions* between 'possible' and 'forbidden' ranges seems to be essential because the existence of the 'forbidden range' of impossible morphologies informs us about constraints of the model. Actually, it would be possible to modify the geometric model to eliminate the 'forbiden range' by assuming that foraminal paths (lines connecting apertures) cannot leave a simulated test, thus, cannot go outside the test. A simpler way would be to exclude parameter values higher or lower than a certain critical value. Nevertheless, in both cases, we would arbitrarily 'forbid' certain ranges of parameters, thus, we would still use the concept of the 'forbidden range'.
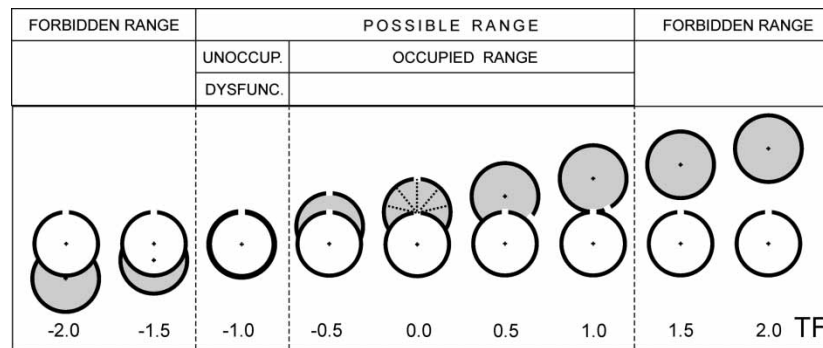
Fig. 5. One-dimensional cross-section of theoretical 2-chambered foraminiferal shells along changing translation factors (*TF*). Grey chambers represent a second chamber. Dotted lines at 0.0 *TF*-value indicate 'undetermination' of the shortest distance (LCP) from the previous aperture to the chamber surface. Different ranges of the morphospace are explained in the text.

Existent vs. nonexistent morphologies

All the lower rank ranges (Fig. 6) can only be distinguished based on comparison of theoretical morphospace with empirical morphologies. This comparison is qualitative at this stage of investigation because so far there is no quantitative method comparing theoretical and empirical foraminiferal morphologies. Such a qualitative approach is, nevertheless, worthwhile because it verifies the model.

If we start exploring a possible range of the morphospace in comparison to the empiric data, we see that this part of the morphospace is further split into two parts, including an 'occupied range' and an 'unoccupied range'. The occupied part incorporates all existing forms known from reality (see Schindel 1990). Unfortunately, empiric foraminiferal morphologies cannot be compared in detail, thus, we can only focus on general arrangements of chambers. Nonetheless, the conclusion is that nearly all theoretical forms simulated by the

implemented model (Łabaj *et al.* 2003) are already known from reality. This 'occupied' part of the morphospace validates the model, even if most morphotypes just roughly resemble empirical morphologies. There are also areas of the morphospace which do not have empirical counterparts. This 'unoccupied morphospace' range is essential for the understanding of morphogenesis. It can be used to explore the limits of geometric constraints associated with a given model and the logical consequences of the fundamental consequences of the model (K. Niklas, quoted in McGhee 2001). General comparison of empirical morphologies with theoretical morphologies generated in the 'unoccupied range' allows distinguishing three lower rank categories (Fig. 6):

(1) 'vacant range' – an empty range that is most likely fully functional, but so far not recorded within empirical morphologies;
(2) 'dysfunctional range' – geometrically possible, but dysfunctional morphologies; e.g. parts of the morphospace with extreme values of parameters, such as non-functional proportions of chambers with very high scaling ratios or strongly limited chamber volume (see Fig. 5);
(3) 'deficient range' – geometrically possible, but probably partly dysfunctional morphologies due to unconsidered (usually unknown) rules of the model.
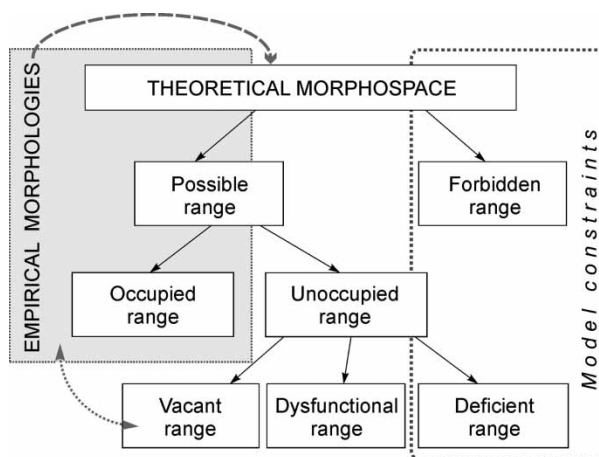
The 'vacant range' may assist in predicting possible but unknown morphologies. Another option is that real evolution may not have discovered all possible morphologies due to temporal constraints (the term after McGhee 1999). Foraminifera simply have had not enough time to evolve into the vacant region of the morphospace (McGhee 2001). Actually, this range seems to be limited in case of the foraminiferal morphospace. Overall comparison of the theoretical morphospace and

Fig. 6. Subdivision of the theoretical morphospace into different ranges based on their relationships to empirical morphologies. 'Forbidden range' and 'deficient range' are interpreted to depict model constraints (see text for further explanation).

empirical foraminiferal morphotypes suggests that evolution of small polythalamous foraminifers probably have 'discovered' nearly the whole theoretical morphospace. Even 'coiled biserial' forms, that seem to be nonexistent (Figs 2, 3), are known from reality as *Plectorecurvoides* – the genus representing a completely coiled biserial agglutinated foraminifer, or the whole superfamily Cassidulinacea, characterized by enrolled biserial or secondarily uncoiled biserial calcareous tests (Loeblich & Tappan 1988).

The 'deficient range' includes some simulated forms (Tyszka *et al*. 2005, fig. 2) that almost certainly never existed in reality, but resemble specific abnormal shells switching or swinging from the biserial growth mode to spiral one. Some of them show every-2-chamber rhythms from left to right coiling, resembling a pseudo-biserial arrangement. Such arrangements are theoretically possible, but probably not optimal in their functionality. We suppose that this presented geometric model does not integrate all factors or mechanisms controlling foraminiferal morphogenesis. For instance, the model does not include the morphogenetic role of apertures in shaping chambers. Real foraminal paths often tend to follow linear streaming of cytoplasm supported by cytoskeleton. This may be observed during ontogenesis of various morphotypes, which avoid strong bending as soon they reach rectilinear foraminal paths. This means that uncoiling forms are relatively common and they do not switch to the coiling mode during ontogenesis (e.g. *Ammobaculites*, *Astacolus*, *Marginulinopsis* etc.). A similar pattern is known from complex foraminifers, which show intercameral foramina situated along straight lines facilitating protoplasmic streaming between successive chambers and/or their chamberlets (Hottinger 1978, 1986, 2000, 2005; Hohenegger 1999; Tyszka & Topa 2005; Tyszka *et al*. 2005). This phenomenon should be further investigated based on empirical examples and then built into the future model. We should also conclude that separation of the 'deficient range' concept gives a chance for further corrections and development of the model because most models do not include all rules, behaviours and/or mechanisms.

In actuality, the 'forbidden range' resembles the 'deficient range' because both ranges are dysfunctional due to constraints of the model. The only (although fundamental!) difference is that the 'forbidden range' is out of the range of possible morphologies defined in the model, thus, the range which does not fulfil assumptions of the model. In our case, the preconditions of the foraminiferal model state that all chambers should be attached to the same single shell and all successive chambers ought to be connected through foramina (succession of apertures).

Discussion

There are two basic approaches to study evolution and phylogenetic relationships within Foraminiferida: (1) the classical 'morphological approach' focused on morphology and composition of foraminiferal tests and (2) the 'molecular approach' based on similarities between molecular data, such as DNA, RNA, proteins (Pawlowski 2000). Theoretical morphology links both approaches, bridging the gap between them. Genetic information indirectly defines basic parameters emerging from the integrated cascade of processes, e.g. spatio-temporal interactions between proteins. It can be supposed that many genes influence each variable, parameter or morphogenetic process (Kauffman 1993). Phenotypic characteristics are therefore generated by a network of interacting gene products (Salazar-Ciudad & Jernvall 2004). The resultant morphology is something what we observe and describe based on the morphological approach. The problem is that neither empirical nor virtual foraminifera have a quantitative method that can completely describe their morphology. Analyses of the theoretical morphospace are, therefore, still qualitative. It is also difficult to measure complex 3-dimensional morphologies. One can imagine several methods, based on image analyses and pattern recognition systems, for obtaining quantitative measures of morphologies. Such measurements could be statistically evaluated using multivariate statistics. In the end, similar morphologies would be grouped around the same morphocluster. Thus, the quantitative aspects of theoretical foraminiferal morphospace and their comparison to empirical morphospaces needs further investigation.

Additional ranges in the theoretical morphospace have been introduced, based on the comparison between theoretical and empirical morphologies. The question is whether one can learn anything about the morphogenetic processes based on separation of all the described ranges of the theoretical foraminiferal morphospace. It should be admitted that mapping of these regions of the morphospace is essential for the verification, understanding and further development of this or any other morphogenetic model. The model does not just simulate similar shapes, it simulates real processes behind, if simple geometric abstractions mimic real morphogenesis. Based on morphospace analyses, it is clear that the model does not take into account all necessary morphogenetic rules. If we leave artificial geometric rules and define a new more 'in depth' model, the overlap of the theoretical morphospace and empirical morphologies would be much larger. The recent model, and the related morphospace, does not include foraminifers with the maximal communication paths

(*Lenticulina*-like forms), multi-apertural forms, and complex foraminiferal architectures.

A general idea of such a new emergent model is presented in Figure 7 (Tyszka *et al.* 2005). A new chamber in this model is formed at the tips of fan-shaped rhizopodia. The rhizopodial fan, formed by microtubules spreads from the last aperture, has been observed in several independent studies (Hemleben 1969; Spindler & Röttger 1973; Bé *et al.* 1979; Hottinger 1986; Hemleben *et al.* 1989). In this way a new chamber cannot be detached from the shell and cannot grow without direct contact with the last aperture (the arrow in Fig. 7). The new model should focus on realistic rhizopodial dynamics, avoiding arbitrarily defined chamber shapes (for further discussions see Tyszka & Topa 2005; Tyszka *et al.* 2005). The forbidden range, detachment of chambers and/or disconnection of for-aminiferal paths, can be limited if more realistic models focused on morphogenetic processes are used. The presence of the 'forbidden range' in the morphospace therefore seems to suggest that the model is not perfect and probably does not take into account all crucial morphogenetic 'rules'. One can also expect that 'in depth' models would reveal other types of 'forbidden ranges' that would exclude certain configurations of parameters governing rhizopodial networks. Nonetheless, the concept of the 'forbidden range' still serves as an essential tool of theoretical morphology.

The point has been made that there is no necessary link between theoretical morphology and adaptation (McGhee 1999; Eble 2000). On the other hand, we cannot forget about the functionality of virtual and empirical forms. Discrimination of 'dysfunctional' or 'deficient' ranges in the morphospace is partly based on the function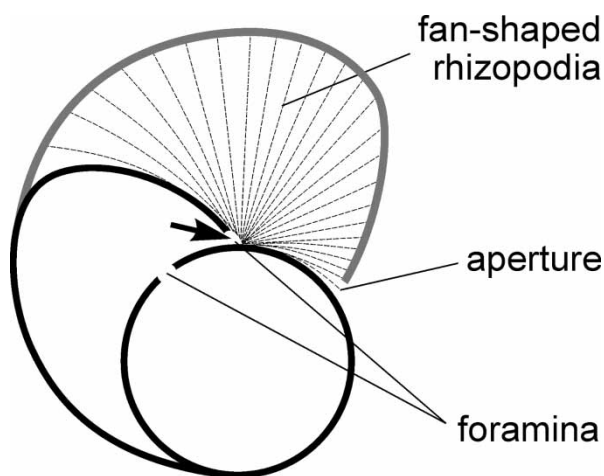al morphology of foraminiferal skeletons. If we build a theoretical model of morphogenesis, focusing on apertures as local moving references with optimised distances between them, we have to rely on functional consequences based on the economy of cell energetics (Hottinger 1978; Brasier 1982, 1995; Hohenegger 1999). This functional minimization of the distance between the last aperture and a new aperture is logical but still very theoretical. This optimising paradigm, built into the model (Topa & Tyszka 2002), was verified based on the large overlap of the resultant theoretical morphospace with the empirical morphologies. In this way we can suppose that at least certain foraminiferal groups use this mechanism, which seems to be functional, as playing a fundamental role in morphogenesis.

It is surprising that the morphologies of small polythalamous foraminifers probably overlap nearly all possible theoretical morphotypes. It may indicate that most of the theoretical morphotypes are functional as protective envelopes. An opposite interpretation assumes that a type of chamber arrangement is not essential for evolutionary success, even if we consider some morphotypes as more suitable for particular modes of life, such as planktonic or deep infaunal habitats. We can speculate that the real evolution of small foraminifera took advantage of nearly all theoretical options that would result from a relatively flat topography of the fitness landscape. It means that it is likely that evolutionary processes 'shaping' small foraminifera can choose from a huge variety of shell shapes that may have similar adaptive values. Biserial and trocho/spiral forms serve as a good example. Both morphotypes are known from very different habitats including endobenthic, epibenthic and planktonic modes of life (Loeblich & Tappan 1988; Culver 1993). It looks like both chamber arrangements are optimal enough in inhabiting very different habitats. Smout (1954, p. 15; see Scott 1974, p. 139) stated that "the final form of the test is of little biological importance" and "the diversity of morphology within this superfamily (the Rotaliidea) is itself a proof of the slight importance of the final shape of the test". "Does it mean that shell form is in fact not subjected to the machinery of natural selection?" (Kucera 1999, p. 4).

The matter of the discontinuities within the theoretical morphospace of foraminiferal tests, and all other morphospaces, is fascinating in itself. There are no doubts that *morphophases* and *morphophase transitions* are immanent in all theoretical models based on optimisation algorithms and/or models sensitive to initial conditions. Such theoretical models have already been described for quite a few groups of organisms, such as silicoflagellate rod-skeletons (McCartney & Loper 1989), centric diatoms (Parkinson *et al.* 1999); stroma-toporoids (Kershaw & Riding 1978) seaweeds, sponges, corals (Kaandorp 1994; Hammer 1998; Kaandorp &

Fig. 7. Simplified idea of the emergent model of foraminiferal morphogenesis. A new model should incorporate cytoskeleton dynamics, which is responsible for chamber formation (see Tyszka *et al.* 2005).

Kuebler 2001; Stolarski *et al*. 2004), and plants (Niklas 1982; Prusinkiewicz & Lindenmayer 1990). Theoretical morphospaces based on these models reveal or may reveal *morphophase transitions* between different morphologic patterns (*morphophases*).

Furthermore, it would be essential to set up systematics for theoretical foraminiferal shells. Such a 'virtual taxonomy' could further be compared with various taxonomic schemes classifying the Foraminiferida (Loeblich & Tappan 1988; Sen Gupta 1999; Mikhalevich 2000). This comparison should be based on the quantitative evaluation of real and theoretical morphologies. Unfortunately, such a statistical approach is something that is missing in morphospace analysis. The problem is how to quantify and analyse morphospaces statistically (Hutchinson 1999). The presented morphospace analysis is still qualitative, however, it would be worthwhile to find specific mathematical tools for further investigations of *morphophase transitions*, as well as the comparison of theoretical and empirical results. It is therefore assumed that any kind of theoretical systematics introduced in this study would be still very preliminary. We can suppose that all sharp *morphospace transitions* could separate morphologies attributed to higher rank taxonomic units. In contrast, placement of taxonomic boundaries at gradual *morphospace transitions* would always be very subjective. In the future, it is planned to simulate an artificial evolution of theoretical foraminifera based on simple and realistic rules. Potential results should give better insight into systematic, phylogenetic, and macroevolutionary studies.

Conclusions

(1) The model of foraminiferal shells used in this study focuses on the understanding of morphogenetic process. In contrast to fixed reference models, it is based on apertures as moving reference frames (Fig. 1). The resultant simulations have proved that this moving reference approach is accurate and fulfils basic model requirements. In consequence, we conclude that foraminiferal apertures are critical in the morphogenesis of foraminifera and essential for studying their taxonomic or phylogenetic relationships.

(2) Variants of the theoretical morphospace of foraminiferal shells have been presented in two manners, i.e. a 3-dimensional box model (Figs 2, 3) and a theoretical morphospace tree, simply called a *morphotree*. Constructing *morphotrees* with branches representing different dimensions (parameters) of the model seems to be a useful method for the exploration of multi-dimensional morphospaces (Fig. 4).

(3) The theoretical morphospace of foraminifera reveals regions including similar morphological forms (Fig. 3). These specific fields in the morphospace, called *morphophases*, are separated from each other by either sharp or gradual *morphophase transitions*. The sharp *morphophase transitions* reveal sensitivity of the model to slight parameter changes. *Morphophase transitions* are caused, in this case, by optimized (minimized) emplacement of foraminiferal apertures.

(4) Comparison of the theoretical morphospace and empirical foraminiferal morphologies suggests that in evolution the small polythalamous foraminifers probably have discovered nearly all morphological options simulated in the theoretical morphospace. It means that most of the simulated morphotypes are actually known from reality and the 'vacant range' of the morphophase is very limited. In spite of these conclusions, we should keep in mind that the model does not include some morphological features, such as multiple apertures, complex chamber shapes and chamber internal structures.

(5) The theoretical morphospace is split into various ranges based on comparison with empirical morphologies (Figs 5, 6). The 'forbidden range' (*sensu* Berger 1969) includes all theoretical forms which do not fulfil basic model assumptions. The 'possible range' covers all forms that are theoretically correct. This 'possible range' can be either 'occupied' by existent morphologies or 'unoccupied' by nonexistent forms. Within the 'unoccupied range', one can distinguish 'vacant range' (empty range), 'dysfunctional range' (geometrically possible, but dysfunctional morphologies), and 'deficient range' (geometrically possible, but partly dysfunctional due to unconsidered rules). Mapping these regions of the morphospace is essential for the verification, understanding and further development of this model. This conclusion is most likely valid for all other morphogenetic models as well.

(6) "Theoretical morphospace is silent about adaptation" (McGhee 1999, quoted in Eble 2000, p. 524), nonetheless, examination of functional significances at every step of the theoretical morphological approach is essential for the understanding of morphogenetic processes and further model development.

(7) Future models of foraminiferal shells should explore morphogenetic processes focused on cytoskeleton selforganization (Tyszka *et al*. 2005). Such models ought to introduce new rules

simulating emergent morphogenetic processes, however, they should never overlook apertures as critical morphogenetic factors (Fig. 7). Therefore, future models should still be based on the moving reference approach focused on single or multiple apertures.

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