Logarithmic expression of *Globigerina bulloides* shell evolution through the biometric analysis: Paleoceanographic implications for the late Quaternary

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**Abstract.** Fossil foraminifera are a treasure trove of information in applications ranging from microevolution to paleoclimatology. The architecture of their tests is of the key importance in systematic and phylogenetic studies and can reveal micro-evolutionary traits through the biometric analyses. In the present paper, we analyze the laws of growth that control planktonic foraminifera shell morphology. We report the results of a biometric study of the temporal variation in the shell shape and chamber size of the cosmopolitan, subpolar to temperate species *Globigerina bulloides* d'Orbigny from core top sediments in the eastern tropical Atlantic Ocean. Morphological variation in terms of test shape and adult chamber size in *G. bulloides*, has been measured in 116 down core sediment samples from the tropical waters (19°N) of the northern Antarctic Ocean and has resulted in a model that simulates the basic morphology (chamber size and spatial arrangement) of planktonic foraminiferal shells of that species. The investigated samples comprise a continuous record that spans the last 200 krys. The specimens for this morphometric study were picked from a restricted sieve fraction and were mounted for Scanning Electron Microscopy (SEM) analysis. The restricted size of the specimens constrained the analysis to adult specimens and minimized ontogenic effects while allowing the documentation of very small overall changes in the parameters under investigation in time. The dimensions that were measured for each test were its height, width and the diameters of the last seven chambers. This allowed the determination of chamber centers and their analogies resulting in a mathematical model based on a logarithmic spiral equation that describes the evolution of the test with the growth during their adult phases. The model presented herein belongs to a family of so-called “fixed-axis” coiling models.

1. Introduction

Marine protists play an important role in oceanic ecosystems and biogeochemical cycles. In particular, biomineral shell-bearing protists, like planktic foraminifera, are ideal study candidates to develop a combined approach of genetic, morphological, and geochemical traits, reflecting environmental and ecological characteristics [1-3]. Their shells are used as paleontological and paleoenvironmental study subjects [4-15] because they fossilize and preserve well in marine sediments. However, in the ocean, mechanisms behind morphological evolution and speciation remain particularly elusive. It is, therefore, essential to understand how the environment interacts with intrinsic constraints over the development of an organism to generate new forms.
Planktic foraminifera provide excellent material to investigate the influence of development on morphological disparity, as they grow by the sequential accretion of chambers on to their test. Consequently, each successive stage of growth remains an integral part of the growing structure [16], occasionally accompanied by additional overgrowth, thickening, or selective resorption of previously deposited calcite [17]. Biometric studies incorporating environmental information in this group have demonstrated a close relationship between morphology and environmental parameters, such as temperature, salinity, density, and productivity variations, both in the fossil and the modern record [12,18-20]. The analysis of the relationships between size and shape are of primary importance for understanding planktic foraminiferal shell architecture [19,21], while additional properties like biomass, shell mass, calcification effort, and respiration rate could also be produced [22,23]. The internal architecture of their tests, which is crucial in systematic and phylogenetic studies, can also reveal micro-evolutionary traits through biometric analyses [24]. The most detailed information on foraminiferal internal architecture is commonly obtained through observations by Scanning Electron Microscopy (SEM). Furthermore, isometric growth or the principle of geometric similitude is the only reasonable way to explain log-spiral patterns of shell coiling [25,26]. Properties that are characteristic of log-spirally coiling shells, such as a constant ratio between the diameters of consecutive chambers, have been reported for several planktonic foraminiferal species [27,28].

2. Material and methods

The present investigation is based on samples from core GeoB 8502-2 from the lower northwest African continental slope in the northeastern tropical Atlantic. Core GeoB 8502-2 was recovered from the lower continental slope and contains hemipelagic sediments. GeoB 8502-2 is 14.78 m long, 12 cm in diameter with an average sedimentation rate of 7 cm/kyr [29]. The core was sampled for the scope at a resolution of less than 2000 years (samples were taken at 10 cm interval) by extracting a slice of the material, 1 cm in thickness, which represents approximately 170 annual cycles. The sediment samples were initially wet sieved through the 63 μm mesh sieve and the dried coarse fraction was subsequently sieved in eight different fractions.

The current morphometric analysis was performed on normal form *Globigerina bulloides* specimens from 116 down-core samples that describe time slices of the last 200 kyrs. 30 specimens, picked from the 315-355 μm sieve fraction, were mounted, from their spiral side, on an SEM stab and were coated with Gold/Palladium for analysis. In total, the morphology of 3,480 specimens was examined at a 100× magnification. The shells were also investigated at a maximum magnification of 3000× to study in detail both the shell surface and whole test morphology, with a Zeiss DSM 940 A at a 10 mm working distance and 10kN accelerating voltage. The morphometrical investigation led to a number of findings concerning the model of shell formation and its chamber analogies, while the ultrastructural examination revealed the preservation state of the fossils.

2.1. Shell geometry

*Globigerina bulloides* evolves shells by adding spherical chambers and their shape is constant throughout ontogeny. For the morphometrical analysis the following dimensions were measured on the GeoB 8502-2 specimens (Figure 1):

- H: Height of *G. bulloides* test,
- W: Width of *G. bulloides* test,
- C1: Diameter of the 1st chamber (final chamber),
- C2: Diameter of the 2nd chamber,
- C3: Diameter of the 3rd chamber,
- C4: Diameter of the 4th chamber, that was prominent and with greater uncertainty
- C5: Diameter of the 5th chamber,
- C6: Diameter of the 6th chamber, and
- C7: Diameter of the 7th chamber.
Figure 1. Position of measurements a) of height (H) and width (W) and b) C1-C4 in individuals of *Globigerina bulloides*. The dashed lines in b) in front of chamber 2 and 4 are the actual chamber diameter while with solid lines the measured diameters are signified.

As shown in Figure 1 for illustration the dimension of chamber 2 and 4 are most of the times underestimated because due to technical reasons the measured diameter (solid line) was smaller than the actual one (dashed line). The degree of divergence is highly variable due to shell’s ontogenic geometry. An Equivalent Circular Diameter (ECD) of a test was calculated. This theoretical number is an estimate of the diameter of a circle that encloses area equal to the area of the rectangle with sides W and H, i.e.

\[
WH = S_A \quad \text{(Eq. 1)}
\]

\[
S_A = \pi r_{eq}^2 \quad \text{(Eq. 2)}
\]

\[
ECD = 2r_{eq} \quad \text{(Eq. 3)}
\]

The ECD provides a linear dimension to refer to the mean size of a test for comparison simplification. Since no kummerforms were considered, the ECD is a reference to a linear length to describe variation than the width alone considered by Malmgren & Kennett [30]. The Width/Height (W/H) ratio may serve as a measure of shell’s eccentricity. It describes the geometry of the general outline of the shell and when this ratio equals unity (1) the shell is globular enough and it can be subscribed within a square. The determination of this ratio in the record thus provides a measure of departure from normality of a test.

This species is thought to grow isometrically [30], a notion which is further strengthened in the present study. Isometric growth is achieved when the effective chamber shape is constant and the volumes of consecutive chambers are in geometric progression [28]. When projected on a single plane the chambers of a whorl are tangent to the coiling axis and outline four circles every two which osculate. This geometry makes this organism ideal for growth model determination. The addition of diameters C1 and C3 constitute segment C13 and of C2 and C4 segment C24 (Figure 2). Thus:

\[
C1 + C3 = C13 \quad \text{(Eq. 4)}
\]

\[
C2 + C4 = C24 \quad \text{(Eq. 5)}
\]

The determination of the center of the chambers (Figure 2b) along with their proportions relatively to the general shell geometry allowed the determination of a logarithmic spiral equation of shell evolution. Furthermore the coincidence of two opposite chamber dimension on the same line, due to
shell’s isometry, allows the determination of the ratio of each chamber dimension (i.e. \(C2\) and \(C4\)) to the whole (i.e. \(C24\)). If \(C13\) is to \(C1\) as \(C1\) is to \(C3\) then the golden ratio is met (Eq. 6):

\[
\frac{C13}{C1} = \frac{C1}{C3} \equiv \phi = 1.61804
\]  
(Eq. 6)

Figure 2. a) Segmentation of the test following its basic geometry, b) an abstract model that may encompass the mean \(G.\) bulloides shell. K1-K4 points are the theoretical centers of the chambers

The Golden ratio is a special number found by dividing a line into two parts so that the longer part divided by the smaller part is also equal to the whole length divided by the longer part. It is often symbolized using the Greek letter \(\phi\) (phi) and in the equation form is:

\[
a/b = (a+b)/a = 1.6180339887498948420…
\]  
(Eq. 7)

In patterns in nature, the golden ratio is operating as a universal constant [31, 32]. This proportion is expressed in the arrangement of parts from leaves and branches along the stems of plants, to the skeletons of animals and the branchings of their veins and nerves, the proportions of chemical compounds and the geometry of crystals, to the use of proportion in artistic endeavors and even in our genome [33].

3. Results and discussions

The results from the morphometrical analysis of \(G.\) bulloides shells under the SEM are presented below in Figure 3. Although the causes behind these size measurements are difficult to identify, since they were performed on specimens of a single size class, they are presented here for future reference. On the other hand, it is logical to assume that specimens of a specific narrow size mesh class (at present 315-355 \(\mu\)m) have always the same number of chambers. Thus, when small changes in the chamber diameter take place, these may be traced in the analysis below but big changes in the specimen’s diameter require an addition of a new chamber which would thus move the specimen to a greater mesh class. In this way, the contribution that the diameters of the chambers have in relation to the number of chambers on the overall size of the specimens can be assessed and we thus may conclude whether a distinct variation in shell size originates from an increase in the diameter of the chambers or an increase in the total number of chambers.
Figure 3. Downcore ECD, width, height and W/H ratio of *G. bulloides* shells from core GeoB 8502-2

The first three measurements are size indicators while the last one refers to shell geometry. In the first column presented is the downcore variation of the equivalent circular diameter (ECD) of the tests, in the second column is the variation of mean measured test height, in the third the mean test width and in the fourth the width/height ratio. It is interesting to note that although the size measurements were performed on 315-355 μm mesh sized sieves the above measured and calculated linear dimensions are greater than 355 μm. This must be because the diagonal of the mesh of this size class is between 445 and 502 μm and thus which species pass through the sieve or not depend on their specific shell geometry. Nevertheless, a general overall decrease in specimen’s size, during the last 200 kyr, is evident from the above Figure. All three size signals show the same trend with the ECD estimate to provide a good intermediate indicator. *G. bulloides* increases slightly in size until middle MIS 5e while after this size maximum with the onset of MIS 5d its size continuously decreases. In particular, *G. bulloides* size increases during the first half of MIS 6 with minimum recorded values at 186,524 years and a local maximum at MIE 6.4. After 152,782 years size decreases until 137,359 years and increase is recorded during Termination (II) and a bit later. A local minimum at year 113,813 precedes
the overall maximum in size of 105,768 years after which a continuous decrease is evident for the rest of the years. The increased size is evident during the LGM and a pronounced minimum at MIE 2.2. In general, the variation of shell width is more pronounced than that of height. The increase in size during MIS 4 observed in width is not evident at its height and as a consequence at the ECD estimate.

Figure 4. Mean diameter of each of the umbilical chambers of GeoB 8502-2 specimens measured during SEM analysis

The width/height ratio (W/H), shown in the last column, refers to the geometry of *G. bulloides* shell with 0.85 being the most frequent, normal, proportion of all samples. With dark grey are the samples which have proportions less than 0.85 and thus decreased eccentricity. The smallest shells produced at 186,524 years are also characterized by low eccentricity. Shell eccentricity is high during the early half of MIS 6 and gradually decreases until the late MIS 5d. After MIE 5.4 shell eccentricity has an increasing trend until MIS 4 with a pronounced maximum at year 85,743 and a subsequent minimum during 62 Ka. After 62 Ka shell eccentricity increases until the early half of MIS 2 and then values oscillate around the mean with no particular trend. The chamber diameter measurements on samples of this core are not considered accurate and are not presented here as the view did not allow exact chamber measurements. The variation in the mean diameter size of the last four more prominent chambers through time are shown in Figure 4.
The frequencies of appearance of the shell chamber of a certain length for the last six chambers are shown in Figure 5. The last chamber does exhibit bimodality with most of the chambers being 280 μm in length while the peak of the first mode of the distribution with almost the same number of appearance is 288 μm. The penultimate chamber is most frequently 255 μm; the fourth chamber from the end is 147 or 150 μm long and the fifth 124 μm. The sixth is mostly 82 μm with the peak of the first mode of the distribution at 92 μm and where possible measurements of the seventh from the end chamber (which are not shown here) found it mostly 69 μm. According to the above by putting the measured lengths on a Cartesian system (x,y) points and by solving the logarithmic spiral equation, with polar coordinates, the following equation, for *G. bulloides* was derived:

\[ r = 1.94 \times 1.61^{(1.79/\pi)\theta} \]  

(Eq. 8)

**Figure 5.** Diagrams showing the frequency of different lengths of the last six shell chambers

The measurement of the length of the last seven shell chambers allowed the calculation and the statistical manifestation of the ratio of diametrically opposed chambers. Both the sum of the diameter of the opposite chambers to the longest one of the two \((C_i+C_{i+2})/C_i\) (Figure 2) and the simple ratio of the opposed chamber \((C_i/C_{i+2})\) were calculated and their frequencies are presented in Figure 6. The ratio \((C_i+C_{i+2})/C_i\) was calculated for four pair of chambers and the values from all pairs were summed. This sum provides the identification of the most frequently found ratio value between all chambers. The same was applied for the opposed chamber ratio \((C_i/C_{i+2})\). Their frequency of appearance is presented in Figures 6a and 6b respectively. It becomes apparent that both distribution peak around 1.62 which is the golden proportion. This is clearly evident in Figure 6a, where the most frequent ratio value is indeed 1.62 although it is not at the crest of the distribution. From Figure 6b, it is apparent that the most frequent ratio \((C_i/C_{i+2})\) is 1.64. This discrepancy between the two ratio values is believed to be due to measurement uncertainties. In the first ratio \((C_i+C_{i+2})/C_i\) amongst others, the length of the larger distance is emphasized and this length is always better measured in this microscale, while the addition and subsequent division of the lengths function as averaging and normalization. Nevertheless, there is strong evidence that the golden proportion plays a major role in the architectural plan of *G. bulloides* shell construction.
4. Conclusions

Variation in the test size, shape, and individual successive chamber diameters of *Globigerina bulloides*, as studied in 116 downcore sediment samples from the eastern subtropical North Antarctic waters for the last 200 kyrs reveal the existence of the golden proportion in the construction plan of foraminifera shells. Furthermore, based on the measurements of the diameters of the successive chambers, a logarithmic equation of shell’s evolution is here proposed.

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