Marine Micropaleontology 96–97 (2012) 105–122

Contents lists available at SciVerse ScienceDirect

Marine Micropaleontology

journal homepage: www.elsevier.com/locate/marmicro

Multispiral growth in *Nummulites* Paleobiological implications

Carles Ferràndez-Cañadell *

Dept. Estratigrafia, Paleontologia i Geociències Marines, Facultat de Geologia, Universitat de Barcelona, Martí Franqués s/n 08028 Barcelona, Spain

ARTICLE INFO

Article history:
Received 28 February 2012
Received in revised form 30 August 2012
Accepted 3 September 2012

Keywords:
Larger Foraminifera
Nummulites
Assilina
Multispiral growth
Growth rate
K-strategy
Eocene

ABSTRACT

An analysis of multispiral growth in Eocene nummulitids was performed. The ontogeny of some multispiral specimens was reconstructed, quantified and modeled, and the occurrence of multispiral growth in the different *Nummulites* and *Assilina* species has been reviewed. The results showed that all larger species display multispiral growth. In *Nummulites*, multispiral growth appears independently in each group when a critical size of about 15 mm as the minimum test diameter of B-Forms is reached. In multispiral tests, up to 20 different spirals may grow simultaneously, so that several chamberlets are formed in each growth step. Multispiral growth thus produces a considerable increase in the growth rate, in terms of volume added in each growth step, of up to 500% in *N. gizehensis* and 570% in *N. millecaput*, yielding a test near seven times larger than a single-spiralled test with the same number of growth steps. The gigantic sizes of 5 to 15 cm reached by Nummulites are produced mainly by the increase in growth rate provided by multispiral growth, and only secondarily by an increase in longevity that is thought to be of less than 6 years. The current view of larger foraminifera as slow growing, long-living, extreme K-strategists is questioned and discussed.

There is no fact in Palaeontology more striking than the sudden and enormous development of the nummulitic type in the early part of the Tertiary period and its almost equally sudden diminution bordering on extinction.
Carpenter et al. (1862, p. 276)

1. Introduction

Larger foraminifera are defined by the structural complexity of their test rather than by their test size, which usually reaches several centimetres and on occasion can exceed diameters of 10 cm. Several lineages of larger foraminifera have appeared recurrently from small, simple microforaminifers throughout geological history (Hottinger, 1982, 1984; McGowran and Li, 2000). As seen in recent species, the increase in size and complexity is due to the relationship with symbiotic unicellular algae, which convert them into another sort of organism, modifying their metabolism and their ecological adaptations and evolutionary features.

Nummulites is the most representative genus of the larger foraminifera, due to its abundance in the Eocene (called the *nummulitique* period after d'Archiac, 1850) and because it shows the largest size attained by foraminifera, with a test of up to 19 cm in diameter (Pavlovec, 1987). Whereas the test of small species presents chambers arranged in a single spire, a characteristic feature of large *Nummulites* species is a multispiral type of growth.

Multispiral growth in *Nummulites* has been recorded since at least 1832, when Boubée named a new species as *N. millecaput* ("thousand-heads") because of this character (*intùs multispiratâ, spiris dicothomis*). However, multispiral growth has not received much attention in nummulitid studies, often being considered a mere growth irregularity. Most papers reviewing the taxonomic characters used in the systematics of the group have paid little attention to this feature (e.g. Puri, 1956; Golev, 1965; Arni, 1967; Blondeau et al., 1974; Schaub, 1981), or alternatively have considered it a character of secondary importance. However, multispiral growth is a widespread feature in *Nummulites* species and has important consequences for the growth rate and size of the test, which have been noted by a few authors, such as Rozlozsnik (1927) or Bartholdy (2002).

This paper reviews the presence and particular features of multispiral growth in *Nummulites* species, with observations on another nummulitid genus, *Assilina*. The results contradict current ideas on larger foraminifera paleobiology, indicating that multispiral growth is related to increased growth rates.

2. Materials and methods

This study was initially based on the drawings and pictures figured in Schaub's monograph (1981), but was later extended to consider other equatorial sections available in the literature, as well as some own material. The revision of the available published papers

* Tel.: +34 934021383; fax: +34 934021340.
E-mail address: carlesferrandez@ub.edu.

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http://dx.doi.org/10.1016/j.marmicro.2012.09.001

provided about 340 different equatorial sections of more than 50 *Nummulites* species and 10 *Assilina* (Appendix A). These figures were used to conduct an analysis of the features of multispiral growth, considering the number of spirals, their appearance in the ontogeny, their regularity and the presence of spirals growing in inverse or in both directions. In some specimens, the ontogeny could be reconstructed in detail, enabling a reconstruction of the spiral configuration throughout ontogeny, quantification of the number of compartments and growth steps and, consequently, inference of growth rates. Since this has consequences for the interpretation of multispiral growth, it is important to stress that the ontogenetic diagrams figured here are reconstructions, not interpretations.

In order to reconstruct the ontogeny, the growth step in which supplementary spirals are added must be determined. This is a difficult task because theoretically the step can only be inferred from two test features: (1) through identifying the last chamberlets of the different spires (formed simultaneously in the last growth step) and numbering all of the growth steps backwards, from the last to the initial one; and (2) through identifying the chamberlets of the same chamber from the lamellar structure, as all the chamberlets of the same chamber will share the same outer lamella (Fig. 1). However, these methods are practically impossible to apply because the last chambers are usually broken in large specimens, the lamellar construction is cryptic and the lamellae are difficult to identify and follow.

An approximation of the ontogenetic formation of the test can be obtained by taking the chamber closest to the next inner spiral as the growth step which originated the supplementary spiral (e.g. Bartholdy, 2002). Although this provides an idea of the origination of supplementary spirals throughout the ontogeny, the method is inexact and in outer whorls may produce errors of more than 100 growth steps.

To reconstruct the ontogeny, the trial and error method was used, which enabled deduction of the growth step in which a supplementary spiral is added with a much smaller error (<10 growth steps). This method is based on two assumptions: (1) when a new chamber is formed, a new *chamberlet* is added at the end of each spiral, and (2) the initial spiral records the complete ontogeny of the test. The former statement implies that in multispiral *Nummulites*, all the compartments, except for the initial ones growing in a single spiral, are chamberlets (i.e. structures which form a part of a chamber, following the definition by Hottinger, 1978, 2006a).

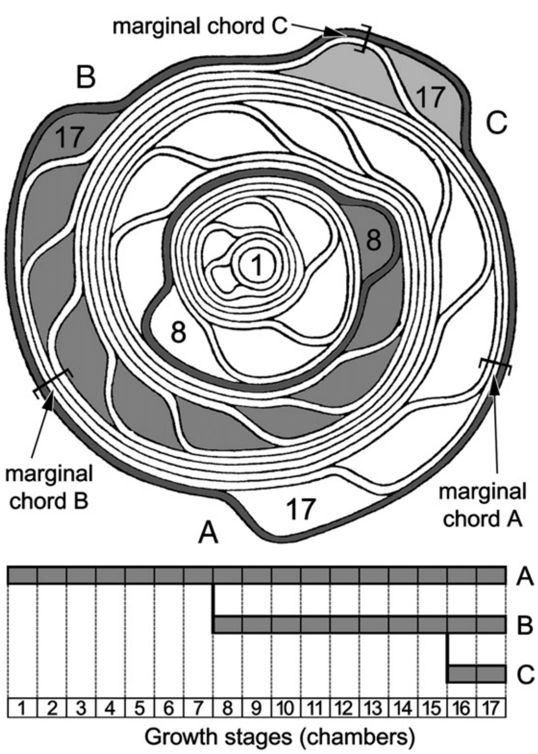

Fig. 1. Lamellar structure of a multispiral hyaline test with three spirals (A, B, C), and the ontogenetic linear diagram. Numbers indicate the growth stage. The second spiral starts at growth stage (chamber) 8th and the third spiral starts at growth stage (chamber) 16th. The 8th to 16th chambers have two chamberlets; the 9th to 17th chambers have three chamberlets. Note the splitting of the marginal chord. (Modified from Smout, 1954, Text-Fig. 37).

The second statement implies that the ontogeny of a test cannot be reconstructed if the initial spiral ends, as is the case in some specimens.

According to these statements, the reconstruction of the test was performed as follows:

(1) In a good drawing of the equatorial section, spirals were painted in different colours. This provided a much clearer picture of the multispiral pattern.
(2) The chambers and chamberlets of the initial spiral were numbered sequentially as growth steps. The number of the tiny initial chambers, not drawn, was estimated from comparison of similar test diameters from good SEM images of microspheric forms. In Schaub's drawings (1981), this initial part usually corresponded to 25–30 chambers.
(3) The chamberlets of the other spirals were numbered.
(4) The first additional spiral may have originated in any of the growth steps (chambers) of the internal whorl of the initial, internal spire. One of these possible growth steps was taken as the hypothesis for the origination of the first additional spiral (i.e. the 1st chamberlet of the spire is related to a growth step of the initial spiral). Next, the relative position of the 1st and 2nd spirals after a number of growth steps was checked. If an impossible situation was found (e.g. an external spiral that was longer than the one beneath, another hypothesis (a previous or later chamber in the 1st spiral)) was taken and checked, and the process was repeated until the possibilities were reduced to a minimum set of chambers (growth steps).
(5) The same procedure was applied to the 3rd spiral. This often led to corrections in the hypotheses of the origin of the 2nd spiral previously obtained. The process was repeated with the rest of spirals, applying the necessary corrections to previous results until a possible scenario was obtained.

Although it does not yield a completely exact reconstruction of ontogeny, this method considerably reduces the possible growth steps involved in creating the spires and provides a good approximation of the real ontogeny. Once these growth steps have been identified, a rectilinear, two-dimensional graphic image of the different spires can be drawn showing the time of origination (growth step) and the continuity of the new spires (Figs. 2–4). As the spirals are growing simultaneously, the incomplete spirals in the broken periphery are extrapolated (adding chamberlets) to equal the longest one, which provides a minimum number of growth steps.

Reconstruction of the ontogeny makes it possible to:

(1) graphically display the pattern of appearance of supplementary spirals throughout the ontogeny and the number of simultaneously growing spirals (Figs. 2, 3);
(2) deduce how many chambers are missing in the broken periphery and thus complete the ontogeny;
(3) display the reconstruction of the test in a determined growth step and thus the distribution of the different spirals in the periphery of the test (Fig. 4).

Because the initial spiral provides the reference for the growth steps, the ontogeny of specimens in which this first spiral ends cannot be reconstructed. In some specimens, especially those with a high number of spirals (up to 19), the complete ontogeny could not be reconstructed.

From the reconstructions, several parameters of the test were quantified (Section 3.2.2), such as diameter of the test when multispiral growth starts, the total number of spirals, the number of incomplete