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Research paper

Identification of life-history stages in fusulinid foraminifera

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ABSTRACT

The whorls of fusulinid foraminifera preserve a record of each individual's ontogeny, and therefore provide access to aspects of morphological life-history patterns. Outline-based morphometric analyses of representative fusulinid specimens assigned to *Robustoschwagerina*, *Sphaeroschwagerina*, *and Schwagerina* show that these genera exhibit characteristically different ontogenetic trajectories within a space defined by test size, test shape, and whorl number. In *Robustoschwagerina* and *Sphaeroschwagerina* the shape of the test altered during development, first exhibiting a spherical prolocular character, transforming to a fusiform shape, and then reverting to a secondary spherical form. In contrast, *Schwagerina* exhibits only the first two stages. Development-based morphological transitions also vary among these genera concerning the test size change. Moreover, these patterns appear to be taxon-specific, and so have potential utility for taxonomic identification as well as for understanding fusulinid life history. The distinct test inflation of the spherical pseudoschwagerines during their ontogeny raised the question whether there is a habitat shift in a certain developmental stage. Intriguingly, the patterns of their ontogenetic shape variation appear reminiscent of the morphological reversion that occurs in several small benthic genera such as *Tretomphalus* for which a late ontogenetic planktonic phase has been proposed. This similarity may have implications for the functional interpretation of spherical fusulinid tests.

1. Introduction

Foraminifera are a group of single-celled marine protists, most of which grow hard, internal, single- or multi-chambered shells (referred to as tests) throughout their life span. Fusulinid foraminifers inhabited shallow sea bottoms during the Late Paleozoic, exhibiting fusiform, spherical or lenticular tests composed of multiple involute and planispiral chambers (Fig. 1). Because of their rapid morphological change and the association between morphological forms and depositional environments, fusulinids have gained a well-deserved reputation as index fossils for Late Paleozoic biostratigraphic and palaeoecological investigations. However, only a few studies on any aspect of fusulinid palaeobiology have been published to date.

Foraminifer tests exhibit an enormous variety of sizes and shapes. In multi-chambered species (such as fusulinids) chambers are added through growth and often assumed to reflect the size and shape of the protoplasmic body. However, foraminiferal tests are internal skeletons, held entirely within the protoplasm during life. While it may be the case that, for many species, the amount of cytoplasm located outside the test is minimal such that the test performs the function of giving shape to the body (especially in benthic species), this is not always the situation (e.g., *Hastigerina*). Nevertheless, the chambers of multi-cameral foraminiferal tests can be regarded as physiognomic in the sense of reflecting aspects of the organism's phylogeny, current taxonomy, ecology, and development.

Generations of taxonomists have observed and commented on the fact that the sequence of chambers comprising an individual fusulinid test often undergoes various morphological transitions, with changes that appear to be species-specific. Indeed, ontogeny-based morphological transitions have been used as key diagnostic characters for species identification (e.g., *Bolivia*, *Heterohelix*, *Tetrataxis*, *Orbulina*). Moreover, the sequential and episodic nature of chamber formation can be used to subdivide – at least conceptually – the organism's life history into discrete stages (Brummer et al., 1986, 1987). Our interest lies in exploring how the tools of morphometric analysis can be used to test hypotheses related to developmental aspects of fusulinid palaeobiology.

Many researchers have applied morphometric analyses to living and fossilized foraminifera to investigate shell development dynamics, living strategies, and ontogeny (e.g. Brummer et al., 1986; Galeotti and Coccioni, 2001; Hemleben et al., 1985, 1989; Malmgren and Kennett, 1972; Showers, 1980; Yang and Hao, 1991). Most of these investigations have focused on geometric relationships between adult test forms and

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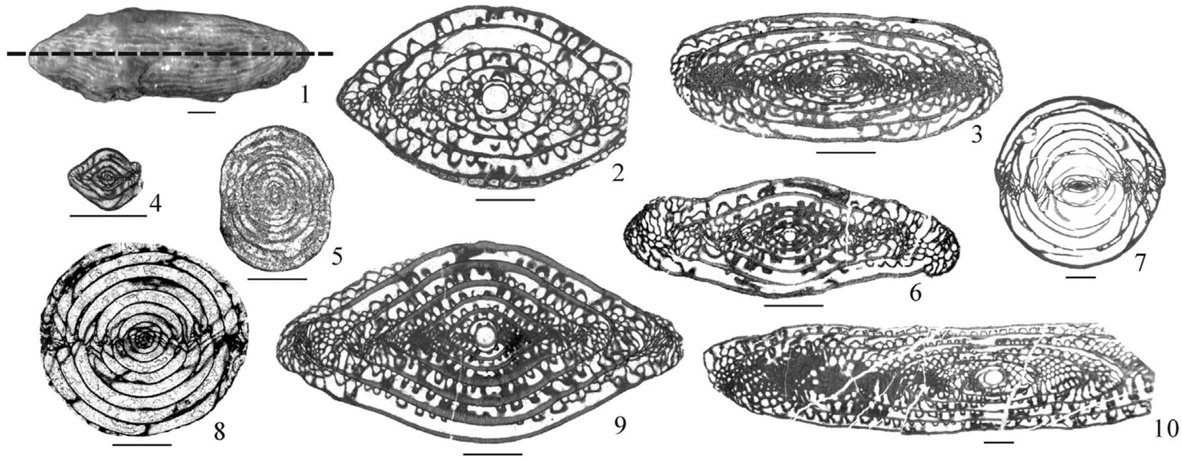

Fig. 1. The whole exterior test and axial thin sections of fusulinids exhibiting variable forms. 1. *Parafusulina* displaying the coiling axis, from Middle Permian of Huagong, Guizhou; 2. *Pseudofusulina* from Early Permian of Zongdi, Guizhou; 3. *Eoparafusulina* from the Early Permian of Zongdi; 4. *Schubertella* from the Middle Permian of Zongdi; 5. *Staffella* from the Early Permian of Zongdi; 6. *Triticites* from Early Permian of Zongdi; 7. *Sphaeroschwagerina* from the Early Permian of Zongdi; 8. *Verbeekina* from the Middle Permian of Huopu; 9. *Schwagerina* from the Early Permian of Zongdi; 10. *Monodiexodina* from the Middle Permian of Xiaoxinzhai, Yunnan. Scale = 1 mm.

either taxonomic or environmental parameters. Linear distance measurements (e.g., test diameter, test height) of particular developmental stages (e.g., prolocular diameter), have normally been used for this purpose. Such measurements are typically made using a microscope (Brummer et al., 1987; Galeotti and Coccioni, 2001; Hemleben et al., 1985; Malmgren and Kennett, 1972; Scott, 1973; Showers, 1980). Recent developments in high-resolution X-ray tomography now provide researchers with access to the forms of every foraminiferal chamber, and therefore more morphological characters among foraminiferal ontogeny were successfully captured in three dimensions and revealed more details concerning the test geometry (Briguglio and Hohenegger, 2014; Hohenegger and Briguglio, 2012; Speijer et al., 2008).

A few researchers have collected and/or analyzed information bearing directly on the geometry of test or chamber form by digitizing outlines of tests or landmark coordinate locations. To date however, specific studies of foraminiferal ontogeny, including the definition of developmental stages, have been made in a very approximate and qualitative manner, and so have led to ambiguous, difficult-to-interpret results (e.g. Pharr and Williams, 1987; Shan et al., 2006; Yang and Hao, 1991). So far as we are aware Yang and Hao (1991) constitutes the only published example of a fusulinid ontogenetic investigation that has been approached from a comprehensively geometric point-of-view. Nevertheless, the abundance of fusulinid fossil materials, along with great quantities of published images of fusulinid fossil cross-sections that expose the varying form of the test through developmental time, make fusulinids ideal subjects for ontogenetic study.

On the subject of fusulinid palaeobiology and biostratigraphy, species assigned to the subfamily Pseudoschwagerininae have always received extra attention. This is not only because of their quick diversification as an Early Permian index taxon (Shi et al., 2009; Yang et al., 2005), but also for the distinctive test-shape shift, from a fusiform to a subspherical or spherical morphology (Yang and Hao, 1991; Zhou et al., 1997). Fusulinid researchers have long suspected that this shift signals a change from a benthic to a planktonic life habit (Dunbar, 1963; Ross, 1982; Yang and Hao, 1991). While this hypothesis cannot be tested directly, it can be assessed indirectly with regard to its morphological character, and evaluated against various predictions drawn from sedimentary particle physics and the life histories of putative modern analogs.

Here, we address this issue within the pseudoschwagerine by conducting a geometric morphometric investigation to describe the morphological test ontogeny of three genera. Accordingly, the primary goals of this investigation are to: (1) explore the potential of modern morphometric approaches of morphological analysis to quantify life history transitions in foraminifera, (2) develop methods of analysis that can be applied quickly and easily to the characterization of foraminiferal life-history patterns, and (3) evaluate the potential of such results to make finer and more comprehensive biologically based distinctions between foraminiferal genera and species, including the identification of cryptic species.

2. Materials & methods

2.1. Materials

The pseudoschwagerine genera, *Robustoschwagerina* and *Sphaeroschwagerina*, both with spherical adult tests, were chosen in this preliminary investigation along with the fusiform schwagerine genus *Schwagerina* representing a morphological outgroup. The bulk of our specimens were collected from the Asselian-Sakmarian strata of Zongdi section in Guizhou Province, illustrated in part by Shi et al. (2012), and from the Yishan section in Guangxi Autonomous Region of South China. Several illustrations of published specimens, mostly types, were also included in our dataset. Specimens with more chambers and, more importantly, clear images in published articles, were selected preferentially. All specimens are listed in Table 1

Robustoschwagerina tumida and *Sphaeroschwagerina karnica* are type species of their genera. The type species of *Schwagerina* was, unfortunately, excluded from this investigation owing to the poor quality of its published photographs.

Images of axial sections through these specimens were used to quantify form variation throughout ontogeny. These were made by grinding the specimen parallel to the coiling axial until the middle of the proloculus was exposed. The resulting section allowed the sizes and shapes of the chambers comprising the whorl to be seen and photographed. While it was not possible to assess all the chambers that formed during the individual's lifespan using these sections, axial sections are the standard sections from which taxonomists assess the individual's internal morphology for the purpose of taxonomic identification, ecological inference, and phylogeny reconstruction. Digital images of each specimen from the Zongdi and Yishan localities were collected using cameras attached to a transmitted light microscope with digital resolutions of 150 dots per inch (dpi) and 72 dpi, respectively.

2.2. Morphometric methods

The whorl stage number was set by counting the number of chamber outlines exposed in each axial section with each chamber being