



New supraordinal classification of Foraminifera: Molecules meet morphology

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ABSTRACT

The limitations of a traditional morphology-based classification of Foraminifera have been demonstrated by molecular phylogenetic studies for several years now. Despite the accumulation of molecular data, no alternative higher-level taxonomic system incorporating these data has been proposed yet. Here, we present a new supraordinal classification of Foraminifera based on an updated SSU rDNA phylogeny completed with the description of major morphological trends in the evolution of this group. According to the new system, multi-chambered orders are grouped in two new classes: Tubothalamea and Globothalamea. Naked and single-chambered Foraminifera possessing agglutinated or organic-walled tests are arranged into a paraphyletic assemblage of “monothalamids”. The new system maintains some multi-chambered calcareous orders, such as Rotaliida, Miliolida, Robertinida and Spirillinida, although their definitions have been modified in some cases to include agglutinated taxa. The representatives of the planktonic order Globigerinida are tentatively included in the order Rotaliida. The agglutinated Textulariida are probably paraphyletic. The position of the order Lagenida is uncertain because reliable molecular data are only available for one species. The new classification system separates orders or families, which differ in basic chamber shapes, prevailing mode of coiling and distance between successive apertures. It appears that these features correspond better to the main evolutionary trends in Foraminifera than wall composition and structure, both used in traditional classification.

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1. Introduction

The classification of Foraminifera has a long history going back to the beginning of the 19th century and the work of d'Orbigny (1826) who established the order Foraminifera and proposed the first taxonomic system based on the growth plan of foraminiferal tests. d'Orbigny's successors have developed diverse systems based on the morphology of fossil and recent tests, differing principally by the importance given to form and chamber arrangement versus wall composition and structure (reviewed in Cifelli, 1990). The primary division of Foraminifera into single-chambered Monothalamia and multi-chambered Polythalamia (Schultze, 1854) was progressively replaced by a classification based on the presence or absence of pores (Reuss, 1861; Carpenter et al., 1862). In the 20th century, wall characteristics gained more and more importance and became the main criterion to distinguish higher-level groups in Foraminifera (Pokorny, 1963; Loeblich and Tappan, 1964; Hohenegger and Piller, 1975). In the seminal work of Loeblich and Tappan (1988, 1989, 1992), Foraminifera were divided into 12 suborders that mainly differ by mineralogical and ultrastructural features of the test wall. In the most recent modifications of this classification (Sen Gupta, 1999; Mikhalevich, 2004; Kaminski, 2005), the number of orders (or classes/

subclasses) increased to 16, but the foundations of this system remained unchanged (Table 1).

A few important attempts were carried out to group suborders into higher level taxa (Hohenegger and Baal, 2004; Hohenegger, 2011). The noticeable classification proposed by Mikhalevich (1998, 2000, 2004) and Mikhalevich and Debenay (2001) was based on a “macro-system” dividing Foraminifera into seven classes and resting upon “the whole organization of the test” rather than composition and ultrastructure of the test wall. This system revealed some interesting tendencies in the evolution of Foraminifera mainly based on morphological test patterns. Many taxonomic studies of Foraminifera concerned revisions of lower-level taxa (e.g., Hottinger, 1980; Gudmundson, 1994; Revets, 1996) but only a few tried to build up a more general system, such as the classification of agglutinated foraminiferans, whose updated versions are published on a regular basis (Kaminski, 2004).

The lack of progress in higher-level classifications of Foraminifera was mainly due to difficulties in inferring evolutionary relationships between major groups defined exclusively by morphological features and the sheer number of taxa involved. Despite the excellent fossil record, phylogenetic schemes of foraminiferal evolution are limited to textural and morphologic characters of tests (e.g., Cushman, 1948; Grigelis, 1978; Tappan and Loeblich, 1988; Vachard et al., 2010). This situation has changed with the advent of molecular studies that shed new light on the evolution of Foraminifera (Pawłowski, 2000; Bowser et al., 2006). The majority of molecular phylogenies were

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Table 1
Recent morphology-based high-rank classifications of Foraminifera.

Loeblich and Tappan (1988)	Sen Gupta (1999)	Mikhalevich (2004)	Kaminski (2005)
<i>Order</i>	<i>Class</i>	<i>Phylum</i>	<i>Class</i>
Foraminifera	Foraminifera	Foraminifera	Foraminifera
<i>Suborders</i>	<i>Orders</i>	<i>Classes</i>	<i>Orders</i>
Allogromiina	Allogromiida	Astrorhizata	Allogromiida
Textulariina	Astrorhizida	Lagynana	Astrorhizida
Fusulinina	Lituolida	Astrorhizana	Lituolida
Involutinina	Trochamminida	Spirillinata	Loftusiida
Spirillinina	Textulariida	Ammodiscana	Textulariida
Carterinina	Fusulinida	Spirillinana	Fusulinida
Miliolina	Miliolida	Miliolata	Miliolida
Silicoloculinina	Carterinida	Miliamminana	Silicoloculinida
Lagenina	Spirillinida	Miliolana	Involutinida
Robertinina	Lagenida	Nodosariata	Robertinida
Globigerinina	Rotaliida	Hormosinana	Favusellida
Rotaliina	Buliminida	Nodosariana	Spirillinida
	Globigerinida	Rotaliata	Lagenida
	Involutinida	Textulariana	Buliminida
	Robertinida	Rotaliana	Rotaliida
	Silicoloculinida	Globigerinana	Globigerinida

based on analyses of partial SSU and LSU rDNA sequences (Holzmann and Pawlowski, 2000; Pawlowski, 2000, 2002a,b, 2003). Because of their unusual length (>3000 nucleotides) complete SSU sequences were only obtained for a few species, mainly representatives of the order Rotaliida (Pawlowski et al., 1996; Schweizer et al., 2008). Molecular phylogenies were also inferred from actin (Flakowski et al., 2005), tubulin (Habura et al., 2006) and RNA polymerase (Longet and Pawlowski, 2007), but the number of species analyzed in these studies was very small. Recent analysis of combined sequence data confirmed major trends in the evolution of Foraminifera inferred from single gene phylogenies (Groussin et al., 2011). However, up to now no formal attempt has been made to modify the higher-level classification of Foraminifera by including molecular data.

Here, we propose a new higher-level system of Foraminifera, based on molecular data. We present an updated version of a SSU rDNA phylogeny based on complete sequences obtained from representatives of almost all foraminiferal orders, including 23 new sequences. We discuss this phylogeny with reference to other multigene studies and we describe the basic morphological features for new molecular groupings.

2. Material and methods

2.1. DNA extraction, amplification, cloning and sequencing

DNA was extracted using guanidine lysis buffer (Pawlowski, 2000), and each extraction was performed with a single specimen. The DNA collection numbers, collection sites and taxonomic references for all analyzed species are given in Table 2. PCR amplifications of the complete SSU rDNA were performed using several primer pairs (Table 3). The amplified PCR products were purified using High Pure PCR Purification Kit (Roche Diagnostics), cloned with the TOPO TA Cloning Kit (Invitrogen) following the manufacturer's instructions and transformed into competent *Escherichia coli*. Sequencing reactions were performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and analyzed on a 3130XL Genetic Analyser (Applied Biosystems). The new sequences reported in this paper were deposited in the EMBL/GenBank data base and their accession numbers are listed in Table 2.

2.2. Phylogenetic analyses

The obtained sequences were aligned to an existing database using Seaview vs 4.3.3. (Gouy et al., 2010). After elimination of highly

variable regions, 1904 sites were left for analysis. Based on MEGA5 (Tamura et al., 2011), a GTR + G model of evolutionary changes was selected. A phylogenetic tree was constructed using maximum likelihood (ML) method using RAxML as implemented in BlackBox (Stamatakis et al., 2008). Bayesian inference (BI) was performed with MrBayes 3.2.1 (Huelsenbeck and Ronquist, 2001). The analysis consisted of four simultaneous chains that were run for 10,000,000 generations, and 10,000 trees were sampled, 2000 of which were discarded as burn-in. Posterior probabilities at all nodes were estimated for the remaining trees.

The results of phylogenetic analyses were compared to morphological trends revealed from fundamental shell features characterized all analyzed taxa, including unilocularity vs. bi- and multilocularity, basic shape of chambers, and composition of the wall (organic, agglutinated and calcareous). These features were indicated in a phylogenetic tree and discussed based on recent knowledge on morphogenetic patterns responsible for the foraminiferal shell formation.

3. Results and discussion

3.1. Molecular phylogeny

The ML and BI analyses of complete SSU rDNA sequences show congruent results (Fig. 1). The foraminiferal tree comprises two large clades of multi-chambered species. The first multi-chambered clade, called here the Globothalamea, is composed of species belonging to the orders Rotaliida, Robertinida and Textulariida. Rotaliida form a relatively well-supported clade (81% BV, 0.96 PP) that also includes the sequences of planktonic Globigerinida. *Robertina arctica*, the only representative of the order Robertinida branches at the base of Rotaliida, together with *Leptohalysis scotti*. Another textulariid, *Reophax* sp. branches independently as sister to all Globothalamea, in both ML and BI analyses. The Globothalamea group together in all analyses, but their clade is not well supported. This is partly due to the genetic similarity between globothalamids and the monothalamous clades A + C that branch as sister group to them. The support for Globothalamea is much stronger when the highly divergent sequences are removed and a larger number of sites are analyzed.

The second multi-chambered clade, called here the Tubothalamea, is composed of Miliolida, Spirillinida and Ammodiscidae, the latter two groups being represented by the genera *Spirillina* and *Ammodiscus*, respectively. *Spirillina* and *Ammodiscus* form a strongly supported (100%) clade branching as sister to Miliolida. The relations within Miliolida are well supported, except for the position of *Cornuspira*, that branches as sister to other species, but without a strong support in both ML and BI analyses. The agglutinated genus *Miliammina* was shown to be related to miliolids in previous studies (Fahrni et al., 1997; Habura et al., 2006) but has not been included in our analyses, as the authenticity of its SSU rDNA sequence could not be ascertained. Nevertheless, actin and tubulin molecular records (Fahrni et al., 1997; Habura et al., 2006), as well as a clearly tubular shape of chambers still support its close affinity to miliolids and the Tubothalamea.

All multi-chambered species could be placed in one of the two clades, except for the sequence of *Glandulina antarctica*, the only representative of the order Lagenida reliably documented so far. DNA amplification of lagenid specimens has very low success rates, even when attempting a fragment of the SSU rDNA that in general yields positive results for all other tested groups of Foraminifera. The lack of broader taxon sampling in Lagenida makes the accurate establishment of its phylogenetic position difficult. Yet, the sequence of *G. antarctica* is so different from other multi-chambered taxa that Lagenida possibly form a separate group that evolved independently from an unknown monothalamous lineage. This is also supported by a different morphology of lagenid chambers and the structure of their tests (see below).

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