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Actin phylogeny of foraminifera and intron evolution

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Molecular phylogenies of foraminifera are commonly inferred from the ribosomal rRNA genes, which can easily be obtained from single cell isolates. The ribosomal phylogenies, however, are often biased by heterogeneity of substitution rates, and their resolution of higher level relationships is often very low. The sequences of protein-coding genes provide an important alternative source of phylogenetic information, yet their availability from foraminifera has been limited until now. Here, we present the first extensive protein sequence data for foraminifera, which comprises 90 actin sequences for 27 species representing five major foraminiferan groups. Our analysis allows to group foraminiferan actins into two main paralogs, ACT1 (actin type 1) and ACT2 (actin type 2), and several actin-deviating proteins. Phylogenetic analyses of ACT1 and ACT2 confirm the general structure of foraminiferan phylogenies inferred from SSU rDNA sequences. In particular, actin phylogenies support:

1) the paraphyly of monothalamous foraminifera,
2) the independent divergence of miliolids and their close relationship to *Miliammina*,
3) the monophyly of rotalids, and finally
4) the rotalid ancestry of globigerinids.

Some foraminiferan taxa can be distinguished in actin sequences by the presence or absence of specific spliceosomal introns. We identified 24 introns dispersed along the sequence of two foraminiferan actin paralogs. Comparison of intron positions indicates that 20 out of 24 introns are specific to foraminifera. Four introns shared between foraminifera and other eukaryotes were interpreted as parallel gains because they have been found only in single species belonging to phylogenetically distinctive lineages. Moreover, additional recent intron gain due to the transfer between the actin paralogs was observed in two cultured species. Based on a relaxed molecular clock timescale, we conclude that intron gains in actin took place throughout the evolution of foraminifera, with the oldest introns inserted between 550 and 500 million years ago and the youngest ones acquired less than 100 million years ago.