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FORAMS 2006

Systematics and Evolution of Protists: Fossils, Morphology and Molecules

A Cushman Symposium in Memory
of Alfred Loeblich and Hellen Tappan

Chaired by Jere Lipps and Susan T. Goldstein

This symposium brings together experts to discuss the latest in systematic and evolutionary research on various protists, especially foraminifera. Morphology, molecular phylogenetics, stratigraphic analyses of evolutionary trends, cladistic analyses, biogeographic patterns of evolution, life history evolution, and mechanisms of major evolutionary changes (radiations, mass extinctions) as well as other suitable subjects will be considered in a day-long symposium.



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Helen Tappan and Alfred R. Loeblich, Jr. Micropaleontologists

Jere H. Lipps

*Museum of Paleontology, University of California, Berkeley, CA 94720, U.S.A.
jlipps@berkeley.edu*

Helen Tappan (1917-2004) and Alfred R. Loeblich, Jr., (1914-1994) are surely among the greatest micropaleontologists of all time. Their names will stand along with those of the founders of modern micropaleontology: Christian G. Ehrenberg (1795-1876, Germany), Alcide d'Orbigny (1802-1857; France), Henry B. Brady (1835-1891, England), and Joseph A. Cushman (1881-1949, United States). These were great men whose work Loeblich and Tappan admired and built upon. While the others were explorers in the systematics and biostratigraphy of microfossils, foraminifera in particular, Al and Helen were synthesizers as well as systematists par excellence. For this reason, we honor them by dedicating Forams2006 to Al Loeblich's and Helen Tappan's memory.

Although we will never know how successful they might have been separately (but I am sure it would have been substantial), their relationship, cemented by marriage in 1939, was a synergistic one in which the final outcome was certainly greater than their sum separately could ever be. You could see the energy that radiated between them as they worked side by side on their dining room table, Al commonly looking down the microscope and Helen writing notes and text. In the field, they were overwhelming with Al collecting very large sacks full of samples and Helen writing notes and plotting localities. Those were lessons well learned by their students too, for Al impressed us with the need to get enough material so we wouldn't ever have to go back and Helen with the need to document it all very carefully. Of course, none of us could do both things as well as the two of them could do it, so often they would do it all for us too. Helen because of her professorial position at the University of California, Los Angeles, could have students while Al working for Chevron Research Corporation could not. Nevertheless, each student had Al as a major professor too, for their synergism could not be curtailed by mere job boundaries. Helen's students were Al's students. Both thought that their students were

their major contribution and we all benefited from long discussions with them at their home, in the field, in their labs, and especially in seminars where the latest words in micropaleontology were discussed. In later years, Helen and Al did occasionally publish projects separately. Helen's monumental book, *The Paleobiology of Plant Protists*, was backed and encouraged by Al who also helped her with all aspects of it. He was as proud of her work as he was of his own.

In the six decades that they worked, they described many species of microfossils and used them in biostratigraphy. But their chief contributions were books that compiled and interpreted enormous amounts of literature and data. All micropaleontologists know of their 1964 Treatise on Invertebrate Paleontology two volume set that described and reclassified all foraminiferal genera. The Treatise was a very original contribution and in short order it became the discipline-wide reference. It is still one of the most cited works in micropaleontology today. They worked for years in libraries and museums in the United States and Europe. As the original multi-authored book developed, Al and Helen told Ray Moore, the editor of the Treatise, that they would do the entire job themselves. Ray understood the synergism and agreed. The Treatise is a complete record of all foraminiferal genera published to the time the books went to press. No single person could have done this job. Helen worked mainly in the library and on manuscripts while Al mainly examined specimens and illustrations, but together they did the analyses and drew the conclusions. Nearly 25 years later, they returned to a compilation of foraminifera in their *Foraminiferal genera and classification*, published also in two volumes, one on the description and classification of foraminiferal genera and the other devoted to illustrations of each genus. In the Treatise, they assessed each genus and placed some as synonyms, but in the later volumes they accepted each newly and validly described genus based on morphologic differences alone regardless of population variations. They did not want to suppress genera that might in fact be determined to be valid in later studies. Al and Helen knew their works were stepping stones to better understanding of microfossils, not the final word. Al often said, if you don't agree, write it up so everyone knows what you think. They both respected studies well done, but had little use for sloppy or quick work.

Everyone noticed the differences between Al and Helen. Al was loud and critical while Helen was quiet and kind. Both would listen, but Al was their conduit to controversy. Helen never shrugged off controversy and criticism, but her way of dealing with it was to quietly reexamine issues and find a solution, after discussion with Al. Again the synergism of two different styles served them well.

Micropaleontology has been lucky to have had the Loeblich's in its service. There has never been a partnership in the field or in paleontology generally that provided so much basic information and interpretation, or such impetus for further work. All micropaleontologists use their work, and it seems doubtful that the monumental studies they published in book form will ever be repeated.

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Figure 1 Helen Tappan Loeblich and Alfred R. Loeblich, Jr.



Figure 2 Alfred R. Loeblich, Jr.,
in the field in Europe.



Figure 3 Helen Tappan Loeblich resting in the field
between sampling sites in Europe.



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Rethinking the test: Functional and evolutionary implications

S.S. Bowser¹; A. Habura¹; J.M. Bernhard² & J. Pawlowski³

¹Wadsworth Center, NY State Department of Health, Albany, NY 12201, U.S.A.
bowser@wadsworth.org

²Woods Hole Oceanographic Institution, Woods Hole, MA 02543 U.S.A.

³University of Geneva, 1211 Genève 4, CH, Switzerland

Foraminiferal tests are often regarded as simple protective coverings. Other test functions have been proposed, e.g., serving as ballast to resist hydrodynamic forces, or to help “guide” the development of pseudopodia. The function of test ornamentations is less obvious. Certain features, such as apertural teeth, may help disaggregate food particles as they pass along their surfaces, but the function of other ornamentation remains elusive.

Our recent work with “primitive” unilocular foraminiferans, involving 3D microscopy and nanofabricated substrates, has revealed a potentially unifying concept regarding test function and evolution. The ability of reticulopodia to extend over great distances (due, in part, to the evolution of their unique tubulin storage polymorph) enables forams to employ elevated substrates to capture suspended particles with enhanced efficiency. We view this basic pseudopodial function as a powerful driving force for the evolution of the test and many of its features, starting with those associated with “simple” agglutinated forams (e.g., *Hemisphaerammina*) and progressing toward the most complex topologies, e.g., as seen in *Homotrema*.

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Genomic view on origin of foraminifera and their relationships with other amoeboid protists

Fabien Burki & Jan Pawlowski

*Department of Zoology and Animal Biology, University of Geneva, Switzerland
Fabien.Burki@zoo.unige.ch*

Until recently the molecular phylogeny of eukaryotes was mainly based on analyses of single or very few genes. The availability of genomic sequences from a broad range of eukaryotic phyla brought new perspectives and provided a more reliable view of the evolutionary relationships among eukaryotes. In particular, the phylogenomic analyses helped to resolve the eukaryote tree into a topology with a rather small number of major groups. Nevertheless, the evolutionary relationships of many groups of protists, including foraminifera, are yet to be confirmed.

Based on rRNA sequences, foraminifera were at first thought to be an early diverging lineage among eukaryotes. This view has been challenged by analyses of actin, polyubiquitin and RNA polymerase sequences, which consistently demonstrated phylogenetic affinities of foraminifera to Cercozoa, a heterogeneous assemblage of filose testate amoebae, cercozoans, amoeboflagellates, chlorarachniophytes, gromiids, as well as certain protistan parasites Plasmodiophoriida (plants) and Haplosporidia (invertebrates). Among these groups, foraminifera appear to be most closely related to Gromiida, Plasmodiophoriida and Haplosporidia. Later studies showed that foraminifera and Cercozoa are sister group to radiolarians (Polycystinea & Acantharea) and a new supergroup Rhizaria comprising radiolaria, foraminifera, and Cercozoa was established.

Although Rhizaria has been well accepted as being one of the major groups of eukaryotes, their representatives are missing in all the multigene phylogenies published yet. To fill this gap we sequenced around 1900 Expressed Sequence Tags (ESTs) from the freshwater naked foraminiferan *Reticulomyxa filosa*. Using our foraminiferan EST dataset as well as the other ESTs available for a chlorarachniophyte, *Bigelowiella natans*, we constructed a 96 gene eukaryote phylogeny which includes for the first time the supergroup Rhizaria. The overall topology of our trees is in agreement with previously published studies, showing the split between opisthokonts (animals + fungi) and bikonts

(Plantae, Stramenopiles, Alveolates, Excavates), and with Amoebozoa branching close to the root of eukaryotes. Our results confirm the monophyly of Rhizaria (Foraminifera + Cercozoa) with very high statistical support in all analyses. Furthermore, Rhizaria branch consistently as sister group of the Stramenopiles, which includes, among others, the diatoms, the brown algae and the actinophryid heliozoans.



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The coiling direction paradox in *Neogloboquadrina pachyderma*

Kate Darling¹; Michal Kucera² & Chris Wade³

¹*Grant Institute of Earth Science/Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, U.K. Kate.Darling@ed.ac.uk*

²*Institut für Geowissenschaften, Eberhard-Karls Universität Tübingen, Tübingen, Germany*

³*Institute of Genetics, University of Nottingham, Nottingham, U.K.*

Planktonic foraminifera with trochospirally arranged chambers can produce shells with two different coiling directions. Some morphospecies show a strong preference for either right-handed (dextral) or left-handed (sinistral) coiling, while other morphospecies appear in mixed coiling proportions varying around a midpoint value. Some display a pattern of distinct shifts in their coiling ratios spatially and through time. Although the underlying mechanisms controlling coiling direction are not understood, many workers have assumed it to be a morphological feature reflecting ecophenotypic variation and have used coiling ratios extensively for paleoenvironmental reconstruction. Recent genetic studies now clearly demonstrate that coiling direction in planktonic foraminifera is a genetic trait, heritable through time and not environmentally controlled. Previously reported links between coiling and environmental factors result from the different ecological preferences of the genetically distinct coiling types.

Neogloboquadrina pachyderma is the most important provider of paleoproxies on the state and variation of high latitude oceans in the Quaternary. It has two distinct coiling forms with virtually exclusive distributions that appear to be controlled by water temperature. The genetic evidence shows that the two opposite coiling morphotypes diverged many millions of years ago and they have distinctly different ecologies. In combination with fossil evidence, biogeography and ecology, the degree of genetic distinction between the two coiling types of *N. pachyderma* strongly implies that they should be considered different species. The genetic evidence also demonstrates a low level (< 3%) aberrant coiling associated with each morphotype posing a serious nomenclature problem for taxonomists and paleoceanographers alike. The presence of aberrant coiling and the continual need for paleoceanographers to refer to coiling direction in the literature demands the re-classification of the right coiling *N. pachyderma* genotypes as a distinct species to simplify nomenclature and reference. We propose the adoption of the widely recognized name *incompta* for the dextral morphospecies.



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Molecular and morphological studies of *Streptochilus* from the Arabian Sea

Kate Darling¹; Ellen Thomas² & Chris Wade³

¹Grant Institute of Earth Science/Institute of Evolutionary Biology,
University of Edinburgh, Edinburgh, U.K. Kate.Darling@ed.ac.uk

²Department of Geology & Geophysics, Yale University, New Haven, U.S.A.

³Institute of Genetics, University of Nottingham, Nottingham, U.K.

Specimens of the biserial planktonic foraminiferal genus *Streptochilus* were collected 540 nautical miles offshore in the central Arabian Sea during the summer monsoon of 2003. Samples were collected from 5m water depth in waters with an average depth of 3,500 metres. All living specimens had bright orange coloured cytoplasm and sizes ranged from juvenile to fully mature. Ancestral relationships were determined by comparing their small subunit ribosomal DNA sequences with related and morphologically similar taxa. Living benthic foraminifers are commonly found suspended in the plankton in high energy turbulent waters, particularly over shallow shelf regions. Expatriation into the open ocean may also occur providing turbulence is sufficient to keep them in suspension. Using molecular, morphological and ecological evidence, we explore whether *Streptochilus* is solely planktonic in habit, whether it exploits both planktonic and benthic habitats during its life cycle or whether it is an expatriated benthic form from the shelf regions of the Arabian Sea.



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Actin phylogeny of foraminifera and intron evolution

J. Flakowski; J. Fahrni; I. Bolivar & J. Pawlowski

*Department of Zoology and Animal Biology, University of Geneva, Switzerland
Jan.Pawlowski@zoo.unige.ch*

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.



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Allogromiid test construction

Susan T. Goldstein¹; Samuel S. Bowser²;
Andrea Habura² & Elizabeth A. Richardson³

¹*Department of Geology, University of Georgia, Athens, GA 30602, USA
sgoldst@gly.uga.edu;*

²*Wadsworth Center, New York State Department of Health, Albany, NY 12201, USA*

³*Department of Plant Biology, University of Georgia, Athens, GA 30602, USA*

Allogromiid Foraminifera include a diverse array of predominantly monothalamous taxa that occur from freshwater settings to the deep sea. Their simple morphological appearance belies their underlying diversity reflected in test construction, molecular genetics, and modes of life. Recent molecular studies (Pawlowski *et al.*, 2002. *JFR*, 32(4):334-343) have shown that the traditional morphological approach to current allogromiid classification is not valid and that allogromiid classification is in need of major revision. In addition, allogromiid molecular phylotypes far outnumber described species (Habura *et al.*, 2004. *J. Eukaryotic Microbiol.*, 51(2):173-179), illustrating just how little we know about the allogromiids.

The application of a variety of fine structural methods delineates a series of fundamental allogromiid test constructions (*e.g.*, Goldstein & Richardson, 2002. *JFR*, 32(4):375-383): herringbone structure in an organic test (*e.g.*, *Allogromia laticollaris*), a herringbone organic inner test or “theca” with an organic (*e.g.*, *Iridia lucida*) or agglutinated outer covering (*e.g.*, *Astrammia* spp.), a granulofibrillar inner theca with an agglutinated outer covering (*e.g.*, *Notodendrodes* spp.), a flexible agglutinated construction with a featureless to fibrous inner organic lining (*e.g.*, *Cribrorhammina alba*, *Ovammia opaca*), an agglutinated covering without a bioadhesive (*e.g.*, *Crithionina*), and a “hyperamminid” construction with an agglutinated layer and inner organic lining comprised of crescent-shaped fibers. Ideally, we would like to compare the fine structure of test construction with membership in the various molecular clades. However, the current dataset is far too incomplete: we do not yet have both sequences and a fine-structural characterization for a sufficient number of species. Nonetheless, our growing information on test construction tends to support the validity of certain molecular clades. Allogromiid Clade E, for example, includes the sand-ingesting allogromiids (*Psammophaga* spp.) and new representatives from coastal Georgia. These representatives share a common test construction characterized by an agglutinated layer rich in clay platelets underlain by a finely fibrous inner organic lining that is in direct contact

with the plasma membrane. At least a portion of the Clade I allogromiids (*Astrammia rara*, *A. triangularis*, *Pelosina* sp.) also share a common test construction characterized by a herringbone organic inner theca with an agglutinated outer covering. Clade J likewise includes a suite of morphologically well-constrained species, although the characteristic *Crithionina*-like gross morphology may occur in some Clade M representatives. Clade L allogromiids (*Ovammia opaca*, *Cribrothalammina alba*) have a narrowly defined constructional theme: the agglutinated layer, rich in fine quartz grains and diatom fragments, is underlain by a prominent inner organic lining, portions of which may extend into the cytoplasm forming partial partitions, and secondary pores form in the test during gametogenesis. Some clades, however, are represented by a remarkable range of morphologies (e.g., Clade C), and we need to know more about the morphological constructions involved. Clearly more work is needed before a new allogromiid classification can be established. Such a new classification will need to integrate structure over multiple scales. Supported in part by NSF grant DEB0445181.



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Molecular evolution of the foraminiferal SSU rDNA: Prospects and pitfalls

Guido W. Grimm¹; Dennis Sprenger¹; Christoph Hemleben¹ & Vera Hemleben²

¹*Institute of Geosciences, University of Tübingen, Sigwartstrasse 10, 72076 Tübingen, Germany* guido.grimm@uni-tuebingen.de

²*Department of General Genetics, Centre of Plant Molecular Biology (ZMBP), University of Tübingen, Auf der Morgenstelle 28, 72076 Tübingen, Germany*

Ribosomal DNA (rDNA) sequences have been extensively used for benthic and pelagic foraminifera as a molecular marker to infer phylogenetic hypotheses. However, molecular phylogenetic studies on a broad taxonomic set of foraminifera are characterized by a generally low resolution caused by the low sequence divergence within the conserved sequence regions that can be unambiguously aligned. Only a few moderately to well-supported lineages (e.g. miliolids, “polythalamous clade”, spinose planktonic taxa) have been identified; the phylogenetic backbone remains completely unresolved. Furthermore, the phylograms’ topologies and the inference of an “all foraminiferal root” appear to be heavily influenced by taxon sampling and outgroup taxa that are used. Using phylogenetic networks, we can visualize the extent and systematic bias induced by incompatible phylogenetic splits that are predominant within the generally alignable portions of SSU (small subunit) rDNA data and thus hindered phylogenetic tree building up to now. We can demonstrate that SSU sequence data of foraminifers cannot be used *ad hoc* to infer an “all-foraminiferal” phylogenetic hypothesis. However, the particular data structure of the foraminiferal SSU showing an alteration between highly conserved and highly divergent sequence portions provides a possibility to evaluate phylogenetic alternatives indicated by network analysis. Identification of evolutionary hotspots for different taxonomic levels can reveal deep insights in the pathways of molecular evolution of the foraminiferal SSU. Sequence motives, e.g. in the DNA region coding for the terminal loop of helix 44, and alignability of variable regions are diagnostic for many taxonomic groups. Thus, an adequate pre-analyses filtering and organisation of the SSU rDNA data and taxa analysed can help to produce a data set assessable for phylogenetic studies, which focuses on particular relationships and evolutionary hypotheses.



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Accelerated rates of foraminiferal origination and extinction during the Late Paleozoic Ice Age

John R. Groves

*Department of Earth Science, University of Northern Iowa, Cedar Falls,
IA 50614-0335, U.S.A john.groves@uni.edu*

The Late Paleozoic Ice Age (LPIA) was an interval from Late Mississippian through Early Permian time (~50 million years in duration) during which continental glaciers were widespread throughout the Southern Hemisphere. Marine invertebrates experienced unusually low rates of origination and extinction during this period. An explanation for this phenomenon is that cooler and more seasonal climates of the LPIA would have led to an increase in the stability of marine communities, as well as increases in the environmental tolerances, geographic ranges, and population sizes of marine species. Species with these attributes are resistant to extinction and also less likely to speciate via ecological divergence or geographic isolation; thus, the suppressed rates of evolution. Detailed work (by others) on brachiopods showed that the biotic effects of the LPIA were most pronounced at low latitudes, and that these invertebrates did, in fact, exhibit broader latitudinal ranges and longer stratigraphic ranges during the LPIA than during earlier and later non-glacial times.

In contrast to marine invertebrates, foraminifers experienced increased rates of origination and extinction during the LPIA. Analysis of foraminiferal occurrence records shows that their rates of origination and extinction accelerated in latest Mississippian time, fluctuated at relatively high levels throughout most of Pennsylvanian time before another episode of rapid acceleration at the Pennsylvanian-Permian boundary, and then gradually declined during the remainder of Early Permian time. These results suggest that not all marine organisms responded similarly to environmental changes during the LPIA and (or) that factors other than climate may have influenced foraminiferal evolution. Examples of non-climatic factors include:

- 1) global tectonic events that are known to have caused changes in marine circulation patterns and provinciality;
- 2) repeated glacio-eustatic sea-level changes that caused instability and shifting of neritic habitats.

It is also possible that high rates of foraminiferal evolution during the LPIA may have been triggered by a chance evolutionary innovation, such as the acquisition of fusiform morphology, followed by rapid diversification within the order Fusulinida. A prominent feature of the foraminiferal data is the close correlation between rates of origination and rates of extinction throughout the LPIA.



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Molecular evolution of foraminiferal tubulins

Andrea Habura^{1,2}; Laura W. Parfrey³; Sarah Broderick¹ & Samuel S. Bowser^{1,2}

¹*Division of Molecular Medicine, Wadsworth Center, New York State
Department of Health, Albany, NY 12201, U.S.A.*

habura@wadsworth.org; bowser@wadsworth.org

²*Departments of ²Biomedical Sciences and ³Biology, University at Albany,
1400 Washington Avenue, Albany, New York 12222, U.S.A.*

Foraminiferans are known to be highly divergent in several normally conserved genes. Although the best-understood example of this phenomenon is the ribosomal small subunit (Pawlowski, 2000; Habura *et al.*, 2004), other genes also show evidence of strong modifications. These modifications are generally conserved within the Foraminifera but are found in no other organism, which presents several opportunities for foraminiferal molecular research. From a phylogenetic standpoint, these genes are useful for estimating relationships between different groups of foraminiferans. In addition, the identification of close relatives of the Foraminifera (particularly *Gromia*, but also other members of the Rhizaria; Adl *et al.*, 2005) should permit identification of some of the particular evolutionary changes that resulted in the emergence of morphologically-distinctive foraminiferans by the early Cambrian. Study of the physical implications of changes in conserved genes will also result in enhanced understanding of foraminiferal cell biology.

Foraminiferal beta-tubulins are a case in point. These genes are highly useful for phylogeny, and can be used to test ideas about foraminiferal relationships that are hard to resolve using SSU rDNA data (Habura *et al.*, 2006). In addition, foraminiferal beta-tubulins are highly modified compared to those from other organisms, in ways which have implications for foraminiferal microtubule assembly (Habura *et al.*, 2005). Because these genes are so unusual, specific primers can be used to identify foraminiferal tubulins in environmental DNA samples. This approach allows rapid testing of hypotheses about environmental influences on tubulin assembly, such as low temperatures.

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Micro*scope and the Star*sand database

Andrea Habura^{1,3}; David L. Patterson² & Samuel S. Bowser^{1,3}

*¹Division of Molecular Medicine, Wadsworth Center, New York State
Department of Health, Albany, NY 12201, U.S.A.*

habura@wadsworth.org; bowser@wadsworth.org

²Marine Biological Laboratory, Woods Hole, MA 02543, U.S.A.

*³Department of Biomedical Sciences, University at Albany,
1400 Washington Avenue, Albany, New York 12222, U.S.A.*

The Micro*scope project, hosted by the Marine Biological Laboratory (Woods Hole, MA, USA), is a communal database of information about microbial life. Micro*scope uses name-based tools within a layered architecture to organize local and distributed organismal data. This data is structured using “taxonomic intelligence” principles. Content is assembled into hierarchical arrays by annotating incoming data with names to integrate the content taxonomically. Additional databases contain other descriptive information, such as geographical data. The databases are designed to be synchronizable through SOAP calls, enabling communities of contributors to assemble large content environments. The Micro*scope tools can be used to gather, structure and dynamically annotate information from other Web resources, such as published literature.

The Star*sand project is a micro*scope database focused on the Foraminifera and other Granuloreticulosea. It contains a substantial amount of original data, provided by the Star*sand team of contributors, and also offers a number of powerful search tools of use to foraminiferal researchers. Hands-on demonstrations of the content environment will be available.

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Global timing and architecture of the last major extinction period in the deep sea

Bruce W. Hayward; Shungo Kawagata; Aswahaq T. Sabaa & Hugh R. Grenfell

*Geomarine Research, 49 Swainston Rd, St Johns, Auckland, New Zealand
b.hayward@geomarine.org.nz*

The last episode of enhanced global extinction in the deep sea is recorded by the disappearance of nearly 100, mostly cosmopolitan, bathyal and abyssal species of elongate benthic foraminifera, starting in the late Pliocene and peaking during the mid-Pleistocene Climate Transition (MPT, 1.2-0.55 Ma). We have documented these disappearances in 20 well-dated sites bathed in various water masses in different parts of the world's oceans. In most sites the absolute abundance and diversity of this group of elongate foraminifera declined during glacial periods, particularly during the MPT, with recovery or partial recoveries in interglacials. Stable isotope studies suggest that these species were infaunal and prior to their disappearance their abundance usually fluctuated in concert with benthic foraminiferal indicators of enhanced food flux. In the MPT the abundance of these elongate species declined dramatically, whereas that of the higher food flux species did not.

The decline and disappearances began first in deeper sites bathed by deep southern-component water (c. 2.5 Ma, 1.7 Ma), followed later in the mid-Pleistocene in northern-component deep water and southern and northern-sourced intermediate water sites. This pattern paralleled the glacial expansion of first the Antarctic ice sheet (late Pliocene), then later the North Atlantic ice sheet, with their consequent impact on the production of deep water and later intermediate water. In the northern hemisphere the onset of the decline in the mid-Pleistocene may have coincided with onset of the production of Glacial North Atlantic Intermediate Water and the hypothesised North Pacific Deep Water. This coincidence in timing suggests that the causes of the extinctions were related to glacial changes in some properties of the water masses accompanying equatorial shifts in their source areas. The extinctions occurred latest in AAIW in the Caribbean and off New Zealand in furthest-traveled intermediate water (AAIW or NPIW). This suggests that the culprit degraded in the water mass as it moved along and took several hundred thousand years before reaching lethal levels in downstream regions.

Whatever caused the extinctions was clearly related to global cooling, and had to change progressively and permanently as otherwise areas where species had been killed off would have been recolonised during interglacials. It was unlikely to have been changes in the amount or seasonality of food supply raining down from above, as these would not have altered sufficiently everywhere in the deep oceans to cause world-wide extinctions. While carbonate dissolution increased in some deeper sites during MPT glacials, this was not sufficiently universal to be implicated. We have suggested that increased dissolved oxygen in colder water formed during glacials may be responsible, but would this have been truly global and permanent to have prevented recolonisation from refugia during interglacials? The decline and extinction of this group of foraminifera coincided with pulsed overall global cooling, but how might this have caused its demise? Maybe the specialised nature of the apertures of these extinct foraminifera provides a clue. Were these apertures an adaptation to consuming a specific kind of food (*e.g.* chemosynthetic bacteria) that may have been progressively killed off during the MPT? Maybe these elongate species were just not able to cope with the increasing severity and speed of changes in the deep sea that accompanied the progressive onset of the present Ice Ages, or was it just competition from other foraminifera.

This study provides an insight into the architecture of the extinction of cosmopolitan deep-sea foraminifera, and maybe also the evolution of the deep-sea water masses, through the progressive contraction in their bathymetric and geographic ranges prior to their final disappearance at 0.55-0.7 Ma.



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Phylogeny of normal perforate Cenozoic planktonic foraminifera based on wall texture

Christoph Hemleben¹ & Richard K. Olsson²

¹*Institut und Museum für Geologie und Palaontologie der Universität Tübingen, D- 7400 Tübingen, Germany christoph.hemleben@uni-tuebingen.de*

²*Department of Geological Sciences, Rutgers University, Piscataway, NJ 08855, U.S.A.*

The recovery of early Paleocene planktonic foraminifera after the end Cretaceous mass extinctions led to fundamental changes in the wall structure of the test, changes linked to the way in which the earliest Paleocene species were adapted to the water mass environment. These changes in wall structure, consequently, reflect biological activity. The great mass of planktonic foraminiferal species that occupied the Paleocene oceans is derived from two survivors of the normal perforate genus *Hedbergella* that rapidly gave rise to distinct lineages. Since wall texture, e.g. surface texture, keel development, spines etc. reflect in part the adaptive strategies exhibited in the biological activity of living species it provides a means for a biological classification and, in turn, it is an important guide to phylogenetic study. We regard this interrelationship as a unifying concept in the classification and phylogenetic study of Cenozoic planktonic foraminifera. The basic features are expressed in the spinose and non-spinose groups. The cancellate spinose wall, which is a distinctive and diagnostic feature of the Cenozoic, is perhaps the most notable development in the Danian. This was an adaptation for more efficient food gathering (carnivory) and was widespread in species of *Eoglobigerina*, *Globigerina*, *Parasubbotina*, and *Subbotina*. The following spinose wall textures are recognized: *sacculifer*-type, *ruber*-type, *sacculifer/ruber* transition-type, *Turborotalita*-type, *bulloides*-type, and *Clavigerinella*-type. The *Clavigerinella*-type is subdivided into a *Hantkenina*-subtype in which spines have apparently been lost, except perhaps in some juvenile stages. Another type of cancellate wall texture that evolved in the Danian is seen in the non-spinose genus *Praemurica* that is comparable with the living species *Neogloboquadrina*, in which the cancellate pattern is due to the formation of subparallel low ridges that are connected by short ridges. It is a very common structure in Paleogene and Neogene planktonic foraminifera. Two other types of noncancellate wall texture are characterized by a smooth non-spinose wall with more or less scattered pustules and a heavily pustulose wall. The smooth wall type is seen in species of *Globanomalina* and in the Eocene *Turborotalia*.

The heavily pustulose (muricate) wall texture occurs in the genera *Acarinina* and *Morozovella*. A less pustulose, honeycombed *Globoquadrina*-type wall observed in the Eocene-Oligocene genus *Dentoglobigerina* possibly evolved from the muricate genus *Acarinina*.

Diagenetic alterations of primary wall texture of planktonic foraminifera, such as dissolution, degradation of layered wall structure, and recrystallization, may obscure the recognition and interpretation of wall texture.



FORAMS 2006

Evaluating support for eukaryotic supergroups and the search for sister groups of foraminifera

Laura Wegener Parfrey¹; Erika Barbero²; Elyse Lasser²;
Jessica Grant²; David J Patterson³ & Laura A Katz^{1,2}

¹*Program in Organismic and Evolutionary Biology, University of Massachusetts
Amherst, MA, U.S.A. lwegener@nsm.umass.edu*

²*Department of Biological Sciences, Smith College, Massachusetts, MA, U.S.A.*

³*Bay Paul Center for Genomics, Marine Biological Laboratory, Massachusetts, MA, U.S.A.*

Perspectives on eukaryotic diversity have recently shifted towards a supergroup system. We analyze two facets of supergroup robustness and find variable levels of support from molecular genealogies and considerable taxonomic instability. Destabilized factors include issues of eukaryotic complexity, limited data, nomenclatural ambiguity, and sparse taxonomic sampling. We argue that low taxonomic sampling of diverse free living microbial lineages is the most critical factor, as the resulting molecular genealogies substantially underrepresent diversity. Hence, statements of monophyly may be premature. In conjunction the EuTree consortium, we are testing organismal relationships within the putative supergroup 'Rhizaria' by expanded sampling of understudied lineages and a multigene approach. 'Rhizaria' encompasses Foraminifera, members of the polyphyletic Radiolaria, and a heterogeneous collection of amoebae and flagellates. Support for 'Rhizaria' comes entirely from molecular studies, although the resulting tree topologies vary tremendously with taxon sampling and the method of tree construction. Our work aims to elucidate the sister groups of the Foraminifera, as molecular studies have pointed to at least four groups as the sister taxon. This incongruity is largely due to highly divergent Foraminifera genes (Habura *et al.*, 2005. *Mol. Biol. and Evo.* 22:2000-2009). Expanding sampling of taxa and genes may clarify these relationships.



FORAMS 2006

Miliolid wall structures: Implications for classification of the miliolida

Justin H. Parker

*School of Earth & Geographical Sciences, The University of Western Australia,
35 Stirling Highway (M004), 6009 CRAWLEY W.A., Australia
jparker@segs.uwa.edu.au*

High-resolution scanning electron microscopy of the outer wall structure of eighty species of Holocene Miliolida from Western Australia and southern England has revealed similarities between genera that have traditionally been separated based on larger scaled morphological differences (including coiling mode and aperture type). Three principal outer wall structural types are identified among the studied species including: (1) no outer wall layer; (2) a pavement constructed of many calcite crystals; and (3) a pavement constructed possibly of a single crystal of calcite. The outer wall type that is constructed of a pavement of individual crystals is broken up into four different structural classes and six different subclasses. The structural classes refer to the main crystal shapes used in construction of the outer wall layer and include plates, laths, rods and needles. Structural subclasses are based on the arrangement of crystals in the pavement and include packing style (open, loose or tight), crystal arrangement (parquet, mosaic or bundled), crystal imbrication (imbricate or not), crystal alignment (random, roughly aligned or longitudinally aligned), supplementary layers (present or absent) and perforations of the outer wall layers. Perforations include those $< 0.5 \mu\text{m}$ in diameter (where the outer wall layer is called perforate). Where the outer wall shows no perforations or has pseudo-pores $> 0.5 \mu\text{m}$ (here considered ornament), the outer wall is classed as imperforate. Further characterisation of these subclasses can be elucidated from analysis of specific length/width ratios of individual crystals. The classes and subclasses are independent of wall ornament.

Examination of several deconstructed specimens has revealed that the outer wall structure is maintained throughout ontogeny, with the outer wall layer of the proloculus having the same structural characteristics as the outer wall layer of the final chamber. The structure of the outer wall layer is often preserved in species that develop a chamber floor. The calcite plate pavement is common to more species than is presently recognised and is shown to occur

in species with roughly textured walls that are the result of plate modification or of supplementary calcite layers. A newly recognized open-mosaic wall texture is shown for some species of *Quinqueloculina*.

Different genera and different species have the same outer wall structure, and it is not possible to make taxonomic identifications based solely on this structure. However, affinities between species within large genera (particularly *Quinqueloculina*) and other genera including *Miliolinella* and *Triloculina* seem to be evidenced in the test construction of the species. Affinities based on the structural characteristics of the outer-wall structure are examined and related to morphological variation to assist in the understanding of the classification of the Miliolida.



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Molecular phylogeny and higher-level classification of foraminifera

J. Pawlowski

*Department of Zoology and Animal Biology, University of Geneva, Switzerland
Jan.Pawlowski@zoo.unige.ch*

Loeblich and Tappan's 1987 classification of foraminifera laid foundations for an ordinal system, which remained almost unchanged until today and is widely used in current foraminiferal systematics. They distinguished 15 foraminiferal suborders and superfamilies based on the composition and structure of the test walls. Recent molecular phylogenetic studies, based on small-subunit ribosomal DNA sequences available for 11 out of the 13 modern orders, indicate that some of these suprageneric taxa are not monophyletic. Among others, molecular studies revealed phylogenetic groupings between:

- 1) Allogromiida and Astrorhizida
- 2) Miliolida and Spirillinida
- 3) Rotaliida, Robertinida, Lituolida, Trochamminida and Textulariida

Based on these molecular data, the taxonomic status of some foraminiferal suborders has been revised and a new supraordinal classification has been proposed.



FORAMS 2006

Molecular evolution of soritid symbionts

X. Pochon & J. Pawlowski

*Department of Zoology and Animal Biology, University of Geneva, Switzerland
Jan.Pawlowski@zoo.unige.ch*

Coral reef ecosystems worldwide gather a myriad of invertebrates, including sponges, jellyfishes, anemones, corals, and mollusks that are hosts to a diverse group of dinoflagellates of the genus *Symbiodinium*. Among protists, *Symbiodinium* endosymbionts have been reported in ciliates and large soritid foraminifera. Recent molecular phylogenetic studies on the symbionts of soritids have revealed an extraordinary diversity of *Symbiodinium* lineages, most of which are specifically associated with this relatively small group of foraminifera. Additional ecological and evolutionary studies have shown that:

- 1) the specificity between soritids and *Symbiodinium* is greater than previously thought and can also be found at a lower taxonomic level within Soritinae,
- 2) the diversity of soritid-specific *Symbiodinium* spp. is much greater in the Indo-Pacific than in Western Atlantic, hence correlates positively with the distribution of soritid diversity,
- 3) soritid symbionts did not present faster evolutionary rates compared to the metazoan symbionts, suggesting that other factors such as the predominantly vertical transmission of symbionts and/or biogeographic isolation may be responsible for the host-symbiont specificity and diversity observed in Soritinae.

Furthermore, a relaxed molecular clock method of the eight existing *Symbiodinium* lineages, suggested that the genus originated in early Eocene, and that the majority of extant lineages diversified since mid-Miocene, about 15 million years ago.



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Modularity and morphological evolution in foraminifera

Susan L. Richardson

*Wilkes Honors College, Florida Atlantic University, 5353 Parkside Drive,
Jupiter, FL 33458, U.S.A. richards@fau.edu & Department of
Paleobiology, National Museum of Natural History, Washington, DC, 20560, U.S.A.
richardson@si.edu*

Foraminiferans are unique among members of the unicellular clade Rhizaria in having evolved large, complex, multi-chambered tests. The complexity of the derived foraminiferal test results from the modularity of its constituent chambers. Individual chambers can be thought of as structurally and/or functionally distinct parts of a whole test, and can be classified as morphological, developmental, and/or evolutionary modules. As morphological modules, chambers are the “building blocks” of the multi-chambered test, elements that can be recombined in a diversity of complex arrangements. As developmental modules, chambers are iteratively expressed during the ontogeny of the organism. As evolutionary modules, chambers represent parts that have been independently modified during the course of evolution.

As has been hypothesized for Metazoa, modularity in Foraminifera is an evolved property. From within the framework of a cladistic phylogeny of living and fossil taxa, multi-chambered tests appear to have arisen independently in the two derived subclades of Foraminifera: an unnamed subclade comprised of Lituolida (in part) + Spirillinida + Silicoloculinida + Miliolida + Fusulinida, and an unnamed subclade comprised of Lituolida (in part) + Textulariida + Lagenida + Buliminida + Trochamminida + Rotaliida + Globigerinida + Robertinida. In both subclades, multi-chambered tests are derived from basal taxa with undifferentiated, episodic accretionary growth, in which successive intervals of test material are added as lamellae to the open end of a tubular second chamber. The evolution of tests with iterated discrete chambers is hypothesized to have resulted in restricted cytoplasmic communication between successive chambers, thereby increasing the autonomy of cellular functions within an individual chamber.

The largest and most complex foraminiferal tests are found in those clades that possess algal endosymbionts. The symbiotic integration of cells of different origin is one way to acquire modularity at the genetic level. Endosymbiotic associations with photosynthetic unicellular eukaryotes are

observed in several groups of modern benthic foraminiferal clades, including Soritacea (rhodophytes, chlorophytes and dinoflagellates), Alveolinacea (diatoms), Nummulitacea (diatoms), Calcarinidae (diatoms), and Amphisteginidae (diatoms). Foraminiferans with photosymbionts possess enhanced calcification rates, as well as an endogenous source of nutrition that allows them to allocate more energy resources to cell growth and maintenance. Thus, in comparison to aposymbiotic taxa, foraminiferans with endosymbionts grow to larger test sizes comprised of more numerous chambers that are organized into more complex arrangements. In addition, these taxa frequently possess other modular morphological components that can be combined during an individual's ontogeny to generate a complex test (e.g., multiple apertures per chamber, internal chamber compartments and elements, and/or complex, multilayered spines).

At the phenotypic level, the acquisition of a modular organization to the foraminiferal test appears to have been a novelty that enhanced evolution in Foraminifera, and facilitated the morphological diversification of the clade.



FORAMS 2006

**Genus *Stensioina* (benthic foraminifera) from
Turonian-Santonian deposits of the Eastern European
Platform: Species distribution,
taxonomy and morphological evolution**

Aleksey Yu. Sadekov¹; Vladimir N. Beniamovski & Aleksandr S. Alekseev

Australiana National University, Mills road. J7, 0200 Canberra/ACT, Australia

¹ *aleksey.sadekov@anu.edu.au*

Stensioina species have very wide biogeographical distribution and are common within epicontinental benthic foraminiferal assemblages of the Early Cretaceous. As a consequence the evolution of *Stensioina* species been widely used to determine the stratigraphy of Upper Cretaceous sequences (Koch, 1977. *Geol. Jb.* A38: 11-123; Olferiev & Alekseev, 2003. *Stratigraphia i geol. korelacia*, 11 (2): 75-101). We have studied the morphology and stratigraphic distribution of Turonian- Santonian *Stensioina* species from various outcrops and boreholes of the Eastern European platform. Our results indicate the occurrence of two periods of species evolution within the studied area. The first period, from the middle Turonian to middle Coniacian, includes the development of *S. praexsculpta* - *S. granulata* and *S. praexsculpta* - *S. emsherica* lineages and represents evolutionary change in the test spiral surface morphology. The second period, from the middle Coniacian to later Santonian, reflects the evolution of the test umbilical area within the *S. exsculpta* - *S. incondita*- *S. pommerana* lineage. The general patterns in early *Stensioina* evolutionary paleobiogeography can be traced based on the stratigraphic distribution of species. early Turonian endemic species like *S. pokorny* suggest that *Stensioina* first evolved in Western Europe and subsequently, around middle-later Turonian, appeared in the eastern parts of the European paleobiogeographical realm (Koch, 1977). During Coniacian time *Stensioina* complexes from Western Europe show predominance of members from *S. praexsculpta* - *S. granulata* lineage (Bailey, 2005) whereas foraminiferal assemblages from Eastern Europe are strongly dominated by species from the *S. praexsculpta* - *S. emsherica* lineage. The last member of this lineage reached the Caspian region only at middle Coniacian time. These differences in species development in Eastern and Western regions probably reflect patterns of geographical isolation in the early evolution of *Stensioina*. Despite the complex evolution of these benthic foraminifera, they stand to enhance present biostratigraphic schemes for the Upper Cretaceous.



FORAMS 2006

Molecular phylogeny of Rotaliida based on the SSU rDNA and focus on two genera (*Cibicides* and *Uvigerina*)

Magali Schweizer*^{1,2}; J. Pawlowski²; T.J. Kouwenhoven¹ & G.J. Van Der Zwaan^{1,3}

¹Department of Earth Sciences, Utrecht University, Netherlands
magali.schweizer@bluewin.ch

²Department of Zoology and Animal Biology, University of Geneva, Switzerland

³Department of Biogeology, Radboud University Nijmegen, Netherlands

*Present address: Swiss Federal Institute of Technology Zurich (ETH), Geological Institute,
ETH-Z, CAB E 64, Universitätsstr. 6, CH-8092 Zürich, Swiss

In traditional morphology-based classifications of foraminifera the hyaline calcareous species are either grouped in the order Rotaliida or split between the orders Rotaliida and Buliminida, which differ by the presence or absence of a tooth-plate, the shape of the aperture and the height of trochospiral coiling. To investigate the higher-level relationships between hyaline calcareous foraminifera we obtained partial and complete small-subunit (SSU) rDNA sequences from 59 and 23 species, respectively. The analysis of complete SSU sequences revealed the presence of four major groups of rotaliids, which cut across the distinction between Rotaliida and Bulimina. Analyses performed with shorter fragments of the SSU (1/3 or 2/3) also identified these four main groups but failed to obtain statistically significant support, which was achieved with the complete SSU.

In addition, we analyzed in more detail two rotaliid genera which are widely used in paleoecological reconstructions: *Cibicides* and *Uvigerina*. In spite of the fact that they are important proxies, their evolutionary relationships are not well known. The different species are distinguished on morphological criteria, but it is not always easy to ascertain whether morphotypes belong to the same or to different species. The six species of *Cibicides* which gave DNA have been historically classified, on morphological grounds, in five different genera belonging to three different superfamilies. For *Uvigerina*, the situation is less complex: the three studied species are classified within the same genus. Furthermore, two species belonging to closely related genera (*Trifarina* and *Rectuvigerina*) were added to the molecular analysis of *Uvigerina*.

The molecular results based on two fragments representing 2/3 of the complete SSU show that the six species of *Cibicides* we obtained form a monophyletic group. Further studies performed with one fragment representing 1/3 of the SSU showed that *Cibicides lobatulus* and *C. refulgens* are two

different species, separated in distinct groups that possibly represent cryptic species. On the other hand, *C. pachyderma* and *C. kullenbergi* could belong to the same species.

A fragment representing 1/3 of the SSU rDNA was used to investigate the phylogeny of *Uvigerina*. Another fragment of rDNA (the ITS) was studied to explore the variation inside one morphologically highly variable population of *U. peregrina*: the genetic variability was rather low.

These first molecular results provide new viewpoints in the resolution of the taxonomic problems encountered in the classification of Rotaliida.



FORAMS 2006

**Iterative evolution of *Globorotaloides* versus *Clavatorella*:
Examples from the late Oligocene and early Miocene**

Silvia Spezzaferri¹; Helen K. Coxall² & Paul N. Pearson²

¹University of Fribourg, Department of Geosciences, Ch. Du Musée 6,
1700 Fribourg, Switzerland silvia.spezzaferri@unifr.ch

²School of Earth, Ocean and Planetary Sciences, Cardiff University,
Main Building, Park Place, Cardiff CF10 3YE, U.K.

Iterative evolution is the repetition in time of morphological changes in which different species with similar morphologies evolve from similar ancestors. Iterative evolutionary changes in a species or genus may be caused by recurrent environmental variations or ecological adaptations that occur within brief intervals of time.

An example of iterative evolution in planktonic foraminifera involves the well known passage of *Globorotaloides hexagonus* into *Clavatorella bermudezi* in the early Miocene of tropical areas. The five-six chambered *G. hexagonus* evolved into *Clavatorella bermudezi* by developing radially elongated and club-shaped chambers in later ontogenetic stages. The occurrence of *C. bermudezi* spans the interval from Zone N8 to N12.

A similar evolutionary pattern seems to have occurred also in the late Oligocene Zone P22. We document here the passage of a new species of *Globorotaloides* to a new genus and species similar in morphology to *C. bermudezi* but which nevertheless is not believed to be directly related. The evolution of the new genus and species is well documented at ODP Leg 108 Site 667 drilled in the Equatorial Atlantic. The ancestor of the new species of *Globorotaloides* appears to be *G. stainforthi*, which in equatorial zones first occurs in the middle-late Oligocene as documented in Spezzaferri (1994. *Palaeontographia Italica*, 81: 1-187)

The new trochospiral *Globorotaloides* displays 5 to 6 chambers in the last whorl, and an umbilical-extraumbilical aperture that is sometimes covered by a flat bulla. The wall texture is coarsely cancellate. It differs from *Globorotaloides eovariabilis* Huber and Pearson by having a flat and well developed bulla covering the aperture, less coarsely cancellate wall texture, lower arched aperture and 4 to 6 chambers in the last whorl. The new homeomorph of *C. bermudezi* displays a trochospiral tending to a planispiral chamber arrangement, 5 to 6 chambers in the last whorl tending to become triangular and slightly radially elongated. The aperture is a relatively high arch strongly tending to extraumbilical position.

The presence of the *Clavatorella* homeomorph is generally associated with high abundances of radiolarians and sponge spicules, thus suggesting that the iterative evolution in this case may be related to high nutrient concentrations in the seawater.

Multispecies isotope analyses are performed on samples containing the new species/genus to reveal their environmental significance.



FORAMS 2006

Theoretical morphospace of foraminiferal shells: Evolutionary implications

The theoretical morphospace of foraminiferal shells (tests) is constructed based on the moving reference model. The model has introduced apertures as reference points into modeling polythalamous foraminifers (Topa & Tyszka, 2002. *Lecture Notes in Comp. Sci.* 2329: 97–106; Topa & Tyszka, 2005. *Paleobiol.* 31(2): 526–541; Tyszka, 2006. *Lethaia*, 39(1): 1–12). The morphospace includes all forms created by the model with systematically varying parameter values. Some of morphologies are possible others not, in consequence, the overall morphospace splits into the ‘possible range’ and the ‘forbidden range’. The ‘possible range’ includes existent and nonexistent foraminiferal forms separated into ‘vacant’, ‘dysfunctional’, and ‘deficient’ ranges. Analyses of these ranges provide additional knowledge on morphogenesis of foraminifera (Tyszka, 2006). It is surprising that nearly all theoretical foraminiferal morphologies are possible and have been selected in reality. We can therefore suppose that most theoretical morphologies are functional because they were successfully tested by real evolution. That raises a fundamental question whether or how far shell patterns are subjected to natural selection. Biserial foraminifers give an instructive example because they have efficiently colonized the water column, sediment surface, and subsurface sediment. Their elongated test shape seems to facilitate burrowing, nonetheless, this shape does not disturb surface dwelling and floating abilities. We can speculate that evolution of small foraminifera may choose from an enormous variety of shell shapes that may have low or even neutral adaptive values. On the other hand, foraminiferal species usually show relatively stable morphotypes that are most likely controlled by genetic codes. They do not choose morphologies by random as it could be expected from assumption of neutral values of shell patterns.

The classical view considers gradual evolution of foraminiferal morphologies. Cryptic speciations recorded by molecular studies seem to support this paradigm. Nevertheless, the theoretical morphospace of foraminifera reveals regions of the morphospace that include similar morphologies. These specific fields in the morphospace, called *morphophases*, are separated from each other by *morphophase transitions*, which involve sharp or gradual changes in morphology controlled by changes of the model parameters. The morphospace acts as a phase space in which all possible states of a system are represented (Tyszka, 2006). Analysis of the morphospace reveals that similar morphologies may be located in distant parts of the morphospace defined by very different parameters. On the other hand, very different morphologies may be closely related, representing similar

parameters. The straightforward conclusion is that small gradual change of parameters may cause abrupt changes of morphologies. Evolutionary consequences are essential supposing that gradual genetic changes may sometimes generate nongradual morphologic modifications. In this case, optimised emplacement of foraminiferal apertures is responsible for these nongradual morphologic changes represented by *morphophase transitions*. Shall we ask whether Darwin's *natura non facit saltum* has exceptions?

The presented model and its resulted morphospace include morphologies resembling foraminifers classified to Textulariida and Rotaliida. Both groups use the same rules to create similar morphologies. The classical taxonomy based on the wall composition keeps them aside; nonetheless, molecular biologists have proven both groups to be very closely related. Other taxa show similar trends (e.g. miliolids, rzehakinids, ammodiscids) quite consistent with the taxonomic scheme presented by Mikhalevich & Debenay (2001. *J. Micropal.*, 20: 13–28). Further integrated studies seem to be necessary for a comprehensive understanding of foraminiferal “fossils, morphology and molecules”. *This research is sponsored by the Polish Ministry of Education and Science (Grant nr 3 PO4D 048 24).*



FORAMS 2006

Cryptic speciation in planktonic foraminifera: Phylogeny, divergence times and biogeography

Yurika Ujiie¹; Jan Pawlowski¹ & Jere H. Lipps²

¹*University of Geneva, Sciences III, Department of Zoology and Animal Biology
Yurika.Ujiie@zoo.unige.ch*

²*University of California-Berkeley, Museum of Paleontology and Integrative Biology*

Most of the Recent planktonic foraminiferal morphospecies have lived in the world's oceans for the last several million years, despite the dynamic geological and oceanographic changes during the Neogene. However, whether these widespread, extant morphospecies represent single species or not is unknown. Indeed, some morphospecies have bimodal or polymodal habitats and are recognized as eco-phenotypes in paleoceanographic studies. Previous molecular phylogenetic studies on selected planktonic foraminiferal "species", particularly in the Atlantic Ocean, reveal multiple cases of cryptic speciation. To complement these studies, we analyzed 34 new planktonic foraminiferal SSU rDNA (small subunit ribosomal DNA) sequences from the northwestern Pacific Ocean, which represent 13 morphospecies including one newly-sequenced species. Using Bayesian phylogenetic analysis, we identified 27 genetic types including four new types. Moreover, we estimated the divergence times among 14 genetic types in the family Globigerinidae. Almost all genetic types diverged during one of three periods dated to ca. 12, 5-4 and 2 Ma. These periods correspond to the formation of surface water-mass structures related to two major geological events during the Neogene and the beginning of global climate change in the Quaternary. Because most of the genetic types have broad distributions in the world's oceans, the overall pattern of distribution and phylogenetic relationships of the planktonic fauna suggest not only tremendous genetic diversification linked to past global environmental changes but also that considerable gene flow takes place through global thermohaline currents.