Macroevolution Research in IODP: An INVEST White Paper

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Abstract

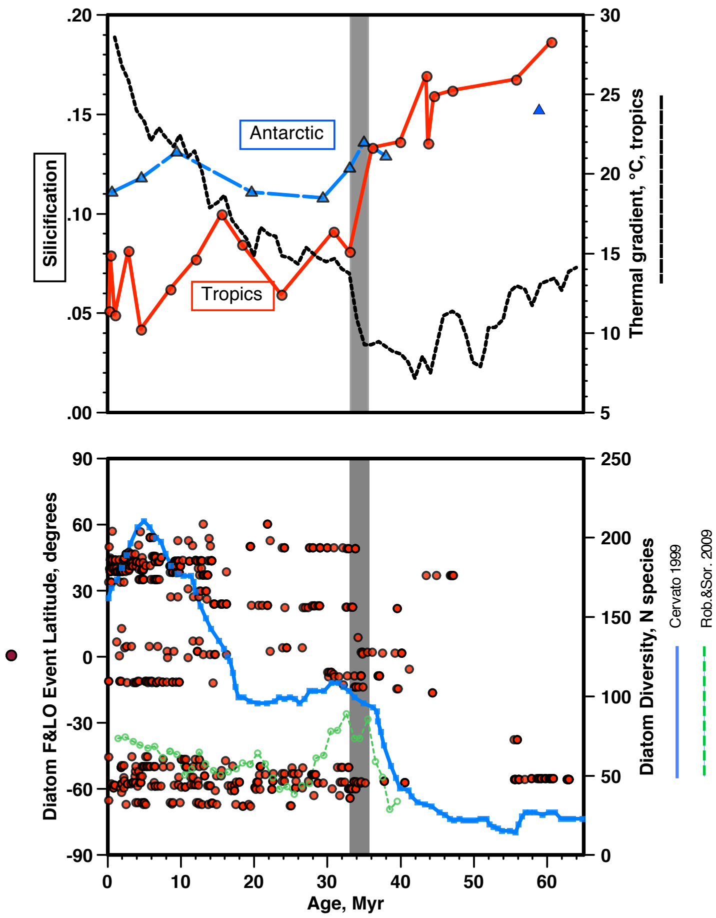
Microfossil studies of macroevolution (patterns and processes of evolution beyond the species-level) provide essential knowledge on how biodiversity will respond to future environmental change, and are a major opportunity to expand IODP science with new links to evolutionary biology and paleontology. Recently developed software tools (e.g. Neptune and PBDB databases) have stimulated several new publications but the completeness and accuracy of data content needs significant improvement to sustain this new research area. Key recommendations are:

- Workshops for micropaleontologists and evolutionary biologists to develop more detailed science questions and technical implementation plans for a program of macroevolutionary study of deep-sea microfossils;
- Improved capture of existing data into Neptune and other databases, approximately doubling coverage of existing sections and including a more comprehensive, regularly updated library of age models for current and newly recovered deep-sea sections;
- New data collection and capture into databases emphasizing complete taxonomic surveys of preserved diversity. Between 10 and 20 composite 0-100 Ma new data sets at ca 500 kyr resolution are needed to minimally capture global patterns of diversity;
- Use of existing collections of microfossil slides (MRC, Museum) for these surveys, supplemented by new sampling and in some cases new drilling to recover gaps in existing deep-sea microfossil records;
- Development of specific drilling proposals for regions / sections with high potential to recover these gaps;
- Support for needed taxonomic infrastructure, including continued descriptive work and reference catalog development for insufficiently studied fossil groups.

Figure 1 - Example of macroevolutionary analysis. Lower panel shows two different estimates of Cenozoic diatom diversity (blue-simple and green-with re-sampling), both from the Neptune database (Cervato 1999; Rabosky and Sorhannus 2009) and geographic patterns of diatom evolution (red dots), from Neptune's age model database (Spencer-Cervato and Burckle 2003). Upper panel shows trends in shell morphology from biometric measurements of radiolarians in MRC and other slides. Grey line marks formation of cold deep water oceans and increase in thermal gradient (black line; Finkel et al 2007). From Lazarus et al. 2009.

Introduction and Summary

Global, integrated earth science studies of deep sea sediments will require significant improvements in our ability to acquire and synthesize large, high quality, globally distributed data, including improved ability to precisely correlate many previously drilled sections in geologic time. One major research goal that exemplifies this, and which should be a specific goal in the next phase of deep sea drilling is macroevolutionary study of microfossils. Macroevolution examines large patterns of evolutionary change in assemblages of fossils over time to determine factors and processes regulating evolution beyond the species level, including both 'normal' factors and responses to extreme events such as extinction and impact recovery. Such knowledge is essential to understand changes in biodiversity due to future change in environments. Microfossils can provide uniquely detailed and complete data at species level for such research. Microfossil studies



complement the long established field of macroevolution research using macrofossils (mostly invertebrates, done at much coarser taxonomic and chronologic resolution). Although long a theme in deep sea microfossil research (Hoffman and Kitchell 1984; Stanley et al. 1988) an accelerating interest is shown by several recently published studies (Bown et al. 2004; Schmidt et al. 2004; Finkel et al. 2005, 2007; Allen and Gillooly 2006; Liow and Stenseth 2007; Foote et al. 2008; Lazarus et al. 2009; Rabosky and Sorhannus 2009; figure 1). Many of these papers are by evolutionary biologists and ecologists newly engaging with deep-sea micropaleontology data, and thus represent an opportunity to significantly expand the scope of future IODP science. Despite this increasing interest such research is not, except as part of other themes, identified as major goal in IODP's current science plan. This is despite macroevolution being repeatedly identified as a major research goal in prior community background planning documents (COSOD II, COMPLEX). The primary reason for this discrepancy has been a lack until recently of suitable analytic tools to achieve the desired research targets. The subject by nature is strongly retrospective and synthetic, primarily shore based and reliant on difficult to construct databases and other software tools, rather than primarily driven by obtaining and analyzing new cores. Appropriate databases and other tools have however been developed in recent years. These, plus continued accumulation of new data/material, and improved understanding in recent years of basic aspects of these groups' biology (genetics, water column distribution/habitat preferences), allow a more realistic research program to be proposed for active implementation in the next phase of deep sea drilling. Many details however need to be developed, and the currently scattered community, which includes many evolutionary biologists as well as more traditional micropaleontologists, needs to come together and develop detailed plans for implementing this research program. IODP involvement is required as most of the primary data comes from materials obtained by IODP drilling, and there is a close relationship between the needs of this research program and general IODP science community needs for age models and other supporting data.

Three main resources are needed for macroevolutionary studies of deep sea microfossils:

• IT tools to integrate in scientifically meaningful ways large data sets of deep-sea microfossil data. These can be, for simpler analyses, just taxa catalogs with geologic range information, but more general research requires detailed occurrence data, using uniform taxon concepts, numeric age and geologic sample location. Both 'range only' type (e.g., for planktonic foraminifera: Stewart and Pearson 2000 - http://palaeo.gly.bris.ac.uk/Data/plankrange.html) and occurrence type databases (for most plankton groups: Neptune - Lazarus 1994; Cervato 1999; http://portal.chronos.org:80/gridsphere/gridsphere?cid=searches) now exist.

• Globally distributed, numerically age dated samples of fossil assemblages covering all, or almost all the time intervals being studied, for new, taxonomically comprehensive surveys of deep sea microfossil occurrences, and collection of non-occurrence type measurements (morphometrics, geochemistry) as these were rarely done for prior, primarily biostratigraphic research. Such collections can be acquired in part by resampling of older materials and, more efficiently, by making use of existing prepared sample sets such as the extensive MRC collections (http://iodp.tamu.edu/curation/mrc.html);

• Limited new drilling to recover remaining gaps in our record of deep sea microfossils over last ca 100 my.

Effective use of these main resources also requires improvement in the accuracy of the two data types typically analyzed in macroevolutionary studies: taxonomic units, and geologic age of occurrences of these taxa. Both databases and reference microfossil collections require a uniform, regularly updated source of chronologic information for deep-sea sections. Such an age-model library is already incorporated into the Neptune system but needs substantial expansion and maintenance. Access to improved age information on the extensive archive of deep-sea drilling materials will also substantially benefit other areas of research beyond evolution studies, e.g. paleoceanography.

All research using microfossils is ultimately dependent on accurate, consistent and complete taxonomy. The current development of this is highly uneven for deep sea microfossils, with relatively mature taxonomy for calcareous plankton groups but much less complete taxonomy for siliceous microfossils. Continued taxonomic research is needed, to complete description of recovered diversity, to build reference catalogs of standardized taxonomic definitions, and to maintain lists of taxonomic names and their synonyms, which serve as key fields for accessing all taxonomically linked primary data within and between different database systems. IODP is currently improving such taxonomic name key lists via their Paleontology Coordination Group (PCG).

Macroevolution

Macroevolution has been the major (arguably the prime) focus of paleontologic research in last decades. Judged by publications, this has been a successful endeavor, with many high profile, high citation publications. Goal of macroevolution research is to examine aspects of evolution that are beyond scope of most living biologic studies (typically of individual species or populations). Molecular biologic study of evolutionary pattern complements but can't replace unique record of past change, including major phenomena e.g extinction. Macroevolutionary research using fossils also provides unique insight on how climate change impacts biosphere (and vice-versa). This subject almost entirely based so far on data from macrofossils, and particularly large databases of taxa occurrences (Sepkoski and successor PBDB). The macrofossil record tho is limited. Despite switch from simple two data point (total taxon range) type database (Sepkoski) to individual sample occurrence databases (PBDB) the incompleteness of the primary fossil record of macroorganisms limits robust studies to relatively high taxonomic levels (e.g families), despite some research on genus level data. Yet most evolutionary processes act at species level, and thus extrapolation is needed to apply species level theory to higher taxonomic levels. This is controversial, as even patterns do not scale linearly from higher to lower taxic levels (Lane and Benton 2003), let alone underlying processes. The correlation of evolutionary pattern to environmental change history is also often weak in macrofossil studies, further limiting understanding of the links between evolutionary change and paleoenvironmental change.

Macroevolution and links to paleoenvironmental change can also be studied with deep sea microfossils, where the completeness of the fossil record at (morpho)species level is much better. This is due to better preservation of species diversity within samples, and to the relatively small number of samples per time interval needed to adequately cover biogeographic variation: plankton provinces are few in number and can be fully sampled by reasonably small numbers of drilled sections. Links to paleoenvironment can be established in detail, often from paleoceanographic studies of the same sections, and better chronology allows much more precise global syntheses, as well as better calculation of rates of change, essential to understanding processes. Macroevolutionary research on marine microfossil has for these reasons been identified as an important theme in several prior IODP planning documents (COSOD II, COMPLEX) and is also included in INVEST (WG1.5 and other working groups in CT1).

Current status and resources

Most earlier research on macroevolution using deep-sea microfossils has been based on either hand compiled data sets of first and last appearances within a single fossil group, often using previously published catalogs of taxa descriptions, particularly for calcareous plankton. Such 'Range only' databases have significant advantages: they consist of relatively compact, easily compiled data which has been taxonomically and stratigraphically quality checked. Limitations however are also substantial and numerous, such as: a relatively subjective compilation methodology; catalog sources used for compilation often lag primary data sources by many years; generally coarse (1-2 my resolution) age estimates. Range only information also severely restricts the methods used and thereby the types of questions that can be addressed. Such studies nonetheless have demonstrated a strong correlation of evolutionary change to paleoenvironmental change, tho which factor(s) are most important (temperature [Allen and Gillooly 2006]; water column stratification [Schmidt et al. 2004; Finkel et al. 2005, 2007]; latitudinal province development [Lazarus 2002]; nutrient availability [Corfield and Shackleton 1988; Lazarus 2002]; or biotic factors e.g. co-evolution [Lazarus et al. 2009]) is not yet clear. More detailed examination of forcing factors, compensation for data imperfections (e.g via subsampling), study of groups for which no suitable catalogs exist (in practice, most groups of deep sea microfossils, including benthic foraminifera, diatoms, and radiolarians) and research on questions needing data other than simple ranges (e.g. within-taxon changes: Liow and Stenseth 2007) all need occurrence type databases. Similar needs motivated the development in macroevolution macrofossil research of the highly successful Paleobiology Database (PBDB) to replace the earlier 'range only' Sepkoski database (Alroy et al. 2001). A counterpart system for deep sea microfossils, Neptune, was initiated in the mid 1990s (Lazarus 1994; Spencer-Cervato 1999) but only became generally available for research in the last few years (ca 2006) via the NSF supported Chronos project. This project placed

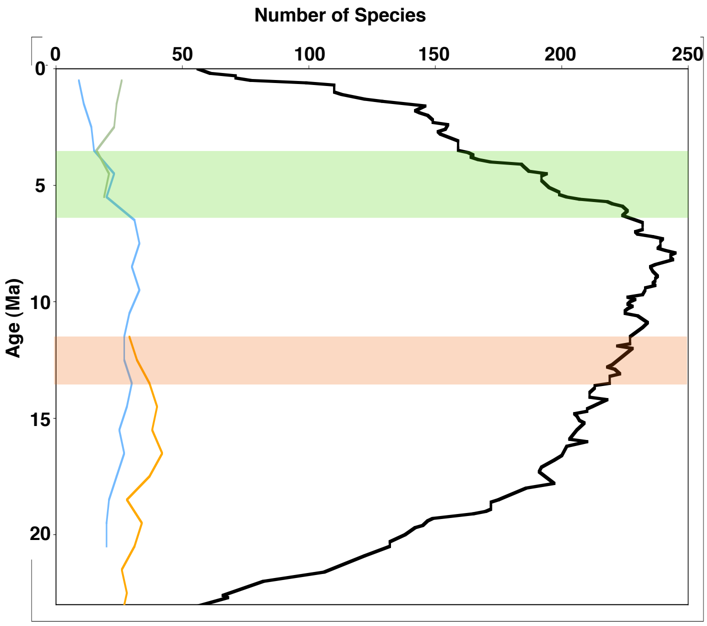


Figure 2 - Example of incompleteness in existing biodiversity data. Blue, orange and green lines are diversity of Antarctic Neogene radiolarians calculated from published ODP biostratigraphic reports of three different authors (Lazarus 2002). Black line is preliminary estimate of diversity history for same sections based on complete taxonomic survey, including numerous small, rare and undescribed species (Renaudie and Lazarus, unpublished, DFG project 1191-81). Not only magnitude but also significant features (e.g., diversity trend in mid Miocene) differ between data sets. (Range-through, no resampling for all curves).

the Neptune system online (www.chronos.org). The PBDB project then codeveloped with Chronos access to Neptune suitable for macroevolutionary research (http://paleodb.org/...dowload/neptune data). Many of the recent papers on macroevolution patterns from deep-sea microfossils cited in the introduction have made use of this new system.

The unique, nearly complete primary preservation and extensive recovery of sediment records by global drilling has provided an extraordinarily detailed record of species, or near species-level evolution for several microfossil groups over the last ca 100 my. However, while the *Potential* for nearly complete data exists, current deep sea microfossil data in database systems such as Neptune are surprisingly incomplete. To give just two examples, most planktic foraminifera (even among reasonably long ranging taxa) are represented in current database by <100 samples, and <10 stratigraphically useful sections (Lazarus, unpubl. analyses); while for the highly endemic Antarctic Neogene radiolarian fauna, the large majority of species first or last occurrences are known from only a single section, and total recorded diversity (DSDP and ODP) is only (fig. 2). There are many reasons for this general data incompleteness. Some are in principle temporary and specific to database development. In particular, no adequate age models exist yet for many (often older) sites, a surprising fact which however can be remedied in many cases by review and re-analysis of existing data. A full review of older sections with new age model development and entry of published taxa occurrences into Neptune would nearly double data density (from currently ca 200 to ca 400 Sites) and is urgently needed. Others are more basic: the primary descriptive taxonomy of some groups (e.g. radiolarians), although sufficient for initial macroevolutionary analyses, still need much work. Much of the problem however is fundamental to the existing available data, which has accumulated over several decades and which was collected primarily for biostratigraphic dating of local sections. These include: incomplete recording of non-stratigraphic marker taxa; rare taxa, often missed in the typical quick-examine slide procedures used biostratigraphy and paleoceanography; the often dramatic increase in numbers of known species over the last 30 years due to continued taxonomic studies; and others. Thus, although improved database technology is leading to renewed interest in such research, unless new data with much better coverage of the actual preserved fossil diversity is collected, the potential of deep-sea drilling to clarify macroevolutionary processes will be hindered.

Requirements and resources for new data collection

A set of samples providing a complete, or nearly complete record of deep-sea microfossil macroevolutionary history would be well preserved, precisely dated assemblages for each fossil group with a substantial preserved record (planktic and benthic foraminifera, calcareous nannofossils, diatoms, radiolarians and dinoflagellates), at temporal resolution equal to or better than all but the shortest ranging taxa (i.e. ca 500 kyr spacing), for each oceanic biotic province (e.g., ca 10-20 globally distributed composite sections), and where each composite section covers the entire in-sediment preserved record (ca last 100 my). Although individual studies normally only need a subset of these materials, the total sample numbers needed (>>1,000) and complex dating/age modeling requirements are prohibitive for individual research projects - if such materials need to be assembled for each study from scratch. Fortunately, substantial libraries of pre-made fossil microslides are available: from former research collections deposited in museums, still active longer-lived micropaleontology research groups, and in particular, the global network of Micropaleontologic Reference Center collections. These resources should be integrated into macroevolutionary research designs to insure effective use of materials and adequate coverage in generating new data sets for analysis.

Although most biotic provinces and time intervals have been adequately sampled by prior drilling, in some cases poor recovery, regional hiatuses, poor primary preservation of microfossils, or other problems have left gaps in the coverage of deep sea microfossil history. Early Paleogene and older intervals, and particularly earlier Paleocene siliceous microfossil assemblages have been inadequately recovered. As part of a macroevolution research program, a prioritized list of desired materials, and a list of ocean regions most likely to yield them should be compiled and developed into specific drilling proposals in conjunction with the drilling plans of other next-phase IODP drilling themes.

Need for Workshops

The lack of a prior program in IODP and involvement of new disciplines with little prior contact means that many subjects still require discussion (details of current data adequacy, future data needs, gaps and drilling targets, tool development, ideas for funding etc). A series of interdisciplinary workshops are thus needed to convert this emerging research theme into a robust IODP science plan.

References

Allen, A.P., and Gillooly, J.F., 2006, Assessing latitudinal gradients in speciation rates and biodiversity at the global scale: Ecology Letters v. 9, p: 947–954.

Alroy, J., et al., 2001, Effects of sampling standardization on estimates of Phanerozoic marine diversification: Proceedings of the National Academy of Sciences v. 98, p: 6261–6266.

Bown, P.R., Lees, J.A., and Young, J.R., 2004, Calcareous nannoplankton evolution and diversity through time, *in* Thierstein, H.R., and Young, J.R., ed., Coccolithophores: From Molecular Processes to Global Impact: Berlin, Springer, p. 481–508.

Cervato, C., and Burckle, L.H., 2003, Pattern of first and last appearance in diatoms: Oceanic circulation and the position of the Polar Fronts during the Cenozoic: Paleoceanography v. 18, p: 1055.

Corfield, R.M., and Shackleton, N.J., 1988, Productivity change as a control on planktonic foraminiferal evolution after the Cretaceous/Tertiary boundary: Historical Biology v. 1, p: 323–343.

Finkel, Z.V., Katz, M.E., Wright, J.D., Schofield, O., and Falkowski, P.G., 2005, Climatically driven macroevolutionary patterns in the size of marine diatoms over the Cenozoic: Proc. Natl. Acad. Sci. USA v. 102, p: 8927–8932.

Finkel, Z.V., Sebbo, J., Feist-Burkhardt, S., Irwin, A.J., Katz, M.E., Schofield, O., Young, J., and Falkowski, P.G., 2007, A universal driver of macroevolutionary change in the size of marine phytoplankton over the Cenozoic: Proc. Natl. Acad. Sci. USA v. 104, p: 20416–20420.

Foote, M., Crampton, J.S., Beu, A.G., and Cooper, R.A., 2008, On the bidirectional relationship between geographic range and taxonomic duration: Paleobiology v. 34, p: 421–433.

Hoffman, A., and Kitchell, J.A., 1984, Evolution in a pelagic planktic system: a paleobiologic test of models of multispecies evolution: Paleobiology v. 10, p: 9–33.

Lane, A., and Benton, M.J., 2003, Taxonomic level as a determinant of the shape of the Phanerozoic marine diversity curve: American Naturalist v. 162, p: 265–276.

Lazarus, D.B., 1994, The Neptune Project - a marine micropaleontology database: Math. Geol. v. 26, p: 817–832.

Lazarus, D.B., 2002, Environmental control of diversity, evolutionary rates, and taxa longevities in Antarctic Neogene Radiolaria: Paleontologica Electronica v. 5, p: ca 30 p. (web).

Lazarus, D., Kotrc, B., Wulf, G., and Schmidt, D.N., 2009, Radiolarians decreased silicification as an evolutionary response to reduced Cenozoic ocean silica availability: Proc. Nat. Acad. Sci. USA v. 106, p: 9333–9338.

Liow, L.H., and Stenseth, N.C., 2007, The rise and fall of species: implications for macroevolutionary and macroecological studies: Proc. Royal Soc. B v. 274, p: 2745–2752.

Rabosky, D.L., and Sohannus, U., 2009, Diversity dynamics of marine planktonic diatoms across the Cenozoic: Nature v. 247, p: 183–187.

Schmidt, D.N., Thierstein, H.R., Bollmann, J., and Schiebel, R., 2004, Abiotic forcing of plankton evolution in the Cenozoic: Science v. 303, p: 207–210.

Spencer-Cervato, C., 1999, The Cenozoic deep sea microfossil record: Explorations of the DSDP/ODP sample set using the Neptune database: Palaeontologica Electronica v. 2, p: web.

Stanley, S.M., Whetmore, K.L., and Kennett, J.P., 1988, Macroevolutionary differences between the two major clades of Neogene planktonic foraminifera: Paleobiology v. 14, p: 235–249.