

Issues in Palaeobiology: a Global View

Interviews and Essays



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Hall

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1. Marcelle BouDagher-Fadel *

1. What are the most important problems in palaeobiology?

For me, the central questions in palaeobiology are the implications of the process of speciation and radiation in space and time. Ever since the articulation of the Darwin-Wallace Theory of Evolution, the nature of biological species within the context of natural evolution - and indeed the process of speciation itself - have been an enduring and key topic. Throughout geological time and up to the present day, life in the ocean shows an exciting and fascinating exuberance of biodiversity. Living biological species are largely genetically identical and capable of inter-breeding but, in the fossil record, morphology and palaeoecological context must be used to infer kinship. All biological characters of the species are then used to infer its origin, its progress in biostratigraphic columns, and its eventual demise. These characteristics also guide the classification and phylogenetic lineages of the group of species and their speciation in time. Hohenegger (2012) defined speciation as the splitting up of a group of genotypes into groups with differing genotypic frequencies, while a unique species is homogeneous in its genetic composition. However, the biological concept of species is still not globally unified and the factors leading to speciation are yet not widely understood.

In my area of study, namely the larger benthic foraminifera and the planktonic foraminifera, we speculate much about palaeobiology, palaeoclimate, palaeogeography, palaeoecology and the possible physiology of extinct forms

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by comparing them to their living analogues. However, in some cases this might be difficult as little or nothing is known about the biology of the skeletal analogues of the majority of living species.

It is clear by now that, while the Darwin-Wallace framework provides a general explanation for natural evolution, the observed pattern of life needs to be analysed in terms of the complex sets of processes that determine the factors that affect the success or failure of a newly evolved species. The origins and processes underpinning parallel evolution and evolutionary convergence, which produce morphologically very similar tests in genetically separated and distinct forms, are contemporary issues debated by many researchers. Without doubt, they result from natural selection, reflecting “persistent selection favouring similar general forms” (Conway Morris, 2003), but there will be a balance between specific predispositions to particular genetic mutations and the ecological factors driven by the consequences of occupying similar habitats (BouDagher-Fadel, 2008). Ecological variables as well as genetic characteristics are the two major problems that need to be analysed in order to understand the palaeobiology and phylogenetic evolution of different species.

The purpose of the protozoan skeleton is related to both the separation of the different parts of the cytoplasm for different but related functions, and to the provision of shape and rigidity. Every feature of the skeleton must, at some stage, have provided a competitive advantage or at least no deleterious effect. For microscopic organisms such as foraminifera, the test can have had little or no defence value because those predators that ingest plankton (namely other, larger marine organisms) would hardly be deterred by such a small calcareous object! However, the foraminiferal test can, for example, provide a basis and

support for the pseudopodia used to capture food particles. Furthermore, there are other obvious ecological variables, such as salinity, temperature, water density, illumination and so on, which have also a marked effect on test shape and structure (Hemleben *et al.*, 1989). With the exception of illumination, the other variables are difficult to determine; temperature may be estimated from the radioisotope ratios, but these have not been calculated for many early taxa.

If more needs to be learned about the probable palaeobiology of an extinct species, then more effort should be made in the biological study of its living analogues. Such comparisons will suggest new interpretations which will radically improve our understanding of the nature, lifestyles, habits and evolution of the extinct foraminiferal species.

2. Which is the most fundamental issue of palaeobiology and evolution that your work addresses?

My work addresses the study of the marine protozoa known as foraminifera, which are single-cell eukaryotes. These single-cell organisms have inhabited the oceans for more than 500 million years. Foraminifera are separated into two types following their life strategy, namely, the planktonic and the benthic foraminifera. The benthic forms occur at all depths in the marine realm. They vary in size from less than 100 μm in diameter to a maximum breadth of many centimetres. Benthic foraminiferal tests may be agglutinated (quartz or other inorganic particles being stuck together by calcitic or organic cements), or may be primarily secreted and composed of calcite, aragonite, or (rarely) silica. They include many species that live attached to a substrate or that live freely, and they

include organic-walled and agglutinated small foraminifera that dominate the deep-sea benthic microfauna, as well as a major group of foraminifera with complicated internal structures, the so-called larger benthic foraminifera (BouDagher-Fadel, 2008), the group that includes the major reef-forming species. However, the other type of foraminifera, which is just as successful as their benthic ancestors, are the planktonic foraminifera. These evolved from benthic forms in the Triassic and have tests made of relatively globular chambers composed of secreted calcite or aragonite. They float freely in the upper water of the world's oceans, with species not exceeding 600 μm in diameter. Today they have a global occurrence and occupy a broad latitudinal and temperature zone. The majority of planktonic foraminifera float in the surface or near-surface waters of the open ocean as part of the marine zooplankton. The depth at which a given species lives is determined in part by the relative mass of its test, with deeper dwelling forms usually having more ornamented and hence more massive tests.

Both living and fossil foraminifera come in a wide variety of shapes and sizes. The Larger Benthic Foraminifera (LBF) in particular exhibit a variety of interesting evolutionary characteristics. In particular, the substantial morphological complexity of their shells, reproduced precisely with each successive generation, form the focus of major study. This complexity (and its evolution in time) is the basis of their geological usefulness, also helping to reveal fundamental issues in palaeobiology and enabling us to trace the phylogenetic details of their evolution. The fossilised tests of larger foraminifera are important rock-forming materials, and foram-limestones are extensively developed in both the Upper Palaeozoic and Cenozoic. Their remarkable abundance

and diversity is due to their ability to grow to a variety of sizes (the largest being up to 160 mm in diameter), to exploit a range of ecological niches, and to transform their shells into greenhouses for symbionts.

Study of the shape and structure of larger foraminifera is an essential tool for biostratigraphy, as their growth history is recorded and preserved as part of the test, and their paleobiological evolution is recorded and defines the geological column. Therefore, well defined palaeobiological lineages can be identified and traced throughout their history. They seem to follow Cope's (1896) Rule (the increase in size of organisms during their evolutionary history) of a trend towards complexity. Primitive forms persisted and survived harsh conditions and major extinction events, but also gave rise gradually to more complex, specialist forms that flourished in stable environments. Cope's Rule has been linked by many authors to 'K-selection' and hypermorphosis (Gould, 1977). The K-strategy mode of life usually occurs in stable environments as it requires delayed maturity, fewer offspring, and life where the asexual mode of reproduction is dominant, sexual maturity usually marking the termination of growth. This is certainly the case for larger foraminifera where sexual reproduction usually occurs just before death (BouDagher-Fadel, 2008).

The fact that a single-cell animal like the LBF can build a large and complicated test is often seen as surprising and challenging. But the fact that they do is of the greatest significance: their study gives unique insights into the understanding of a particular aspect of the history of life and provides many examples that epitomise key aspects of evolution. The most important problems facing those who study this group are relating the anatomy of the test to both molecular biology, and to behaviour in the fossil

record. Researchers have made many attempts to understand the palaeobiology of this group using the oxygen and carbon isotopic compositions of fossil shells (Purton and Brasier, 1999), and have made many inferences based on living assemblages (Saraswati *et al.*, 2003).

During the evolutionary history of LBF, a major increase in size made some forms highly specialised and vulnerable to rapid ecological changes. For this reason, LBF show a tendency to suffer periodic major extinctions. They also have many morphological features that show convergent evolutionary trends. These convergent trends of developing the same characteristics at different times reflect the fact that certain shapes and sizes are optimally suited for the effective exploitation of specific niches. Identical shapes or structures appear again and again within the same lineage, or in parallel lineages from different stocks. An example of such convergence is the fusiform test, which appeared at different times in different lineages (BouDagher-Fadel, 2008). It seems that this morphological evolution occurs as the foraminifera occupied specific environmental or ecological niches, such as reef, backreef or forereef environments (see BouDagher-Fadel, 2008).

Genes, of course, are the fundamental units of life, and determine the genotypical properties of any lifeform. However, environment, ontogeny and the conditions of growth determine the phenotypical character of a species, defining, for example, the individual shape of the test. The interaction between the gene in the embryont and the selection of the external features that the foraminifera develop during growth is an example of this selection process discussed by Gould (2002) in his book *The Structure of Evolutionary Theory*. This process acts on feat-

ures that emerge from complex gene interaction during ontogeny and not from individual genes, and despite the variety of genetic components, certain ecological conditions will favour certain morphological developments.

Many characters in the evolution of foraminifera are gradual and linked to the timing of phases in growth. They could have been started by DNA mutation at one stage of foraminiferal life, and amplified as a consequence of those selection processes related to stress and life in adverse environments. Since Carboniferous times, changes in local or global conditions have caused the highly specialised forms of LBF to go extinct, only for other LBF forms to evolve and fill the vacated niches. The disappearance and reappearance of LBF taxa through geological time illustrates the converging trends highlighted so clearly by Conway Morris (2003). LBF are, therefore, good examples of the creative powers of gene mutation and gene interaction, and can provide case studies for the important role of both genotypical and phenotypical processes.

Through my research and industrial work, I found that it is important to understand the environment of deposition of any carbonate sequence so as to predict the presence, quality and thickness of reservoir, seal and source rocks. LBF associations, along with light-sensitive calcareous algae, are useful as depth and age indicators. Their palaeobiology can be used as an indicator of the locus of facies evolution, palaeogeography and palaeotemperature.

3. *How could continuation or an expansion of your research programme lead to new insights or open new questions in palaeobiology?*

Larger foraminifera thrive in many environments, and their delayed reproductive strategy leads to a long life span, perhaps reaching a hundred years in some large *Nummulites*. This combination of a long lifespan and abundance in the geological record makes them a most valuable tool for biostratigraphy in shallow-water environments. Furthermore, their possession of test features that are under continual evolution makes larger foraminifera useful in the study of the genetic and morphological basis of evolution.

One important future development would be to combine studies of living forms with the valuable and rich fossil record in order to understand the relationship between genetic characteristics and morphology. Work on the origin of the foraminifera and on phylogenetic analysis of verified foraminiferal DNA sequences are already underway (Wray *et al.*, 1995; Holzmann *et al.*, 2003). Genetic analyses are essential to understand phylogenetic relationships among LBF genera and species. They will help to establish whether the characteristics developed by different forms are analogous (i.e. they have the same appearance, but a different origin or function) or homologous (i.e. they have the same origin). The tendency towards evolutionary convergence is something which requires deeper analysis. Culture experiments under controlled environmental conditions such as temperature, salinity, dissolved oxygen content, nutrient content, trace element concentration and isotopic enrichment (building upon the pioneering work of Röttger) should be encouraged in order to better interpret natural ecological behaviour and environmental tolerances. The driving

mechanisms behind LBF evolution have been controlled by changes in palaeoenvironments on a whole range of time scales ranging from those driven by tectonics, through those associated with climate change, and finally to those affected by catastrophic volcanic or impact processes. Controlled experiments on, for example, the tolerance of different forms to water depth could enable estimates of such physical variables as subsidence rates to be made. Finally, it is widely held these days that human activity is destroying coral reefs worldwide. As highlighted by Hallock (2005), more research on the biology of living foraminifera will give us a greater understanding of contemporary reef ecologies and will help us to understand how reef-dwelling fauna respond to changes to environmental parameters caused, for example, by climate change and/or other human generated processes.

Expanding my research about the mode of life, evolutionary trends and the migratory habits of Neogene and living species will give new insights on the palaeobiology of extinct species. The LBF are certainly highly versatile, biologically adaptive and flexible, and so make a challenging and extremely rewarding subject for research. The process of cryptic speciation as compared to the processes that underpin Darwin-Wallace evolution, namely, that genetic divergence and eventual speciation is driven when communities become isolated, colonise different niches, or adopt different strategies for survival, has been exemplified par excellence by these foraminifera as they evolved over geological time to produce the wide diversity of species seen today and in the fossil record.

4. What do you see as the most interesting criticism against your position in discussions about palaeobiology and evolution?

As a micropalaeontologist, I combine a morphological approach to taxa with a phylogenetic interpretation of the fossil record to define the biostratigraphic and environmental significance of foraminifera. However, such fossil-based studies may miss some of the true complexity of the modes of life that the foraminifera exploited when extant. Biologists who work on recent species are now relying on molecular biology to investigate species diversification to help constrain the phylogenetic evolution of recent forms. When studying fossil forms, however, genetic data are not available and only information drawn from test morphology can be used to investigate phylogenetic relationships. In order to solve this problem, we must practice morphologically based studies to describe the foraminiferal species and compare it to the developing genetic understanding of extant species that has been described in the literature. This can be criticised and disputed by those who would like more concrete information such as that provided by molecular biology. However, for the time being more molecular data, covering all known species, are needed to resolve the many issues that remain outstanding. Only then will it be possible to combine the insights from genetics with morphological and fossil data to provide a complete (or as complete as will ever be possible) understanding of the palaeobiological and evolutionary diversification of foraminifera over geological time.

5. Why were you initially drawn to research in palaeobiology?

When young I was always interested in understanding how living creatures ‘worked’, and as a result I wanted to be a doctor and study human biology. Unfortunately, the day I drove to sit the medicine exam, bodies were littering the roads of Beirut; this day, termed ‘Black Saturday’, heralded the start of the Lebanese Civil War. I was unable to attend that examination, and my opportunity to enter the medical profession was shattered by the subsequent break-down of Lebanese society. However, I decided to persevere with study and during the war I obtained a first class degree in biology. I was fortunate to be offered a scholarship that enabled me to travel to England to further my studies. However, in order to thwart the militias who wanted to get their hands on the scholarship, I found myself having to choose to study geology. I decided a micropalaeontology course would be the best way of combining my biological degree with ‘geology’, and so I studied at UCL, first to obtain an MSc and then a PhD.

Micropalaeontology turned out to be an excellent choice as it gave me many insights into the complexity of life, even at the unicellular level. I was fascinated by the physiology of the LBF and their ability to evolve rapidly and fill a range of ecological niches. They build beautiful large tests and seem to be genetically disposed to reproduce many generations by both sexual and asexual modes, thus maintaining the same genes or combining different genes to gradually change the appearance of the species. LBF are biologically complex and highly versatile and their study provided me with an excellent insight into palaeoecology and palaeobiology. It is certainly the case that the ecological sensitivity, or vulnerability, of the LBF

(coupled with the ability of smaller primitive forms to survive and then evolve to repopulate the niches that were left vacant) means that LBF are very good tools for studying global extinction processes. They are very abundant in the fossil record, both robust (having survived in one form or another since the Carboniferous), but also sometimes highly specialised and therefore highly sensitive to their environment. Their study provides, as a result, considerable insight into evolutionary process as well as into the major geological mechanisms associated with extinction and recovery. LBF also have and continue to occupy the very important ecological niche of being a reef-forming group. The worldwide distribution of carbonate biota, especially reef biota, contains important information on the various environmental factors, including oceanographic parameters, that control this most sensitive of habitats. The study of the distribution patterns of this niche, over different time slices, provides valuable information on how the climate of the Earth has evolved in the past 350 million years.

Thus, by chance, I stumbled across a fascinating subject which has provided me with a stimulating and fulfilling scientific career, some of which I have captured in two recent books (BouDagher-Fadel, 2008, 2013).

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Palaeobiology, broadly understood, has grown to be the dominant approach to the study of ancient life. Palaeobiology encompasses a much broader range of topics than classic palaeontology, but in doing so has thrown up challenges to the manner in which palaeontologists are trained, the research topics they consider important, the types of roles they fill in academic, commercial, governmental/regulatory, and scientific communities and the manner in which they relate to their biological and earth science colleagues.

Without question palaeobiology influences some of the most significant developments in fields such as ecology, geology, oceanography, evo-devo and evolutionary biology. But this comes at a price in terms of shifts in the intellectual focus of the study of fossils, including the relative importance accorded to subjects such as biostratigraphy, systematics, and taxonomy. Moreover, the practice of palaeobiology differs between countries, reflecting differences in needs, opportunities, and levels of resources.

What is palaeobiology? Where is it going? How does it relate to classic palaeontology? What motivates people to become palaeobiologists? Twenty-two experts with diverse geographical and thematic back-grounds discuss their personal views on fundamental questions on the goals and issues in palaeobiology. This collection of interviews and additional essays illustrate the diversity of approaches, interests, personalities, backgrounds, and predictions for the future of this intellectually rich discipline.

Interviews with:

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