Issues in Palaeobiology: a Global View

Interviews and Essays

Scidinge Hall

edited by
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Sánchez-Villagra, M.R. & MacLeod, N. (Eds.). Issues in Palaeobiology: A Global View.
Interviews and Essays. Scidinge Hall Verlag Zürich 2014. ISBN: 978-3-905923-17-9

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20. Sergio F. Vizcaíno *

1. What are the most important problems in palaeobiology?

This first question is probably the most difficult to answer and I wouldn't attempt a reply without first providing further context. I do not feel that a single scientist in palaeobiology, or any other branch of science, can generate a list of issues that can be regarded as *the* most important problems confronting the field without also considering the relationship between current paradigms and tendencies *and* the scientist's perspectives and interests. The better the fit between the last two and the first two, the more reasonable and promising the responses may sound; when the fit is not as tight, then responses will require bolstering from additional argumentation to render them credible.

From the next three questions, it seems to me the editors assume evolution as a core idea not under threat of falsification, placing our responses under a Lakatosian perspective. I do not want to (and cannot) make this a deep discussion on the philosophy of palaeobiology, although I have to confess that I'm perfectly fine with this perspective. In any case, I think that, in leading off with this question, the editor's main aim is to identify the most widespread 'programme' (and here I use the typical British spelling, which also aligns well with its Lakatosian sense, in contrast to the more familiar usage in science of research program) that drives current palaeobiological research, so that we might be in a better position to judge

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whether to stick with it or whether we have reached a point where it is more reasonable to switch to a different programme; though I should add, incidentally, that I am unaware that such a programme for palaeobiology has ever been explicitly identified in the literature.

I think that the broadest problems that palaeobiologists face as a community concern the identification of past biodiversity when it comes to organisms that had different ways of life from modern ones. That is, the problem comes from determining the nature of the interactions of the different organisms among themselves, and with their environments; also in how these interactions have changed through time, and what our results might mean as goes the future of life on Earth.

While this may appear to be an overly generalised statement, it hints strongly, though subtly, at the intellectual challenges that have to be overcome in our attempts to reconstruct the palaeobiology of many of the organisms that are the subject of our research: there have been many possible modes of life. Before exploring this, it's worth identifying the main or core theoretical assumptions of palaeobiological research using a few simple examples, mainly from my experience of vertebrate palaeobiology using a form-function correlation approach. Uniformitarianism (or actualism, the idea that materials, conditions and rates of processes have remained relatively constant over time) and analogy (the application of features of modern to ancient organisms) play important roles in palaeobiological interpretation. We certainly can, and should, use them as a guide to the past, but only when we can be reasonably sure that the extinct forms are very similar morphologically, physiologically, and phylogenetically to the extant forms with which we compare them. However, many, if not most, extinct organisms are very different from their closest relatives - among South American Cenozoic mammals, for example, think of fossil sloths as compared to living tree sloths, or glyptodonts compared to armadillos - and in some cases their general morphology is no longer readily represented today - the Burgess Shale fauna springs immediately to mind in this regard. In such cases, these organisms are said to have no modern analogues and, in our efforts to interpret their paleobiology, we cannot rely on a straightforward actualistic reference to the biology of their closest relatives. In such instances, if the use of modern forms is not properly contextualised, our efforts produce highly unsatisfactory or puzzling reconstructions. It is clear, through research done over the past several decades, that non-avian dinosaurs were decidedly not like crocodiles and lizards, and neither did they, as a whole, closely resemble birds, their nearest living relatives. For many cases, then, an overly straightforward approach, relying only on actualism and modern analogs, produces either very predictable results (the jaw mechanisms of some extinct bears are very much like those of some modern bears) or nonsensical reconstructions - the use of a single allometric equation based on the transverse diameter of the femur would produce an estimate of 98 tons of body mass for the elephant-sized ground sloth *Megatherium*. It is the latter cases that merit particular attention. To view things otherwise would be - to paraphrase a common expression - condemning the past to be just like the present. But it is clear that this cannot be true. Our challenge then becomes one of generating innovative hypotheses that are based on more than just actualism and use of analogs, and this requires the use of other approaches. Such a course does not necessitate the refutation of actualism and analogs, but an extension of the palaeobiological research toolkit beyond them. Among the approaches that have the greatest potential promise as goes their relevance to palaeontology are the mechanical ones - those that address form-function relationships but are not necessarily based on already-known biological comparators - and extant analogs not closely related to the fossil. The extension of concepts and methodologies involves both theoretically progressive aspects, the formulation of hypotheses that allow further prediction, and intermittently empirically progressive aspects, observation that does confirm or corroborate new predictions; confirmation can, for example, include consistency with the principles of mechanics.

At this point I hope the editors would permit a short digression from their original question to address a related question: on which aspects would I like to see more palaeobiologists focus their efforts? The answer is, basically, on the reconstruction of biological traits that usually do not or never fossilise, such as soft tissues, physiology, reproduction, sensorial perception and behavior. For instance, the metabolic theory of ecology, or MTE, provides a framework on which it would be very interesting to build palaeoecological reconstructions. The MTE is essentially a modern extension of the Law of Kleiber, based on an interpretation of the relationship between body size, body temperature and metabolic rate for all organisms. The main implication of MTE is that the metabolic rate, and the influence of body size and temperature on metabolic rate, defines the fundamental limitations to ecological processes. If this is true from the individual level to the level of ecosystem processes, then many attributes of life history, population dynamics and ecosystem processes could be explained by the relationship between metabolic rate, body size and body temperature. According to MTE, organismal metabolism level restricts patterns of growth, reproduction and death: small organisms, with fast metabolisms have high feeding rates, exhibit rapid growth, accelerating senescence and early death such that natural selection promotes early breeding. At the ecosystem level, MTE explains the relationship between temperature and biomass. The average rate of biomass production is higher in small organisms than in large orgamisms, which in turn is regulated by temperature. The use of body size data in palaeobiology has increased considerably in recent years and studies of functional morphology and biomechanics frequently employ measures to be correlated with size before functional interpretations are applied to fossils. Therefore, a primary goal for the near future may be to find a way to estimate body temperature and metabolic rate in fossil animals.

Issues like this may imply the development of new techniques and devices, the availability of which - given the meteoric rate at which technology evolves - seems likely for the next generation. However, as my colleague Marta Fernández notes, the evolution of technology outpaces our ability to generate the epistemological frameworks in which the new available palaeobiological information might be understood, thus creating a major problem for palaeobiologists.

Another major problem may be, as suggested above, how we apply what we learn from the past to preserve the future of life on Earth. We have the chance to work with the consequences of global climatic changes at timescales unimaginable to most biologists. Certainly, there are lessons from the past that palaeobiologists have to learn, and I think it is our obligation to pass on our knowledge to colleagues that are in positions to affect policy and make decisions as goes life on Earth.

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

The main approach to palaeobiology of our research group involves the application of the principle of form-function correlation - that, due to a close relationship between form and function, the latter can be predicted from the former - to South American fossil vertebrates, mainly mammals. Beginning with an understanding of the biological design of the animals, we interpret their role in successive geological past ecosystems: this provides crucial information in understanding their evolution, and consequently that of the corresponding palaeoenvironments.

In carrying out our research, we've adopted a protocol that involves the identification of three biological features that are essential for each taxon: body size, diet, and substrate preference and use, including mode of locomotion. Certainly, we frame our definition of design within the context of biological evolution, with the understanding that organisms reflect a duality between adaptation to environmental demands and inherited tendency to remain constant. That is, the morphology of an organism is restricted or moderated by their evolutionary history and is not structured or designed specifically and solely for their habitat. Thus, the phylogeny represents a variable that potentially introduces confusion in the inference of patterns from functional morphology; detailed and critical knowledge is essential for comprehending and 'calibrating' a 'functional morphological signal'. One way to exclude the effects of phylogeny on our analysis is to identify anatomical features that covary with the habit in unrelated lineages. However, when the structures and functions are unique to or autapomorphic of a fossil organism, the phylogenetic framework may not provide palaeobiologically useful information.

We've found that the genus, rather than species, is usually the most useful working taxonomic unit as an object of study. There are several reasons for this. One is that genera are discrete taxonomic units often accepted with little or no debate by most palaeontologists. Another is that palaeobiologic approaches based on morphology are usually not sufficiently sensitive for discriminating among congeneric species when based on a few traits from a restricted part of the skeleton, and intraspecific variation of South American fossil species has not been properly evaluated. At least for fossil vertebrates, in South America, there is a strong typological heritage with roots in the late 19th century seminal work of the Argentine palaeontologist Florentino Ameghino. I distinguish typological from morphological species by recognising that the former may be based on any minor morphological difference; while, for the latter, there should be at least a minimal attempt to correlate the degree of variation with that of accepted biological species. Typological species are virtually useless for palaeobiological studies, but the same point may also be made for other approaches traditionally linked with an evolutionary view, such as phylogeny, distribution and biostratigraphy. This suggests that we need to continue in producing taxonomic revisions that are based on a more 'modern' style of biological thinking.

With these issues constituting our main conceptual core, we edited a volume on the palaeobiology of a high-latitude Early Miocene (Santacrucian Age) continental fauna palaeocommunity of Patagonia during the Middle Miocene Climatic Optimum between 20 and 15 million years ago. The volume represents the best example of our research programme. The Santacrucian is particularly important for understanding a phase in the history of South

American mammals in which the communities consisted of a complex mixture of descendants of ancient lineages and new taxa (primates and rodents) from other landmasses (probably Africa). We've been presented with a precious opportunity for a profound and comprehensive understanding of the palaeobiology and palaeoecology of the region. While reconstructing the palaeoenvironment, we kept in mind that we were examining an interval of time in which the environments must have fluctuated. We therefore selected a series of localities that represent a sufficiently restricted time interval and which yield well-preserved plant and vertebrate specimens; the aim being to develop a palaeosynecological analysis. We have thus established the Santacrucian as a new model that can be applied, in addition of course to extant ones (be they savannas, forests, and so on), to the study of faunas older than the Santacrucian. Two particularly useful aspects of our model are that it is closer phylogenetically, morphologically and in time to members of older faunas. I recognise that this approach, with fossil forms acting as analogues for other fossils belonging to lineages with distant or without living representatives, as an interesting methodological tool for the study of evolutionary palaeobiology.

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

After a long learning process, we now have a clearer framework in which to study the palaeobiology of South American Cenozoic biotas, with an emphasis on the dominating mammalian faunas. In the case of the Santacrucian, we will, in the near future, be expanding our approach to a more complete geographic and chronologic range of the Santa Cruz Formation. In doing so, we will not need to repeat the palaeoautoecological analysis for each taxon, except as warranted by new material, by new taxa, or when novel approaches present themselves. We will, instead, record the different assemblages at different levels and evaluate the ecological changes that occurred during the time of deposition of the formation in different areas. We've also worked on other mammalian faunas (especially the more complete ones that exist for the Pleistocene), and on birds as well as on other vertebrates that lack clear living analogues, like dinosaurs and aetosaurs. All of this opens a gate to the development of multiple new lines of research on the palaeobiology of South American fossil vertebrates. In all of these cases, although we might be equipped with robust phylogenetic scenarios, we should not lose sight of the fact that we do not fully understand all biological rules, nor that evolution has produced many forms that at first sight cannot be completely explained solely by comparison with extant analogues.

Our form-function approach in vertebrates has been largely limited to the functional implications of skeletal and dental morphology, and their consequences on the biological role that the organisms play in their palaeoecosystems. There is, however, much additional information that could explain the coexistence of forms that supposedly occupy the same niche in a past ecosystem. For instance, the size of the orbit has often been used as an indication of diurnal vs nocturnal habits in primates, but it has hardly been applied to other forms.

As suggested above, in the relatively short term it would be crucial to find a practical way to estimate basal metabolism for a more complete evaluation of past ecosystems. The big question is whether - with precise insights on the evolution of past ecosystems - we can distinguish those processes affecting present ecosystems at geological scales from those produced as consequences of human activities.

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

One of the things I find of considerable interest in many discussions about my work is that often my critics seem to believe that I am convinced that I have fully demonstrated something. I may be wrong, but usually my interpretation of this is that she/he is convinced that her/his position is 'truth' rather than a personal understanding of reality that is based on certain lines of evidence and analysed with some specific methodology, and that corresponds to a particular conceptual approach. Surprising as this may sound, we palaeontologists, as well as many other scientists, are often not as objective about our work as we think we are. A frequent example of this is when colleagues that work mostly on phylogeny criticise my morpho-functional or biomechanical interpretations because they consider that they should not be considered adaptations but a result of a phylogenetic heritage. To me, this criticism deserves at least two replies. One is that when I'm trying to produce a sound hypothesis on the habits of an organism and its role in a past ecosystem based on a form-function approach, what matters to me is the biological consequences of a certain feature or system, independent of the organism's history. That's why I deliberately avoid the use of the term adaptation (roughly understood as an apomorphy promoted by natural selection). Another reply is that any cladogram onto which one could map the character to evaluate whether it qualifies as an adaptation is a hypothesis of the relationships among organisms, not the real phylogeny just as my proposal is a hypothesis, not an observation of the behavior.

There are other facts to consider. When the structures and functions are unique or autapomorphic, phylogeny would not be very informative about its biological meaning. In many cases, homologous structures in closely related taxa have different functions, so the more distantly related taxa are, the more likely it is that the relationship between homology and function breaks down. Finally, if a lineage develops a phenotype adapted to a particular environmental condition, it should not necessarily be identical to current models, so no phylogenetic approaches are required.

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

I discovered my preference for palaeobiology in my fifth year of biology at the Universidad de La Plata. Earlier, I had thought that I was destined for a career in marine biology, and by my fourth year I had taken courses in oceanography and marine biology and had even got a diver's license. However, things started to change that year. I had my epiphany, we might say, in the comparative anatomy halls of the Museo de La Plata. I had visited these exhibits often as a child, but in this particular year, following my comparative vertebrate anatomy labs and while studying for the exam in this course, I began to see them in a completely different way. In my last year I was delighted with the vertebrate palaeozoology course offered by Professor Pedro Bondesio, who - in a style very similar to that of Edwin H. Colbert - linked the anatomy of dinosaurs and other vertebrates with much of the biological information that I had learned the previous four years. I then decided that I wanted to do a doctoral dissertation on what I called 'functional anatomy' of an endemic group of South American mammals. It seems my enthusiasm convinced Dr. Gustavo Scillato-Yané and Dr. Eduardo Tonni to advise me in a project on xenarthrans. However, despite my efforts and their open-mindedness and goodwill, it did not really work out as planned, and after my dissertation I became a more traditional palaeontologist for a few years. But in 1993 everything changed for me when I met Richard Fariña, from Uruguay, who was presenting his challenging hypothesis on the bipedality of glyptodonts in an 'orthodox' meeting of vertebrate palaeontology in Argentina. Richard was then an advanced PhD student of Professor McNeill Alexander and was applying a biomechanical approach to the palaeobiology of the South American Pleistocene megafauna. I have to confess that I did not then understand the procedure behind his proposal, but I somehow became convinced that it was what I needed in order to explain several aspects on the mechanics of some armadillos that I had tried to deal with in my dissertation. It was then that I really started working in palaeobiology and began one of the most significant collaborations in my career. Much of what I learned after came from texts and papers, from the collaboration with different colleagues and students and, particularly, from the editors and reviewers of my articles. I had to learn a way of producing articles that were more in line with what is considered 'the' scientific method - the experimental method, essentially - although the general - and equally - scientific method in palaeobiology is the comparative method. It was in palaeobiology where I started to think that I could make a contribution to the understanding of the evolution of past biotas.

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 palaebiology. 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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Scidinge Hall

ISBN: 978-3-905923-17-9
11 £ / 14 € / 16 CHF / 18 US $