Issues in Palaeobiology: a Global View

Interviews and Essays

Scidinge Hall

edited by
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Marcelo R. Sánchez-Villagra

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1. What are the most important problems in palaeobiology?

Disciplines don’t naturally have a single focus and it is therefore hard for me to identify what I think are the most important problems in palaeobiology. Palaeobiology is the study of life through geological time, including the short lives of individual organisms and the great sweeping collective lives of clades. The fossil record provides the strongest direct evidence for when and where events involving organisms took place and what those organisms were like. ‘When’ and ‘where’ are key components of ‘how’ and ‘why’. Palaeobiology’s aim is to understand all facets of past life and, thus, the field’s most important challenge is to foster multifaceted approaches and parallel lines of investigation to achieve this understanding. Important problems remain to be addressed in all areas, including extinction, evolution, phylogeny, climate change, Earth systems, anatomy, functional morphology, development, taphonomy, biogeography, community ecology, and macroecology. Within these areas, the important problems to be addressed are both big and small.

However, there is a fundamental problem facing our field: namely, threats to its observational underpinnings. Regardless of the area of inquiry, palaeobiology ultimately depends on descriptive data - descriptions and illustrations of fossils, documentation of stratigraphy and taphonomy at individual sites, functional morphological inter-

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interpretations of individual taxa, taxonomic revision of poorly synthesised groups. When these are lacking or faulty, the large-scale analysis of regional and global patterns and processes is hampered. For example, we now know from Greenland ice cores that climate in the northern hemisphere has vacillated radically on millennial scales over the last quarter million years. This observation has raised the urgent question to what extent these sharp, sudden fluctuations in climate had an impact on organisms and ecosystems. The palaeobiological answer to this question has been almost intractable because its millenial scale is smaller than the resolution of existing stratigraphic, morphologic, and taxonomic data from the Quaternary. Basic re-evaluation of faunas and redeterminations of ages from thousands of sites and hundreds of thousands of fossils are needed to measure the organismal patterns that might be associated with these important climatic events.

One of the biggest challenges in palaeobiology is, therefore, maintaining the pace of base descriptive work. This work is time consuming and offers few professional rewards other than personal satisfaction. Indeed, descriptive papers are becoming increasingly difficult even to publish because of demands for ‘high impact’ work and are often relegated to comparatively obscure periodicals. The availability of large databases of occurrences, scans, or morphological datasets have not, by any means, replaced descriptive work because they are venues for disseminating already published data, not venues for presenting new data.

Descriptive work yields important rewards, however. Detailed reevaluation of Late Pleistocene sites in northwestern Europe, for example, has given us the first hints of how the millennial scale events recorded in the Greenland ice cores impacted mammalian life. During
one such pulse, Saiga antelope, which live today in the deserts of Central Asia, expanded rapidly across Europe as far as western England and then retreated again. This pulse is only recognisable because of primary taxonomic reassessments of museum material and redating of previously excavated sites. Prior to this recent work, Saiga were simply considered a rare but general component of Late Pleistocene European faunas. Their rarity has now been revealed to be due to the very short time they inhabited the western part of the continent, even though they may have been common during their climate-mediated pulse of expansion. Indeed, several Saiga specimens were found in existing collections misidentified as sheep due to a lack of concerted alpha taxonomic work in the past. The pulse of Saiga is now revealed to have been of very short duration thanks to new methods of dating and chronological refinements of sites that were collected in the 19th and 20th centuries.

Thus, if I were to point to an important problem in palaeobiology, I would point to the threat to our field’s continued ability to conduct primary observational research, not to a particular research problem. The skills and knowledge base needed to make primary taxonomic identifications or to recognise and usefully describe new fossil species have been significantly eroded over the period of my career. The erosion is due to several trends. One is the expansion of our field to institutions that do not have research collections or active field programs that allow students to learn from intimate exposure to the variety of form within and among fossil species. Providing my own students with this kind of primary learning is difficult because I am working at an institution that does not have an adequate vertebrate palaeontology research collection and because my own research programme is
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not strongly field-based. Another trend is the growing preference for ‘high impact’ publications as measures used in academic hiring and promotion. Descriptive work is slow and it is seldom ‘high impact’ in the way that those words imply. The impact of descriptive work is slow but profound. Citations to descriptive papers accumulate slowly, but continually and over long periods of time. Good descriptive work remains relevant even after centuries because it is frequently necessary to go back to original descriptions to reevaluate taxonomic identifications, to code characters, and to make new observations in light of new questions that were not considered by the original author. A third trend is that palaeontology journals themselves are less likely to publish descriptive work than they once were. The academic publishing world has been transformed by pressures introduced by commercialisation, outsourcing, and business finance, as well as by the practices of palaeontologists themselves.

Presses now actively pursue papers that will be broadly interesting and thus increase (or at least sustain) income for the press. Monograph series published by universities and museums have been discontinued because of their imbalance between their cost and the income they generate. Researchers often choose to prioritise non-descriptive work in interdisciplinary journals because if they don’t their careers will not advance. The feedbacks between these factors have escalated the decline of descriptive research as well as the monographic venues in which it can be published. Electronic publication, which has the potential to solve this problem by offering low-cost methods for publishing lengthy, richly illustrated work, has so far failed to deliver a solution because commercial presses, which increasingly publish academic research, need to deliver large returns to shareholders and
so they demand saleable content, and descriptive work is seldom viewed as saleable. If the descriptive phase of our field were anywhere near complete, this issue might not be crippling. But the continued pace of discovery suggests that the decline of descriptive paleontology is an important threat.

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

My work addresses the processes that link morphological evolution, phylogenetic diversification, and community sorting over space and time. Many fossilisable traits, especially the teeth and bones that I work with, have functional properties that are linked to the organism’s way of life. The traits may or may not be ‘adaptive’, as in the caricatured ‘adaptationist paradigm’, but they most certainly constrain the range of function of the organism, and therefore the range of environments in which it is likely to flourish. Traits thus have the potential to influence geographic sorting, which in turn influences community composition. As environments change over time and over space, organisms are likely to be sorted - in a probabilistic sense - by their traits. Traits also evolve. They adapt to changing environments and they are shared by closely related taxa because of phylogenetic history. The origin and evolution of traits is fundamentally a historical process involving populations, species lineages, and clades, not communities. Because the functional properties of traits influence where animals live with respect to one another, they influence community structure, and because species interactions influence the evolution of traits, the community structure influences the
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evolution of trait function. These interactions are not only interesting, but they are poorly studied because they occur at the intersection of the subfields of macroecology, phylogenetics, and functional morphology. My work attempts to bridge these fields to better understand the interactions between evolutionary, functional, and ecological processes on continental scales over time periods of millions or tens of millions of years.

More specifically, my research tackles the problems of quantification needed to address these questions. My research involves the relationship between morphology and developmental, evolutionary, or ecological processes measured on widely varying timescales, none of which is easy to quantify. However, if one wants to ask how the processes acting on one scale (such as divergence between two local populations of a species or anthropogenic changes to the environment) compare to how they unfold at a different scale (such as the rate of evolution through a stratigraphic sequence that is millions of years long, or the rate of community reorganisation during the global temperature spike at the Paleocene-Eocene boundary), one must be able to measure morphology at both scales, relate that morphology to the processes at both scales, and then make direct quantitative comparisons between the scales, despite the sometimes profound differences in granularity and sampling. Much of my research effort has been spent trying to improve the ways in which we can quantitatively make comparisons between morphological datasets collected from the modern world and the palaeontological past.

I have focused on three areas. My first area of focus has been measuring divergence in the morphology of bones and teeth relative to divergence in genetic and molecular markers. Can population-scale divergences be detected in
fossilisable traits of the dentition and skeleton? Or does morphology evolve too slowly to measure these kinds of processes? These questions are fundamental to understanding the limits of morphology and palaeontology. My second area of focus has been modelling the evolution of morphology over geological timescales using population-level processes. If population-level processes can be measured in fossils, how do the rates at which these microevolutionary processes work compare to rates of evolution measured over geologically long periods of time in the fossil record? Some of this work focused on the modelling of how long-term directional selection, stabilising selection, or drift would look if they continued over millions of generations. Quantitative genetics long ago provided the statistical framework for making this leap with univariate characters like body size, but the morphologies of interest in the fossil record include shapes of the occlusal surfaces of teeth, articulations of joints, and structures of limbs. My work with Norman MacLeod on morphometric quantification of three-dimensional surface data was an attempt to push back the boundaries of morphological analysis. My work with Jason Head, Anjali Goswami, Aida Gomez, and Steve Le Comber has tried to push back the boundaries of how complex morphologies can be better analysed to study development, evolution, alpha taxonomy, and climate-organism relationships. My third area of focus has been geographic analysis of climates, environments, and organisms. My work with Michelle Lawing, Jussi Eronen, Jason Head, and Mikael Fortelius has tried to meld approaches from species distribution modelling, functional morphology, and palaeobiogeography to study processes that link species distributions, environmental change, and community composition.
3. How could continuation or an expansion of your research programme lead to new insights or open new questions in palaeobiology?

I hope that my research programme will inspire new questions about the processes that are shared by evolutionary morphology, phylogeny, and macroecology. Each of these fields focuses on questions of its own; I try to ask new questions that fall between or connect them.

I also hope that my research programme will result in improved understanding of the tradeoffs between evolutionary and geographic responses of organisms to changing environments, the rates at which they respond, the effects of the responses on communities, and the likelihood that organisms cannot respond and thus become extinct. This knowledge is interesting in its own right, but it is also relevant to assessing the ecological risks of 21st century climatic and environmental change. The geological record documents environmental transitions large and small. Those events can be used to measure the processes of biotic response, data that can be used to estimate the probabilities and rates of community reorganisation, extinction, speciation, and phenotypic evolution. The scientific uncertainties about the near-future impact of anthropogenic change have made understanding these processes an urgent issue.

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

An unresolved question that has direct implications for my research is whether mathematical transformations of morphology can be used to model developmental and evolutionary transformations. My approach to morpholo-
tical analysis is grounded in standard morphometric practices, namely the use of multivariate morphospaces in which all possible combinations of morphometric variables (that is, all morphologies) have an ordered place. Morphospaces are constructed from variables used to measure morphologies and the mathematical distances between them. A straight line through morphospace corresponds to the shortest distance between morphologies. The ordering of morphologies in morphospace is thus based on mathematical ordering of the numbers used to quantify them. Morphospaces figure importantly in all aspects of quantitative morphology, from estimating a population mean (which is the mathematical center of a group in a morphospace), to testing for differences in mean (which involves the distributions of two groups around their means in a morphospace), to mapping morphology onto a phylogenetic tree (which involves estimating ancestral morphologies in a morphospace and drawing linear evolutionary trajectories between ancestor-descendant pairs of taxa). With simple morphologies that can be summarised with one or two variables - like body mass or molar area - there is no obvious problem with these transformations. However, the problems become more obvious with highly complex morphologies, which are increasingly difficult to quantify.

Take, for example, the morphologies of two hypothetical species of antelope, one with horns on the snout, the other with horns on the braincase. Skulls of these animals can be quantified morphometrically and ordinated in morphospace. Imagine that an ordination of these species places one species on the left and another on the right. If we are interested in the evolution of this group, we might reconstruct its ancestral morphology and measure the rates of evolution in the two lineages. In this
simple, two-taxon example, the most likely ancestral morphology lies equidistant between the two species. Mathematically, the midpoint at which this reconstructed ancestor lies in morphospace corresponds to an antelope with four short horns, two on the nose and two on the braincase. The evolutionary transformations reconstructed within the morphospace will therefore involve lengthening of fore-horns and shortening of hind-horns in one taxon and the reverse in the other. However, there is no strong biological reason to expect this to be the true pattern of ancestor-descendant transformation. It is equally easy to imagine that the ancestor had long horns placed midway between the nose and braincase, or that it had one set of horns that was first lost before the other was gained.

The biologically shortest path (in other words, the transformation that is most easily accomplished in evolution) thus may not be the mathematically shortest path through morphospace. Indeed, in the antelope example, we might have biological knowledge from development that a single species cannot possibly have two sets of horns at once.

If so, then mathematical morphospaces may be fundamentally flawed because the paths through them may not be the paths that are followed by developmental and evolutionary processes.

Salazar-Ciudad and colleagues have shown using computerised models of tooth development that evolutionary transformations in tooth morphology are likely to involve discontinuous jumps through morphospace. They showed that linear changes in gene expression within developing teeth can result in discontinuous transformations in morphology because of the dynamic interactions between cell proliferation, growth, folding, and between-tissue interactions. Thus, the shortest path
through ‘genospace’ is not the shortest path through morphospace, and vice versa. This issue is more than just esoteric; it has profound implications for all studies of quantitative morphology, from allometry, to Raup’s shell coiling space, to geometric morphometrics.

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

I have always been interested in how things came to be. As a child I was interested in dinosaurs and ancient Egypt. As a teenager my historical interests took me deeper and deeper into the roots of the music I listened to: 80s, 70s, 60s, 50s, 40s, and finally to 30s. As an undergraduate my intellectual history followed the same trajectory. I started off studying 19th century history, then moved into folklore, which I saw as a kind of older history, then into anthropology, and then even further back into palaeontology, geology, and evolutionary biology. I didn’t recognise the pattern then, but I do now. But my interest in how things came to be was one of the things that led me into palaeontology.

I have also always been interested in animals and the natural world. My favorite things to do as a child, and even as an adult, were to spend time outdoors, visit zoos and museums, and take care of pets and other domestic animals. I spent hours every week walking over the central Missouri terrain, examining rocks, looking at plants and animals, and mapping topography. Interestingly, those pursuits did not take me directly into biology or geology. Indeed, it was not until halfway through my undergraduate degree that I even considered those fields. Similarly, I didn’t recognise the pattern then, but I do now. My general interest in the natural world is one of the things that led me into palaeobiology.
Finally, I have had a long interest in geometry, computers, and programming. I got my first computer in 1980 when I was 12 years old, and I was first introduced to programming the year before that in an afternoon class at the Boonslick R-1 Vocational Technical School. A man whose name I cannot remember taught a small group of us to write simple programs in the Basic computer language on Apple II computers: for a = 1 to 10; print “Hello!”; next a. That man was probably one of the two most influential teachers that I ever had. Nearly everything I do now, including everything that is mathematical, relies on computation and his class was the only formal training I ever had in programming. Indeed, I barely had a math class after I learned to program. I had always been abysmal at math and I absolutely hated it until then. I had nearly failed the third grade because I could not (or would not) memorise multiplication tables; to this day I am bad at doing simple math in my head, or even on paper. Nevertheless, I sailed through high school algebra, calculus, trigonometry, and physics because I could program functions in Basic and graph the results. Consequently, my understanding of mathematics is more visual than numerical. I have to be able to ‘see’ functions and transformations in my mind before I can address them with equations. This skill (or shortcoming) is both a strength and weakness of my current work in quantitative palaeobiology. Though I didn’t like math per se, I did well enough at it that I placed out of all my university math requirements. That suited me just fine at the time, but it was almost a disaster a few years later when I applied to graduate school where I was considered to have a serious math deficiency. And it wasn’t really until after getting my PhD that I became interested in quantitative approaches. Thus, for a third time, I didn’t recognise the pattern then,
but I do now. My interests in programing and higher math helped lead me into palaeobiology.

It was Timothy Rowe at the University of Texas who specifically got me interested in palaeobiology. I had first been exposed to organismal evolution in an undergraduate physical anthropology class taught by Chad Oliver. Oliver was great. He was an engaging lecturer who taught us about apes by brachiating across the front of the class. He was also a science fiction writer of the 50s generation whose plot device was intercultural first contacts between humans and extraterrestrial civilizations. Prior to his class, I had no knowledge of the fossil record from a scientific perspective. In a very genuine sense I was dumbfounded that there even were fossils, despite having collected Mississippian crinoids and brachiopods from the Burlington Formation while I was growing up. Wanting to know more, I registered for an introductory palaeontology course taught by a new member of the geology faculty, Timothy Rowe. It was in Rowe’s class that all of the interests I described above came together. We learned about the history of life, especially the vertebrate animals that I loved best. We learned about ancestors and the process of evolution. My career fate was sealed when Rowe introduced us to phylogenetics. It being a freshman-level class, he described the process of phylogeny reconstruction as, “You collect data from the fossils, you put it into the computer, and you get out a phylogeny”. Fatal words. Having been programing for more than six years at that point, I could not for the life of me imagine how data from a fossil could be computer-ised or how a program could calculate a phylogenetic tree. To learn more, I stalked Rowe in his office and extracted from him what amounted to a year’s worth of individual tutorials in phylogenetics, morphology, and evolution.
Perhaps it goes without saying that Rowe was the other most influential teacher in my career. In retrospect I estimate that he probably tutored me for about two hours each week, on top of our normal class meetings. He gave me a formative reading list: Niles Eldredge’s *Unfinished Synthesis*, Ed Wiley’s *Phylogenetics*, Al Romer’s *Vertebrate Paleontology*, D’Arcy Thompson’s *On Growth and Form*. Without question, Rowe taught me more about palaeobiology than any other single individual, though I have learned from many. At the end of the semester I asked Rowe if he would advise my undergraduate honours project on phylogeny reconstruction, which I wanted to learn to do myself. He unexpectedly asked me what group I wanted to work on, a question I hadn’t thought to consider in advance. Having grown up liking dogs, cats, and zoos, the words from Wizard of Oz zipped through my mind: “lions, and tigers, and bears, oh my!” My answer was something like, “Uh, I was thinking about Carnivora”. Less than a year later I was privileged to be admitted into the PhD program at Berkeley to work on the phylogeny of fossil carnivores, at which point I had irreversibly been drawn into research in palaeobiology.
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.

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