Book reviews

Just looking at fossils

A review by F. Boero

Evolutionary Patterns. Growth, Form and Tempo in the Fossil Record. J. B. Jackson, S. Lidgard, F. McKinney (Eds), 2001. University of Chicago Press, Chicago, 399 pp. US $30.00/UK £19.00, ISBN 0 226 38931 6.

The evolutionary arena is full of titles that cover 'patterns and processes' for any kind of phenomenon. The quest for generalization induces people to assume general processes from often limited knowledge of patterns. The great debate on human evolution based on fossils is one example of this pattern. There are groups of organisms, however, that have a rich fossil record. Piece by piece, fragment after fragment, scientists reconstruct complete patterns of morphological and (possibly) ecological change of groups like the Bryozoa, the favourite topic of Alan Cheetam, a great palaeontologist to whom this book is dedicated. I am a neontologist and my field of interest is Hydrozoa. There is very little in the fossil record with regard to animals of this group, so I do not have to know much about palaeontology. But I badly need to study the 'parallel' groups, like the Bryozoa, to understand my own.

And I was pleased to see that the first chapter of this book, by Leo Buss, is not on fossils at all but, instead, on colonial hydroids, showing that the fertilization in palaeontology and neontology is intense. The chapter on parts and integration, by Daniel McShea, is thought provoking. It starts from issues taught to freshers in biology (at least in Italy) such as that the complexity of a unicellular organism is higher than that of any cell of a multicellular organism. Slowly, the chapter takes shape, leading to the analysis of 'partness'. It is rare to see how the whole says much more than the single parts, and I do not want to spoil the pleasure of reading this chapter by explaining more. Beth Okamura, Jean-Georges Harmelin and Jeremy Jackson take us to marine caves, introducing distributional patterns linked to colony organization and to the way bryozoan zooids take up their food. It is a pity that Rupert Riedl, the founder of the study of marine caves, who published most of his observations and ideas in German, is left uncited. He has identified, for hydrozoans, some of the patterns identified here for bryozoans and this reinforces the ideas expressed in this excellent contribution.

Nancy Knowlton and Ann Budd deal with species recognition in corals. After the work of J. Veron, species boundaries are less and less clear-cut. Hybridization can lead to the merging of species that, then, can split again, leading to tangled (reticulate) phylogenies. The study of both fossil and recent corals is used as a test of Veron's ideas. The implications of the questions posed are fundamental to understanding how life evolved in the past and will probably evolve in the future.

John Pandolfi, Jeremy Jackson, and Jörn Geister deal with extinction and take two coral species as a paradigm for what might have been the patterns of extinction when man was not around to be blamed for any biotic change. They used a huge data set: this is the pattern of the title of the book. These data tell us that rarity is not a precondition for extinction (the two coral species considered were common and abundant in their golden period) and that, besides punctuated events of speciation, we also have to consider punctuated events of extinction. Extinction can be sudden, and almost unpredictable, hitting apparently healthy species. This is precious information for conservation biologists. Extinction, in its turn, allows character release in species that are phylogenetically related to those that are extinct, speeding up evolutionary change.

Ross Nehm presents a data set on Marginellid gastropods: pages and pages of careful discussion of phylogenetic patterns in this group of molluscs, with tiny shell drawings and lots of measurements. There is no easy route to knowledge. All this leads to the uncovering of parallel patterns of paedomorphic development, showing that a given body plan is a sort of constraint to evolution and even if those who share it are split into different lineages, they will probably evolve in the same way, if exposed to similar conditions. To explain this, it is stated that it is rather unlikely that the separate clades went through the same genetic change to produce very similar morphologies. The alternative explanation is that developmental channelling can lead to the same result from different genetic information! A fascinating hypothesis that should stimulate evolutionary biologists speculating about the value of contingency vs. constraint in determining evolutionary patterns.

The late Steven Gould contributes with a paper on speciation and punctuated equilibrium. The chapter is an appetizer for his ultimate book 'The Structure of Evolutionary Theory'.

Lee-Ann Hayek and Efstathia Bura tackle the taxon range problem with the techniques used by palaeontologists to establish the duration of taxa while looking

at their stratigraphic record: nothing is more pattern-generating than this, but the ways of disentangling the traces of bygone taxa are multifaceted and call for deep analysis. Mike Foote deals with the age distribution of living and extinct taxa, arguing that, as present biodiversity is very rich, extinction rates must have been lower than speciation rates, so that, in spite of several mass extinctions, the rate of diversity is steadily increasing. This is a gross simplification of Foote's message that, in fact, introduces several concepts, such as birth and death cohorts of taxa, and is accompanied by a rigorous mathematical approach with 14 pages of formulas in an appendix. Ann Budd and Kenneth Johnson discuss contrasting patterns in rare and abundant species during evolutionary turnover, using patterns of speciation and extinction of reef-building corals to show how species originate and become extinct. The species, however, is not a closed universe in this contribution (as it often is in genetically based studies), being inserted in the evolution of the environmental setting, with a key role for ecological disturbance over evolutionary time. An amazing seven-page table contains the species list including, for each species, the time range of occurrence in the fossil record, the ecological relevance (distinguishing core and satellite species), the geographical distribution, and the spatial distribution at a local scale.

Eckart Hakansson and Erik Thomsen give a meaning to bryozoan fragments, reconstructing the evidence of the importance of asexual reproduction in bryozoan lineages. Colonies, in fact, can 'lose pieces' that are real propagules playing a key role in species dispersal.

The last chapter, by Frank McKinney, Scott Ligard and Paul Taylor, is on macroevolutionary trends. One of the most convincing results of palaeontology is the enumeration of taxa through time, revealing changes in biodiversity composition. It is with such an approach that we have discovered mass extinctions in marine invertebrates (at a family level), and we have a measure of biodiversity trends. These data are based on lists that take into account the simple presence–absence of taxa. This approach is criticized, by using bryozoans as a tool. The conclusion is that family, genus or species lists are very important but that they are not sufficient, often providing contradictory information according to the chosen taxonomic accuracy. The relative abundances of taxa are proposed as equally important as simple presence–absence data. This result is also very relevant for modern ecologists, tempted by taxonomic sufficiency to avoid the need of knowing organisms in detail.

The book, overall, is a tangle of disparate approaches, does not provide definitive answers and, instead of providing solutions, most often poses further questions; furthermore, it is loaded with data that make it rather difficult to read (but that can be easily skipped). This last sentence could be read as a strong criticism but, instead, is praise for this fine book. Evolution is not a simple matter and requires multifaceted approaches: the accumulation of data often falsifies the generality of ideas that are tempting for their simplicity but that, after all, are not so general, being based on a restricted data set. One of my pet expressions is 'data are boring and ideas are interesting', but after reading this book, I have to admit that data have much to give, if one knows how to collect and interpret them. Palaeontologists do not see much of their objects of study, compared with what we neontologists can see of living organisms. This limit has forced them to look carefully for their organisms and to look at them with even greater care. What they can do by 'just looking' is amazing and well exemplified in this book.

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Looking for direction in bird ecology

A review by B. S. Tullberg

Evolutionary Ecology of Birds – Life Histories, Mating Systems and Extinction. By Peter M. Bennett and Ian P.F. Owens. Oxford University Press, 2002. £24.95. ISBN 0 19 851089 6.

How has our understanding of bird evolutionary ecology developed during the last 34 years? Using Lack's (1968) classic 'Ecological Adaptations for Breeding in Birds' as a point of departure and armed with a huge data set (p. 31) together with methods that correct for phylogenetic dependence, the aim of Bennett & Owens (2002) is to shed light on this question. The book is divided into four parts. The first part is an introduction to the phylogenetic methods used, mainly independent contrasts analyses, and to the specific bird phylogenies used in the analyses. The second part deals with the evolution of life-history characters – the relationship among various characters and the putative ecological variables that form them. The third part deals with sexually selected traits and the evolution of mating systems. The fourth part, finally, is about something that Lack did not dwell so much on, and is connected to the present and urgent topic of conservation biology, namely, extinction risk and species diversity. The chapters in each part usually start with a citation from Lack (1968) and end up with a comparison between his and the authors' present conclusions.

The book is loaded with results from comparative studies by Bennett, Owen and their co-workers – in fact, I was unable to find any table or figure based on studies by other researchers. Some of the presented work is from previously published articles, whereas much refers to unpublished manuscripts. Thus, one could say that this

book has given the authors an excellent opportunity to summarize their own work over many years. The question is – do they reach their goal of giving the reader a general picture of the state of the art of bird ecology? In my opinion the answer to this question is partly yes, partly no, and partly that it is difficult to evaluate.

First, one of the main benefits of the book is its structure and the fact that the authors do cover many of the ideas and hypotheses that have been of importance in bird ecology. Also, a feature that I particularly liked was the 'Further questions' chapter at the end of each part, listing areas and problems that few researchers have penetrated. Thus, if you want ideas about virgin territories in bird ecology, this could be the place to start.

My main criticism has to do with analytical tools used and with the possibility for the reader to evaluate the results presented. These points are highly connected.

One of the objects of the book, according to the authors themselves, is to present the great impact of phylogenetic thinking in comparative biology and to show how phylogenetic comparative methods can alter our understanding of bird ecology. The problem is that, whereas there are a number of ways to use phylogenetic information on character evolution, the authors have chosen, with few exceptions, one method, namely correlation based on independent contrasts. Because the assumptions of this method make it inapplicable to some type of data, data should be subjected to diagnostic tests (e.g. Garland *et al.*, 1992) before analysis. There is no indication that such tests have been carried out before the analyses presented in this book. Moreover, the authors have usually collapsed all branching patterns above family level, thereby loosing a lot of phylogenetic information. The reason given for this procedure is to focus interest on the broad patterns of evolution in the early radiation of bird (on the level of order and family), but it is unclear to me why this necessitates giving up information at other levels. Anyway, this is one of the reasons why a data set consisting of hundreds or thousands of data points may boil down to 20 or fewer contrasts (e.g. Table 5.2). This is a pity. I also need to add, that certain analyses are entirely based on taxonomic rank (the 'hierarchical approach'), and of course, this can hardly be regarded as a phylogenetic method at all.

Given the great emphasis on phylogenetic methods in comparative biology, it is disappointing that the book features no more than two phylogenies depicting a distribution of character states. This type of presentation facilitates an evaluation of the results – for instance in Figure 5.1 I can count to nine contrasts between an open and safe nesting habit whereas the analysis is based on 11 contrasts (Table 5.1). Maybe some branches are excluded from the figure? However, the point I want to make here is that this figure illustrates how the data could be used in a more interesting way than a pure correlation. It is true that for some types of data correlation by independent contrasts is the method *par preference* and could even be the only feasible one. However, in this case we have transitions between two nesting habits and we could easily employ a test to address directional questions of whether reproductive effort (the dependent variable) has increased, decreased or remained constant after various transitions between open and safe nest placement (see for example Lindenfors & Tullberg, 1998). Results from directional analyses have the potential to indicate the direction of causation where mere correlation indicates none. Something for future research.

Actually, some of the most interesting studies from the book were based on a more confined data set and used matched-pairs comparisons instead of correlation. Together with Melinda McNaught and Sonya Clegg the coloration of Australian species was used to investigate whether species isolation is an important force behind sexual signals. The data seem to be based on careful measures of several dimensions of coloration. Several predictions were tested, for instance that sympatric species should diverge more than allopatric ones, and predictions from species recognition hypothesis were compared with those from hypothesis related to the signalling environment (e.g. Endler, 1992). Although I will not reveal the results here and the final evaluation will await the publication of these studies I found their description in the book unusually transparent.

In summing up the pros and cons of this book – would I recommend it? For someone interested in an introduction to phylogenetic methods in ecology I would not. However, the answer is more positive for researchers interested in evolutionary ecology of birds. For them the book can serve as a source of inspiration for future studies, especially studies that set out to check its results and improve its analyses. My feeling is that it could serve this function for some years to come.

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Missing the boat

A review by Roderic D. M. Page

The Nature of Diversity: An Evolutionary Voyage of Discovery. By Daniel R. Brooks and Deborah A. McLennan. University of Chicago Press, 2002. Cloth $85.00 ISBN 0-226-07589-3; paper $35.00 ISBN0-226-07590-7, 668 pp.

This book is a greatly enlarged descendant of 'Phylogeny, Ecology, and Behavior', published in 1991. Looking back over the past decade, the breadth and volume of comparative studies has greatly increased. Phylogenetics now pervades many aspects of the study of evolution, ecology, biogeography, parasitiology and genomics. As a result, the authors of this book have a much larger pool of studies on which to draw, compared with that available in 1991. The other major change in the last decade has been the development of new methods of phylogenetic analysis, particularly those incorporating specific models of character change. Whereas in 1991, parsimony was the dominant tree building method, phylogeneticists today have a wealth of tools, including increasingly sophisticated maximum likelihood and Bayesian methods. This has had an impact not only on the core task of phylogenetics – reconstructing evolutionary trees – but also on reconstructing rates of character change and speciation. Explicitly statistical tests of evolutionary hypotheses (from molecular clocks, through to rates of diversification and the extent of cospeciation) are becoming more widely used (Huelsenbeck & Rannala, 1997). There is also growing interest in methods that endeavour to accommodate uncertainty in phylogenetic trees as part of the analysis.

A striking feature of 'The Nature of Diversity' is how little these developments feature in the book. Methodologically, the authors are happy to rely solely on those tools that were available to them a decade ago. It is as if they were content to voyage around the world in a sailboat, and wish no truck with the new fangled invention 'steam'. An unfortunate consequence is that they give their readers a very limited view of the tools available (and being actively employed) in comparative biology. Brooks and McLennan emphasize parsimony methods, and are dismissive of model-based methods of phylogenetic inference. Indeed, for most of the book they seem distinctly uncomfortable with statistical approaches. They give the impression that model-based methods are not to be trusted, amount to *a priori* manipulation of the data, and should only be considered worthwhile if they agree with parsimony. Although this view has its defenders, it gives the reader a very misleading impression of the current state of play in phylogenetics (as a cursory glance at recent issues of *Systematic Biology* will reveal). Furthermore, although Brooks and McLennan resist models as long as they can, they embrace them in their chapter on radiations. Indeed, the notion of a radiation (a greater rate of diversification than expected due to chance) requires some underlying model of cladogenesis. Surely, if we can use models of cladogenesis we can use models of character evolution? Alternatively, if models of character evolution are bad, why are models of cladogenesis permissible?

A central part of the book is the analysis of historical associations, either between hosts and parasites, or areas and organisms. Brooks and McLennan spend some space outlining improvements to Brooks parsimony analysis (BPA) and criticizing other methods. Here I declare a conflict of interest, for I have been involved in the development of some of the methods that Brooks and McLennan take to task. They characterize BPA as based an 'ontology of complexity', whereas rival methods are flawed because they rely on an 'ontology of simplicity' which betrays their 'orthogenetic roots'. As the reader might gather from this style of argument, the question of which is the best method for analysing historical associations is the subject of active, sometimes heated, debate. For another, somewhat more varied set of perspectives, see the contributions in Page (2002).

In summary, 'The Nature of Diversity' is an interesting update on Brooks and McLennan's 1991 volume. As an overview of the empirical literature it succeeds to some extent, and the catalogue of examples it provides will be mined by lecturers in search of examples for their students (although the practice of citing large numbers of papers in the footnotes makes it hard to know which references are worth chasing up). However, readers seeking a state-of-the-art summary of how phylogeny informs our understanding of evolution will have to look elsewhere. It is a pity that in embarking on their 'evolutionary voyage of discovery' Brooks and McLennan seemed to have missed the boat.

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