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Book Review

Major Transitions in Vertebrate Evolution by J.S. Anderson & H-S Sues (Editors). Indiana: Indiana University Press. 2007. 417 pages. Hardback. ISBN 9780253349262. £35.

In 1988 Bob Carroll wrote a new version of Romer's classic *Vertebrate paleontology*, and achieved the impossible by imposing his own personality on it, yet nevertheless actually improving it (Carroll, 1988); despite its age it remains the standard text book of the subject. Bob is also a prodigious worker within the field, mostly on Palaeozoic tetrapods, and this fine and fitting volume is a Festschrift in honour of his retirement, edited by two of his former students. There are ten contributions and, as is inevitable with the genre, it is not a comprehensive coverage of the field of the title, in the sense that a monograph or text book would be, but it is nevertheless pretty wide ranging, with chapters on vertebrate skeletal tissues, early vertebrates, paired fins, the tetrapod limb, amphibians, basal amniotes, snakes, birds, the Mesozoic mammal radiation, and whales. Each is primarily a review essay. Several of them are very useful contributions indeed, especially those concerning transitions where significant new fossils have come to light in recent years: Philippe Janvier discusses the various candidate stem vertebrate, cyclostome, and gnathostome taxa. Luis Chiappe and Gareth Dyke provide a detailed review of the confusing plethora of feathered 'dinosaurs', near-birds', and early birds of the Cretaceous that have been discovered, most notably in the Jehol Formation of China but also Spain. Amongst mammal taxa, the origin of cetaceans from their terrestrial ancestry has been considerably illuminated in recent years by fossils of limbed whales of the Eocene, as reviewed by Mark Uhen, while Michael Caldwell describes how the early evolution of snakes is starting to be clarified by fossils with small, but patent and just about functional hind limbs.

However the volume as a whole offers a good deal more than just overviews of new fossils, namely a window into the contemporary Zeitgeist of vertebrate palaeontology itself. Something which I believe Bob would wholeheartedly agree with is that for too long now a depressing number of practitioners have been too obsessed by numerical cladistic analysis of anatomical characters for its own sake. While not wishing for a moment to reopen the old battle lines of the 70s (Hull, 1988) and belittle the virtue of objectivity that cladistic methodology brought to systematics as a means of hypothesising and testing real monophyletic groups, two regrettable habits have become widespread. One is loss of sight of the fact that the methodology of cladistic analysis is predicated on acceptance of certain assumptions about characters – that the organism can in principle be atomised into objectively definable, independent characters that are presumed *a priori* to be of equal phylogenetic informativeness. In their historical introduction, Hans-Dieter Sues and Jason Anderson epitomise this standpoint by the comment: 'Recognition of two features as homologous requires analysis not only of those characters but also of *other characters unrelated to* those under consideration.' [my emphasis]. This is based on a manifestly unrealistic model of character evolution, because 'characters' are actually artificial abstractions of integrated systems and therefore fundamentally cannot be independent of one another. In reality some character transformations must be less likely and therefore potentially more informative about relationships than others, depending at least in part on the nature of all the other characters of the phenotype (Budd, 2006). The difficult question has always been how it might be possible to define and recognise patterns of interdependence in real organisms without becoming circular, not whether such patterns exist or not. The second bad habit is forgetting that to most biologists the interesting issues that fossils can be used to address are not branching patterns in their own right, but such 'scenarionic' things as: How does an observed pattern of taxonomic turnover relate to the environment? What is the functional significance of some particular inferred morphological transition? What is the relationship between palaeobiogeographic patterns on the one hand and phylogenetic radiations on the other? For all such questions, additional sources of information beyond character matrices of atomistic characters must be admitted – stratigraphy, plate tectonics, rules of functional design and ontogeny of living organisms, and so on. The most stimulating thing about *Major transitions in vertebrate evolution* is the way in which its pages reflect the existence in the

vertebrate palaeobiology community of appreciation of these problems of character interpretation, and of the wider palaeobiological issues to which their work can contribute. The most explicit example is Philippe Janvier's essay on the character problem in the context of early vertebrate history, for me one of the most important papers in the volume. From being a long-time formal cladist, he now finds himself writing apostatically:

'The weight of optimisation, probabilities, and statistics in phylogeny reconstruction seems to eclipse the consideration of the characters and their definition, limitation, composition, or coding. There are more and more trees, some of which, although most parsimonious, make no sense in terms of plausible character distribution.'

And when the majority of current cladograms based on parsimony imply that the most complex of all his characters, the dorsal nasohypophysis of lampreys and osteostracans is a homoplasy, then he rightly raises his eyebrows. Of course this particular taxon is a very difficult one, for there is rather little in the way of putative intermediate grade fossils between non-vertebrates, cyclostomes, and gnathostomes.

Janvier's writing is sharply contrasted by the attempt of Mark Wilson and his colleagues to track the evolution of paired fins in jawless and early jawed fish (I mean non-tetrapod vertebrates, of course). Because they start by accepting unquestionably a most parsimonious cladogram, they soon find themselves faced with having to force some very dubious-looking supposed fin homologies onto the taxa. In the end, they can only conclude with some bewilderment that:

'These early paired fins should not all be assumed to be the same: we suggest that some taxa have pectoral precursors, and others have pelvic precursors. At least one thelodont had both. Some "agnathan" lineages likely lost either pectoral fins (e.g., furcacaudiforms) or pelvic fins (e.g., osteostracans, perhaps some thelodonts) that were present in their ancestors. Homologues of pectorals and pelvics differed in position and structure even before the origin of jaws, and within most of the major groups of early jawed vertebrates.'

Surely a consideration of fins as functioning biological structures rather than merely as potential trackers of phylogeny would be at least worth attempting in the search for morphological transitions and the implied homologies. This is exactly how Michael Caldwell approaches the well known problem of delimiting homologies of certain cranial bones amongst squamates, such as the jugal, ectopterygoid and postorbital. He reminds us that in such cases 'Debate on the nature, identity, and delimitation of a character . . . is the only method of falsification available for testing cladistic statements.' His very detailed consideration of homology relying on the morphology of skulls of fossil and living squamates rather than slavishly on a cladogram based on poorly defined characters, I find exemplary.

Two of the papers in the collection move us into the rapidly expanding field of evolutionary developmental biology – 'evodevo'. At a traditional level of embryology, Jason Anderson has attacked the perennially unsolved problem of the interrelationships of the three modern orders of amphibians, both amongst themselves and to known Palaeozoic tetrapod taxa, a field in which Bob Carroll himself has been active for many years (e.g. Carroll *et al.*, 2004). Anderson uses features of development as character states to add to the morphological character matrix, states which at least to some extent can be recognised in growth series of fossil species. He discusses the possible difficulties that abbreviation of development and changes in the timing and order of developmental events pose for defining homologous states, but nevertheless implies that such characters may contain a specially useful phylogenetic signal. At any event, he supports a particular diphyletic version of interrelationships in which frogs and salamanders are related to Palaeozoic temnospondyls, and apodans are related to Palaeozoic lepospondyls, a conclusion that Bob will be largely happy with.

Like every other biological discipline, palaeobiology is being revolutionised in some aspects by the molecular biology revolution (Peterson, Summons & Donoghue, 2007), and the second of the 'evodevo' contributions builds on this to look at how understanding the molecular basis of a developmental trajectory in a modern relative can provide support for a hypothetical sequence of phenotypic transitions inferred from the fossil record. Hans Larsson considers the evolution of the autopodium of tetrapods in this light. This is currently the major organ-level transition most likely to yield an answer, because of the combination of a series of intermediate 'fish-tetrapod' grade (i.e. non-tetrapod tetrapodamorph) fossils coupled with the most extensively studied model system for vertebrate development. (Unfortunately the description of the important tetrapodamorph *Tiktaalik* by Daeschler, Shubin & Jenkins, 2006, was too late to be included). Despite the exciting potential, at the moment the conclusion Larsson reaches is necessarily vague. In his own jargon, an evolutionary novelty such as the tetrapod autopodium is a MODE (module of developmental evolution), arising via of a series of a stages called UDE's (units of evolutionary development). Each UDE consists in turn of a pair of entities, a DTS (developmental transitional stage) and an ETS (evolutionary transitional stage). In short, each morphological stage in an evolving structure is associated with a change in the devel-

opmental mechanism. I think we have suspected this for a century, but the progress lies in the active search for the identity of the actual DTSs involved. He finds that specific genes with expression coinciding with three of the embryological stages corresponding to three of the phenotypic stages inferred from the fossils can be identified amongst the Sonic Hedgehog and Hox gene families. Haeckelian as the argument may sound, and noting that it is still a matter of character states and correlations rather than discovered mechanisms, nevertheless this example is surely a pointer towards a fantastic future source of data for understanding major evolutionary transitions.

Whilst most of the authors are still primarily concerned with phylogeny *per se*, refreshingly there are two very interesting exceptions in which the phylogeny is explicitly taken as the starting and not the finishing point of the exercise. In his review of the wonderful set of limbed cetaceans of the Eocene and what they imply biologically about the transition from terrestrial to the obligatory aquatic life of whales, Mark Uhen is concerned about the functional and adaptive significance of the morphological changes inferred from the now well-corroborated cladogram of these animals. He describes two important aspects of the sequence of acquisition of characters. Firstly, changes occur in several different functional systems hand in hand: locomotion, feeding, breathing, and hearing. Secondly, a single trait change can impact on more than one functional system. Thus, for example, he notes that elongation of the premaxilla simultaneously affected feeding by aligning the incisors with the postcanines to create a better design for piscivory, and breathing by bringing the nostril towards the top of the head. He could have mentioned that the change would also have affected the streamlining of the animal and therefore its locomotory characters, and is probably a prior necessity for cetacean style sonar. This pattern of acquisition of derived characters is in keeping with the correlated progression model for the origin of major new taxa, a model that offers the most realistic explanation for how an evolving lineage traverses long distances through morphospace while never losing full functional integration of the transitional phenotypes (Kemp, 2007a).

Xhe-Xi Luo also commences with an established cladogram, namely of the Mesozoic mammaliaform radiation, in what is another of the most important contributions to the volume. No branch of vertebrate palaeontology has been more revolutionised in both material and concept than the Mesozoic mammals. Less than 30 years ago they were regarded as a rare, low-diversity, and therefore not very significant part of the terrestrial fauna. Now we have thirty to forty distinct suprageneric level taxa described (and entirely new ones appearing with great regularity, for example Montellano, Hopson & Clark, 2008) that show a comparable level of dental and locomotory disparity to that seen in the taxa of smaller mammals today: such mammals evidently played just as important a role in the communities of the Jurassic and Cretaceous as they do now. Luo sets himself the task of elucidating the dynamics of the taxonomic turnover of the group by combining the cladogram with the stratigraphy, and also on the admittedly few occasions where it is relevant, the palaeobiogeography, and the molecular systematics of the modern taxa. He finds that most of the mammaliaform phylogenetic tree consists of successive 'explosive' diversification events in which there was an early radiation into a set of short-lived subtaxa. Only occasionally, notably between the Middle and the Late Jurassic, could he infer a 'long-fuse' event in which the subclades of a clade arose early in its history, but maintained a low diversity until radiating much later on. Furthermore, he found no examples of the 'short-fuse' pattern, in which there was an early radiation of what proved to be nevertheless long-lived subtaxa. Although not addressed by Luo in this essay, it is but a short step to seeking correlations between these various categories of taxonomic turnover on the one hand, and palaeoenvironmental, palaeoclimatological, and palaeobiogeographic signals on the other, with a view to developing a comprehensive model of the ecological drivers of a major evolutionary radiation.

The study of the evolutionary processes that result in the origin of major new taxa is a scandalously neglected area of evolutionary biology, subsumed as it usually is by the belief that such long term 'megaevolution' is no more than the population level process of natural selection on an ecological timescale going on for long enough through geological time. This attitude wholly ignores the issue of how a very large number of the characters of a phenotype can change, often to a dramatic extent, yet never lose their extraordinarily high level of functional and structural integration within the phenotype that any viable organism must possess: the integration versus evolvability question. It also ignores the fascinating question of the nature of the environmental circumstances that must exist in order to drive a lineage far enough through morphospace, from some ancestral stage, to become recognisable as a crab, a sea urchin, a turtle, a snake, a frog, a bird, a mammal or whatever (Kemp, 2007b). The vertebrate fossil record, limited as it may be, should be cherished as far and away biology's most important source of evidence for what really happened on this time scale. *Major transitions in vertebrate evolution* reviews the rapidly growing knowledge in several of the most pertinent cases, and it also epitomises much that is good about the present state of the art.

It also happens to be an exceptionally attractive book, for which the editors and publishers should be congratulated. The high quality paper, broad outer margins of the good sized pages, excellently reproduced figures including some fine colour plates, and an agreeable overall sense of literal and metaphorical gravity as one holds it in one's hands lead to a plea that, whatever may be the cost, real books should never be exclusively replaced by e-pages on computer screens.

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