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The shape of evolutionary developmental biology

The Shape of Life: Genes, Development, and the Evolution of Animal Form

by Rudolf A. Raff

University of Chicago Press, 1996.
$55.00 hbk, $29.95 pbk (520 pages)
ISBN 0 226 70265 0

For many biologists, evolution of body plans has always brought to mind that old saying about the weather: everyone talks about it, but nobody ever seems to do anything about it. No longer. In recent years, months, and even weeks, there has been a flurry of important discoveries that have contributed significantly to our conceptual and factual understanding of the evolution of animal body plans, their defining characteristics, and the origin of the higher taxa that they represent[1–3]. Thus, it is hard to imagine a new volume more timely than this one.

The book is a triumph. In an engaging narrative, Raff summarizes a wealth of information from contemporary developmental biology, molecular genetics and paleontology that is pertinent to a mechanistic explanation of the evolution of animal form. Moreover, this information and the accompanying important insights into the developmental basis of evolutionary change are woven together into a coherent story. A vast range of topics are considered: *Hox* genes, Ediacaran fauna, jaws, Baron Cuvier, morphological novelty, key innovations and marsupial frogs are just a few examples. In achieving this breadth of treatment, Raff reveals himself to be a true, modern naturalist; his fascination and passion for the natural world emerge as strongly as his scientific curiosity.

The book is organized around two related themes: the origins of the major animal body plans during the great Cambrian radiation more than 500 million years ago, and the developmental basis of their subsequent evolutionary modification, which continues to the present. To Raff, an essential feature of the origin of body plans is the evolution of morphological novelty, which may define any of several different taxonomic categories. Thus, he does not (as have some authors) restrict body plans to phylum-level differences in anatomy (although characteristic features of body plans are typically most conspicuous at this level). Nor does he postulate the existence of qualitatively different developmental mechanisms that underlie differences in the scale of body plan disparity among various taxonomic categories. Indeed, the implicit suggestion that virtually all instances of morphological evolution in animals derives from perturbation of a common set of developmental genetic processes and principles is among the book's most significant contributions to ongoing debates in evolutionary theory regarding the nature of evolution above the species level, or macroevolution. Building on the theme of biological order developed earlier, and in much greater depth, by Riedl[4], Raff cites modularity as the pre-eminent characteristic of metazoan ontogeny – 'the attribute that most strongly facilitates evolution'.

Together with dissociation, duplication and divergence, and co-option, modularity defines a set of 'principles of evolvability', which may account for phenomena ranging from heterochrony in direct-developing sea urchins to lactose biosynthesis in mammals.

Raff offers a balanced, realistic view of many current research directions and paradigms in the study of development and evolution; his assessments will cause celebration and consternation to members of both camps. For example, in the nearly 20 years since Gould[5] rekindled modern interest in the evolutionary significance of changes in developmental rates and timing, a considerable segment of evolutionary and comparative biologists have come to manifest a virtual preoccupation with heterochrony as a pre-eminent mechanism and mode of evolutionary change in development. Yet Raff, while conceding the pervasiveness of heterochronic changes in ontogenetic pattern and agreeing that such changes may offer important insights into underlying developmental processes, clearly regards this extreme emphasis on heterochrony as undeserved, and, in some instances, even unhelpful. Indeed, "the uncritical attribution of so many of the phenomena observed in the evolution of development to heterochronic 'mechanisms' may be inhibiting a more penetrating investigation of the subject."

He is equally sober in his discussion of the strengths and weaknesses of the 'model systems' approach so beloved by most contemporary developmental biologists – while extremely effective as a paradigm for exploration of basic and common developmental processes, such an approach may have considerable liabilities and biases when employed in a comparative context. To Raff, comprehensive investigation of the relation between evolution and development requires that one's phylogenetic analyses be as rigorous and appropriate as analyses of developmental process and mechanism.

Finally, Raff devotes considerable and deserved attention to homology. Many people working at the interface of evolution and development continue to employ drastically different (in some cases, incompatible) meanings of the word. Such a disparity in terminology (and underlying concepts of similarity and difference) will only become more problematic as research programs continue to converge from disparate academic origins. However, this must be resolved, and in such a way that recognizes both the historical nature and hierarchical organization of biological processes. Raff favors a 'traditional historical and morphological' definition. And while many people (including us) may agree with him, the issue is far from resolved. Everyone must also remain keenly aware of the potentially confounding effects of homoplasy (parallel or convergent evolution) on assessments of homology, and acknowledge that homoplasy can occur in a vast range of features, from the feeding apparatus that defines major body plans[6] to proteins[7].

Many authors have cited the current widespread and intense interest in comparative aspects of ontogeny as heralding the birth of a new field of evolutionary developmental biology[8–10]. Although it will be another several years before these bold claims can be assessed objectively, *The Shape of*

Life offers a very encouraging sign that this nascent field is advancing and maturing with considerable speed, and that already it is beginning to deliver on many of the bold intellectual promises attributed to it.

In writing such an excellent treatment, Rudolf Raff has brought us considerably closer to the many exciting and important discoveries that still lie ahead.

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Life and death at the KT boundary

Dinosaur Extinction and the End of an Era

by J.D. Archibald

Columbia University Press, 1996.
$49.50 hbk, $25.00 pbk (xviii + 237 pages)
ISBN 0 231 07625 8

The Evolution and Extinction of the Dinosaurs

by D.E. Fastovsky and D.B. Weishampel

Cambridge University Press, 1996.
£29.95 hbk (xvi + 460 pages)
ISBN 0 521 44496 9

Dinosaurs are ever-popular, and there must be hundreds of books in print about these fine creatures. However, there are surprisingly few student texts, and these two books are, respectively, the first book to be published on the extinction of the dinosaurs, and the third textbook devoted solely to dinosaurs. Both of them are admirable.

David Archibald has been collecting dinosaurs and other vertebrates close to the Cretaceous–Tertiary (KT) boundary for 20 years, and he has been involved sporadically in the long-running debate about impacts and other killing mechanisms. There are currently three main explanations: (1) gradual climate and sea-level change, (2) impact, and (3) catastrophic volcanism. Archibald previously favoured a model of long-term decline of the dinosaurs, and matching rise of the mammals, associated with climatic cooling and floral changes lasting 1–5 million years (My). He now presents a combined model, in which many vertebrate species were stressed by marine regression, and loss of coastal habitats (from 60 My ago), and the impact (65 My ago), finished off the dinosaurs, pterosaurs and some other groups.

Archibald focuses on his own work in the midwestern USA, where indeed the record of the last dinosaurs is the best and most-studied in the world. It is very hard, as he makes clear, to generalize from Montana to the world. The best parts of the book are those where Archibald provides clear documentation of the declines and extinctions of vertebrates species-by-species. He shows (for example, page 126) that, whereas dinosaurs and sharks showed 0% survival across the KT boundary, amphibians, placental mammals and champsosaurs showed 100% survival, turtles and crocodilians showed better than 75% survival, and bony fishes showed better than 50% survival at the level of species. The multituberculate mammals, marsupials and lizards were hard-hit, but not completely wiped out.

This core of the book is topped and tailed with introductory sections on basic geology of the KT boundary, a history of some of the controversies, and an outline of the dramatis personae. The focus on dinosaurs is unique, since other popular texts[1,2] are more widely focused. Archibald's book is well written, and the computer-generated diagrams are simple and attractive. Unfortunately, there is a shortage of photographs, and the dinosaurs and other creatures are poorly illustrated with rather crude outline diagrams.

Much more richly illustrated is Fastovsky and Weishampel's dinosaur textbook. Dinosaur textbooks are a new phenomenon, spurred by the success of 'rocks for jocks' courses in the USA, where staff in many geology departments earn their bread and butter by teaching huge classes of non-majors the sexy earth science subjects like 'The history of life', 'Volcanoes and earth hazards' or 'Dinosaurs'. This is not the first dinosaur textbook[3,4], but it is clearly more up-to-date, and it is more thoroughly researched.

Fastovsky's and Weishampel's book reflects the rigour of modern palaeontological research, and it will transmit the idea of method and testing to students, especially in terms of cladistic analysis of relationships, studies of macroevolution and of functional morphology. The book also conveys enthusiasm and excitement, two further principles of science that new generations of palaeontologists display in abundance.

The first four chapters outline the methods of dinosaur collecting, taphonomy, stratigraphy, earth history, cladistics and the evolution of vertebrates. A chapter on the origin of the dinosaurs outlines something of the history of concepts of Dinosauria, and this is a good object lesson in the role of cladistics. Up to 1980, most dinosaur experts, when asked either 'what is a dinosaur?' or 'how did dinosaurs evolve?' would shuffle their feet, or launch into a disquisition on the rampancy of convergence and polyphyly. The standard view was that dinosaurs had had several points of origin among Triassic archosaurs, and that the term 'dinosaur' was a convenient label for a rag-bag of large terrestrial Mesozoic archosaurs. Cladists then catalogued the numerous shared features of all dinosaurs, especially related to their upright posture, which entails major modifications to the ankle, knee and hip joints. These characters define a clade Dinosauria. Fastovsky and Weishampel argue that the dinosaurs achieved their initial success by taking advantage of an extinction event some 2225 My ago.

The core of the book, pages 107–321, is devoted to a treatment of dinosaurs group-by-group. Each chapter includes a wealth of information, following a pattern of summarizing the history of collection and geographic distribution of the group, outlining the classification of all valid genera, and then discussing palaeobiology. This treatment means that all 300 valid dinosaurian taxa are included, and hence the book, through its index, offers a complete coverage of genera. The systematic section is developed in the form of one or more cladograms per chapter, and characters that define nodes are listed in the captions. Hence, in all, the cladograms could be strung together to give a cladogram of all dinosaurs, which is some achievement by the authors.

The final three chapters of the book cover the warm-bloodedness debate, dinosaur distributions in space and time, and the KT extinction event. The dinosaur thermoregulation debate has re-surfaced again recently in the literature, with new debates about polar dinosaurs, stable isotope measurements in bone, nasal turbinates, and dinosaurian DNA. The authors opt for a consensus view that the large dinosaurs were inertial homeotherms, and the small theropods might have been endotherms. In their discussion of the KT event, Fastovsky and Weishampel present a good up-to-date account, full of censuses of the last dinosaurs, iridium spikes, asteroid impact in Mexico, and the like. They accept the importance of the impact, the likelihood that dinosaurs, and other organisms, disappeared rapidly and the probability of a link.

The presentation of the book is superb. The writing style is lively, and there are many