
Book Reviews

The Origin of Animal Body Plans: A Study in Evolutionary Developmental Biology. By WALLACE ARTHUR. Cambridge University Press. 1997. ISBN 0 521 55014 9. 338 pages. Price £45.

Every biologist must have heard of homeoboxes and hedgehog genes. Most are probably aware that modern developmental research has something to say about evolution. But what exactly? What is this new discipline of ‘evolutionary developmental biology’ that has emerged (or re-emerged) in biology? Wallace Arthur’s new book tackles these questions, and concludes that the new discipline is far from mature. It is not yet a full integration of evolutionary biology and developmental biology. He notes that there is ample dialogue between embryologists, molecular biologists, phylogeneticists and even palaeontologists, but laments the fact that evolutionary or population geneticists have been noticeably late to the party. Why has research into natural selection paid so little attention to recent findings in development? And does it matter? Arthur argues that it certainly does matter, since the implications of modern developmental biology are so profound (and so consistently ignored by standard evolutionary theory) that the so-called New Synthesis is starting to look distinctly jaded. Perhaps it is time for a New Improved Synthesis in evolutionary biology. Arthur’s book does not provide this synthesis, but it does try to set out the agenda.

Before tackling this, Arthur takes the reader through a careful, but rather slow, review of some key aspects of developmental biology, gene expression analysis, phylogenetics, invertebrate palaeontology and molecular evolution, whilst trying to draw out threads for his later holistic overview. I was disappointed by these sections of the book. My dissatisfaction was not due to the presence of errors, although inevitably there are a few (the cognoscenti will, for example, spot the omission of *Hoxb-13* and of *zen/Hox3* homology, and most would disagree that vertebrate Hox cluster duplications occurred by local processes). My main criticism is that these first eight chapters simply do not convey the genuine excitement of the subject. What happened to the romance of the homeobox, the passion of the Cambrian explosion, or

the revelation of sonic hedgehog? Just why has a generation of developmental biologists been buzzing with excitement? And what made these pioneers of the model systems approach return to their old zoology textbooks to remind themselves what onychophorans, malacostracans, enteropneusts and amphioxus look like? In the same vein, I found Arthur’s choice of milestones in evolutionary developmental biology particularly strange; it omits Lewis’ Bithorax Complex insights, Field *et al.*’s pioneering assault on invertebrate molecular phylogeny and even the discovery of the homeobox! Comparative developmental biology is buoyant and fast-moving, but the reader would hardly guess so from this book.

Fortunately, there are better things in store if you stick with the task or, dare I say it, skip these initial chapters entirely (better still, start by reading Rudy Raff’s ‘The Shape of Life’ published by University of Chicago Press). The final few chapters deal with the crux of the problem in Arthur’s view: how to integrate comparative developmental biology into mainstream evolutionary thinking (or vice versa). He points out that current evolutionary thinking focuses heavily on the destruction of variation, rather than its creation. I agree strongly with this point, which emphasises the constraints imposed by the genotype on the kinds of variants that will be viable, and therefore available for natural selection. A second point stressed by Arthur is that selective forces need not be just external. Internal co-adaptation of genetic pathways or developmental mechanisms may strongly influence which variants are successful; this would represent a new face of natural selection, rooted in developmental biology. Again, I agree, although just how important ‘internal selection’ has been is hard to gauge. In fact, Arthur suggests that its importance may have changed considerably over evolutionary time. He speculates that the developmental control pathways of Vendian animals may have been far less well integrated than those of modern phyla, in which case evolution had a freer rein to remodel body plans in the Precambrian than has ever been possible since. This idea is not new, and is likely to remain a plausible viewpoint if only because it is so difficult to test!

Other suggestions and speculations made by Arthur

are certainly testable, and the final chapter sets out an agenda for future research. It is an eclectic choice, and one far from comprehensive, but it is worth reading. If it further stimulates the fusion of evolutionary and developmental biology then it will have served a useful purpose. I simply hope it does not do the opposite. Arthur's book does tend to stress how far we have to go to achieve a true integration, and this may prove daunting to some. This should not be the case, since so much rapid progress has already been made. I hope that readers of this book will spice it up a little with forays into the primary literature, and thereby gain a more balanced outlook. Evolutionary developmental biology is alive and well, and really rather exciting; the field may benefit from some steering along the lines that Arthur suggests, but let's not kill the excitement.

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Cells, Embryos and Evolution. By JOHN GERHART and MARC KIRSCHNER. Blackwell Science 1997. ISBN 0 86542 574 4. 642 pages. Price £29.50, paper.

Understanding how cells and their products actually bring about evolutionary differences is a key aim of this excellent text book. The immense research activity in recent years in molecular biology and developmental genetics has shown just how well conserved many genes and control pathways are. The initially surprising findings that the same signalling pathways and transcriptional regulators are used time and time again to make cellular decisions during the development of an individual *and* are well conserved in a wide variety of species are now well documented. Yet alone these do not contribute to our understanding of evolution. How do organisms use cellular processes to adapt their form to their environment? This book links together evolution, cell biology and developmental biology in an original and thought-provoking way.

The book covers a huge diversity of topics beginning with a look at how well conserved cellular processes are, even between organisms differing most in body plan, nervous system and the relationship of the egg to reproductive strategies. It shows how conserved building blocks are used to build the great diversity of cell structures and cell types present within and between organisms; and also how the decision-making machinery, such as that regulating the cell cycle, is well conserved, even between organisms using widely differing strategies for controlling cell division – for example single celled organisms dividing in response

to nutrient availability and embryos rapidly becoming cellularized. The basic cellular building blocks like actin and myosin are found in virtually all eukaryotic cells, yet the proteins have been modified to produce the diversity. Secretory mechanisms are also well conserved. The authors describe how conserved developmental pathways can be used in new combinations to bring about novel structures such as wings and limbs, and how there are common transcription factors involved in eye development from insects to vertebrates, despite the huge differences in the anatomy of the eyes and their methods of receiving light.

The book goes on to look in detail at how cells respond to the extracellular and intracellular conditions in which they find themselves. It shows how core proteins or processes respond in very specific ways to the passing of time or changes in the environment. As an organism develops, cells need to respond to a variety of signals by the control of cell cycles, translational control, kinase signalling pathways and other key regulatory mechanisms that link signals to responses, with overall coordination achieved through the nervous and endocrine systems. The authors discuss the roles of G-protein signalling, transcription factors and ion channels. Eukaryotic promoters have evolved to accommodate a large number of binding factors with different sequence specificities and binding affinities to allow temporal and spatial control of gene expression. These complex control regions allow elaborate developmental programming. Among other topics explored by the authors are the capacity of organisms to respond to new environments, animal behaviour, the immune system, sensory perception and the evolution of the brain.

About a third of the way into the book the emphasis shifts to protein evolution, with a fresh look at such topics as exon shuffling and novel controls of protein functions. Cell differentiation and compartmentalization is covered in depth and the evolution of multicellularity investigated. Of particular interest here are discussions on the segregation of the germ line, which remains capable of meiosis, from the rest of the somatic cells, and how localized cell–cell interactions lead to the specific development and differentiation of particular structures. A lot of emphasis is placed on the development of *Drosophila* imaginal disks and how a specific position is selected for the generation of a bristle using a complex set of positive and negative regulators. This shows how first a field of cells becomes competent to differentiate and then how cell–cell interactions and lateral inhibition within the cluster, with further refinements and commitments, finally cause one bristle or sensory organ to differentiate. This section emphasises the importance of the cell's position within a population of cells, its stage in development and its sex and how

these factors call into play specific subsets of the cell's genetic repertoire. The evolution of mechanisms to generate spatial patterns is a crucial step in the evolution of diversity of form.

There are large sections on the development of the body plan and on axis specification, both of which are excellent in their coverage, but not too different from what one could find in other developmental biology texts. Morphogenesis and the final development of the organism has to be built up starting from the embryo with its defined axes and body plan. The transcription factor cascades used in embryonic development to activate different genes in different regions of the embryo are described and related to the body plan genes and the processes of gastrulation and neural development. Much of the research area described in these sections centres on *Drosophila* as would be expected, but the organizing centre of amphibians and neural development in higher organisms are also well represented.

The final chapters look at how body plans have diversified during evolution and how, for example, limb evolution has occurred. Again at the genetic level

this is often exemplified using the studies of *Drosophila* imaginal disks, where organizing centres are set up and gradually refined using transcription regulation and cell–cell signalling interactions. They also address how these kinds of fundamental, compartmentalized, and robust but flexible processes allow evolution to occur in response to selective pressures and environmental change.

The book is not for the faint-hearted. It makes no compromises and to read it you need to be at ease with all the molecular, developmental, cellular, genetic and biochemical details needed to understand the data on which their ideas are based. At times reading is therefore slow, but it is worth it. I think it will be of interest and value to the best students. It is a pleasure to see a topic tackled in a new way and I would certainly recommend that it should be read by all those teaching or doing research in cell biology, developmental biology, evolution or molecular biology.

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