The burden of the bauplan

The Origin of Animal Body Plans

by Wallace Arthur

Cambridge University Press, 1997.
$64.95/£45.00 hbk (xii + 338 pages)
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Cells, Embryos and Evolution

by John Gerhart and Marc Kirschner

Blackwell Science, 1997.
$49.50/£29.50 pbk (xi + 642 pages)
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Evolutionary developmental biology has truly begun to live and breathe as an academic discipline. It has its own dedicated practitioners, its first, but surely not last, journal (*Development, Genes and Evolution*), a goodly number of monographs, and now what appears to be its first textbook. Most of all, it has its own experimental strategy, and one that is producing simply delightful and eminently publishable results. For those rare and strange unfortunates among us who can (while stooped and reeking of formaldehyde) still tell an undergraduate which side of an earthworm is 'up', these are the most exciting times since Alexandr Kovalevskii described the tunicate's tadpole larva, and that was 1866.

But is this enough? The authors of these books seem to think not. For evolutionary developmental biology is evidently a discipline in search of Big Questions, and, unsurprisingly, some have been found. Why did all the animal phyla evolve so long ago? Perhaps phyla evolved in a Cambrian Explosion, perhaps slowly in the unseen depths of the Vendian; whatever the case, it's perfectly obvious that it has been a long, long while since the first member of the last new phylum wriggled out of the ooze. We know this because each new phylum is fortuitously blessed with its very own body plan (or bauplan or phylotype – they're all much of a muchness) which, remarkably enough, seems to have been retained till the modern day. Which brings us to the second Big Question: 'Why are body plans so conserved?'

It is perfectly conceivable that the answers to such questions will be found by studying the evolutionary properties of developmental programmes rather than, say, Phanerozoic ecology. But where the answers come from probably does not matter much if the questions themselves are simply incoherent. Where the early origin and subsequent conservation of body plans seem, to these authors, a marvellous thing in need of special explanations, others have suggested that these patterns may well be an artefact of taxonomy. Phyla are *defined* by the uniqueness of their baupläne, a uniqueness caused by a million missing links. The older two clades are, the more likely the links between them will be missing, hence all phyla and all baupläne are old. Conversely, the reason why some traits are conserved – the classical body plan traits such as coelom formation – may be entirely due to chance alone[1]. Maybe not, but until some serious thought is given to the effects of clade proliferation and extinction upon the phylogenetic distributions of traits, there will be little reason to think that body plans have any existence outside of their natural habitat, the undergraduate zoology text.

Arthur, and Gerhart and Kirschner, at least acknowledge the idea of constructing null models of metazoan evolution against which to test hypotheses for the causes of evolutionary conservation and diversity, but the thought is quickly put aside as an unpalatable statistical quibble. Still, if you believe that all baupläne are old baupläne, then these are books for you. In *The Origin of Animal Body Plans*, Arthur gives the most cogent and detailed explanation that I have yet seen of why the evolutionary processes of the Vendian yore might have differed from those that we see today. He starts with a careful discussion of the properties of developmental mutants, their stage-specific effects, and their effects on fitness. He then argues that mutations that affected early rather than late ontogeny drove the evolution of the first animals, so giving rise to the differences in body plans we see today. Although these mutations permitted the invasion of novel resource niches, they also initiated a period of genomic coadaptation which gave rise to highly integrated creatures in which further early-ontogeny mutations tended to be deleterious; the flood of new body plans then slowed to a trickle.

All in all, it is something that has been sorely needed: a discussion of developmental evolution from the point of view of a population biologist. But, it must be said, Arthur is a population biologist with a slightly idiosyncratic take on his subject. For example, he devotes a good bit of space to reviving the ideas of Lancelot Whyte as expressed in his *Internal Factors in Evolution*[2]. This turns out to be a strange and assertive little book devoid of any but the most primitive conception of population genetics, but one from which Arthur manages to rescue a potentially useful idea, namely, 'internal selection' – that is, selection among genotypes which differ in their degree of 'integration'. This, Arthur believes, has played a great role in the evolution of developmental programmes, but since he does not produce a single example of a real trait that might have evolved by such selection, his discussion leaves one intrigued but not convinced.

Where Arthur's book is clearly a monograph, Gerhart and Kirschner's *Cells, Embryos and Evolution* is (speaking of baupläne) neither fish nor fowl. It has the flavour of a textbook – two-tone diagrams, footnoted citations, and much elementary discussion of axis formation, signal transduction and the like – but the arguments and organization of a monograph, and a fairly radical one at that. No easy textbook progression of topics here ('Gametogenesis', 'Fertilization', 'Cleavage' etc.), but instead a series of chapters, each of which treats some rather abstract property of development in evolution: 'Regulatory Linkage', 'Novelty', 'Conditionality and Compartmentalization', 'Flexibility and Robustness' and so on. The diversity of topics that each chapter encompasses is astonishing. Thus in Chapter 2, 'Contingency', one finds a discussion of the transcription factor NFκB's role in vertebrate immunity and the *Drosophila* axis specification; the regulation of brown adipose tissue metabolism; the embryonic cell cycle of the frog and *Drosophila*; the molecular circuitry of muscle differentiation; receptor tyrosine kinase signal transduction; the sex-determination systems of *C. elegans* and *Drosophila* compared – and that's just a partial list. Such unexpected juxtapositions can, as in this chapter, be illuminating; elsewhere they can seem pointless. Yet the exuberance of given detail lends this book great charm and interest. To be sure, all the cliché stories of developmental evolutionary biology are here – lens crystallins, Hox genes and *Pax-6* – but so is a multitude of far more original examples. Not until I read it in Gerhart and Kirschner, did I realize that the antlers of the Irish elk, the shield of *Triceratops*, the beaks of birds, and the variable visages of vampire bats are probably all due to evolutionary variation in one tissue: the neural crest. Quite unexpectedly, their comparative embryology goes well beyond the five or six model organisms to encompass marsupials, elasmobranchs, molluscs, leeches, onchyphorans and others besides; whiffs of the 19th century all the more delicious after a dozen (excellent) pages on Sensory Organ Precursor [SOP] specification in *Drosophila.*

But make no mistake, this is a tendentious book. Gerhart and Kirschner argue that the major phyla we see today are those with body plans (more precisely, phylotypes) that were especially 'flexible, versatile and robust'; the poor showing of the priapulids and tardigrades in the diversity department is attributed to some unfortunate aspect of their developmental programmes. Such speculations, which emphasize the 'evolution of evolvability' (much as Kauffman[3] and Dawkins[4] before them), are no more or less plausible than Arthur's 'internal selection', and therein lies the problem. Both books contain edifices of ultimate causation built on little more than a collection of anecdotes about the distribution of forms, ontogenies and the molecular mechanisms that underlie them. And at a time when students of the comparative method routinely use powerful statistical tools with which to unravel historical patterns and test hypotheses about evolutionary mechanisms[5], that's just not good enough. Before evolutionary developmental biology can make a substantial contribution to the explanation (rather than the description) of animal diversity, its practitioners are going to have to grapple seriously with the problems of inferring historical causation. To judge from these books, they haven't begun to do so yet.

Armand M. Leroi

Dept of Pure and Applied Biology, Imperial College, Silwood Park, Ascot, Berks, UK SL5 7PY

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Plants in action

Induced Responses to Herbivory

by Richard Karban and Ian T. Baldwin

The University of Chicago Press, 1997. $44.00/£35.25 hbk, $17.95/£14.25 pbk (x + 320 pages)
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Because plants are firmly rooted in the soil and cannot run away from their enemies, they have long been considered passive in interactions with other organisms. This view has been falsified by several decades of research on plant–pathogen and plant–herbivore interactions[1]. In the past 25 years the research field of induced responses of plants to herbivory has been firmly based and developed. It is remarkable that zoologists[2] and biochemists[3], and not botanists, were the pioneers. The mechanistic and functional angles of the field have developed separately. Consequently, detailed knowledge of biochemical and molecular changes in plants in response to wounding or herbivory was often gathered with little reference to their importance in nature, while knowledge about the effects of induced plant responses on plant–herbivore population dynamics and evolution lacked a mechanistic foundation.

Six years ago, an edited volume[4] on the subject appeared, which was a valuable contribution to structuring the field. It brought together mechanistic and functional approaches across a range of very different research programs, and served as a good compendium to illustrate the diversity of responses and systems. Karban and Baldwin, who both contributed to that book, have now written a comprehensive volume that covers mechanistic and functional aspects of induced plant responses. Their backgrounds and experience make them very well suited to write this integrated overview, which is a rich source of information. All together the book includes more than 800 references that are well balanced over functional and mechanistic studies. A third of these references have been published since the appearance of Tallamy and Raupp's book[4].

Karban and Baldwin have succeeded in integrating information from the two rapidly developing subfields. They have produced an excellent book in which emerging patterns, limitations to existing studies, and important issues for future research are presented in a clear framework. Ecological studies, in particular, are critically evaluated. A recurring, though not consistently mentioned, issue is the problem of pseudoreplication. The authors are especially – sometimes overly – critical about studies on communication between plants.

Integration of the functional and mechanistic approach has synergistic rather than additive value. The book is a must for every ecologist in this field, for it gives ample information on mechanisms that may play a role in the ecologist's experiments. Knowledge of mechanisms is important for sound ecological set-ups and the transgenic plants that are constructed by the mechanistic school will be of great value for functional studies. I am not sure whether molecular biologists or biochemists will find the book as useful as ecologists. The many pitfalls in ecological studies, the numerous alternative explanations for the evolution of induced plant responses and the recurring danger of pseudoreplication as indicated in the book, though all important issues, may deter scientists who are not used to such problems from reading the book right through.

The emphasis of the book is on responses of plants, although it is remarkable that the word 'plant' does not appear in the title. Much less attention is paid to the behavioural or physiological reaction of herbivores to the plant responses, although this can be decisive in determining whether the plant's response benefits the plant or not. The effect on animal behaviour is especially important in induced responses that affect herbivores through attraction of their natural enemies. This aspect of induced responses was not included in Tallamy and Raupp's book[4], but does receive attention from Karban and Baldwin on many occasions. Integrating knowledge on the effects of plant responses on herbivores and effects on carnivores will be decisive for a valuable understanding of the costs and benefits of plant responses for herbivores and plants[5]. A further expansion of research in this direction in the future will be especially important for a valid functional analysis of induced plant responses.

Marcel Dicke

Dept of Entomology, Wageningen Agricultural University, PO Box 8031, 6700 EH Wageningen, The Netherlands

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Class, power and propaganda

Huxley: Evolution's High Priest

by Adrian Desmond

Michael Joseph, 1997. £20.00 hbk (xiv + 370 pages)
ISBN 0 7181 38821

This volume completes Adrian Desmond's coruscating biography of Thomas Henry Huxley, the redoubtable scientist 'agnostic' (he coined the word), evolution's annointed 'High Priest', cultural critic, one-man think-tank, political fixer and domestic patriarch; above all, the ultimate professional who harnessed state power to create the modern laboratory and turned science from a gentlemanly pursuit into a salaried career for middle-class men.

Desmond has established his reputation as a leading exponent of the new contextual history of evolutionary science[1,2], an approach which he likens to film-making with himself as director and his Huxley biography as a 'highly-mediated celluloid construct, where the camera pans across a stage (context) to catch actors reading lines, while

