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Book reviews

All is well when right is like left and left is like right

Developmental Instability. Causes and Consequences. By Michal Polak (ed.). Oxford University Press, 2003. ISBN 0-19-514345-0, £66.50

Developmental instability is one of but a handful of concepts which can be said to unify several biological disciplines. The study of developmental instability – and its champion measure Fluctuating Asymmetry (FA) – unites fields as varied as developmental biology, genetics, ecology and evolution. Developmental instability arises because of noise in the developmental pathway of a trait. In a bilateral trait, developmental noise may result in small, random deviations from perfect symmetry, which is termed Fluctuating Asymmetry. Developmental noise is thought to be aggravated by stress and affected by intrinsic factors regulating developmental precision. The role of developmental instability – and especially FA – in ecology and evolution is lively debated and polarizes the opinion of researchers. The main attraction of FA for ecological studies stems from the possible increase in FA with (environmental) stress; FA may be a useful bio-indicator of anthropogenic stress imposed on today's populations of plants and animals. The concept of FA was therefore embraced by many applied ecologists as a cost-effective way to characterize the health of a population. Critics have countered that many studies of FA have been statistically flawed and that FA is, in fact, only mildly related to stress. In more recent years, considerable debate has flared up around the possible role of FA for sexual selection. FA can, in principle, function as a cue for an individual's health and quality, and may therefore play a role in mate quality assessment. According to this (debated) view, the phenomenon of developmental instability has more layers than when viewed as just an indicator of stress, because it is not only affected by extrinsic factors, but also by individual (and therefore heritable) properties that buffer the phenotype against developmental perturbations.

It is against this background of rapidly growing literature and debate that *Developmental Instability* sits down to critically examine the available data and ideas. Periodic assessment is needed, especially since many new ideas and findings have gathered in the late 1990s after the publication of the last syntheses. *Developmental Instability* takes a bottom-up approach and starts with a reductionist's view of the causes behind developmental instability from a developmental and genetic perspective. It covers both an examination of the molecular and cellular sources of developmental instability and the underlying theoretical models, including nonlinear theory and thermodynamics. In this first part, the expected relationship between FA and developmental instability is also scrutinized.

In the second part, the genetics of developmental instability is approached from different angles. After a timely introduction into the history of genetical models for developmental instability, the roles of genomic coadaptation (especially across hybrid zones) and current knowledge of candidate genes are explored. The last two chapters of this part deal with the quantitative genetic base for FA, addressing whether additive genetic variance exists for FA and how future quantitative genetic research should explore this issue further. Uniquely, one chapter deals with nonadditive effects on FA, a field in which surprisingly little research has been done.

The third part of *Developmental Instability* deals with the relationship between FA and fitness. The first chapter explores this relationship in animals and the second one concerns plants. This part culminates in an interesting discussion on the role of FA in sexual selection. It starts from an insightful discussion of this topic in the light of signaling theory, followed by two chapters dealing each with an extensive review of the data on this topic. Interestingly, the authors of these chapters follow a slightly different pathway in analysing the same data to reach markedly different conclusions on the relationship between FA and sexual selection.

Given the historical emphasis on methodology in studies of FA, it is not surprising that the statistical analysis of FA is addressed in detail in the fourth part of *Developmental Instability*. Attention is focused on how to perform a rigorous analysis of FA and what methods are available. This chapter is accompanied by a web-based program that assists in carrying out a robust analysis of data on FA. Further issues include the advantages of mixed effect analyses for certain problems and introduces Bayesian analyses of FA, a relatively unexplored form of analysing FA which clearly has much insight to give.

The last part examines applied aspects of developmental instability. The first chapter of this fifth part readily makes clear that there is a bewildering variety of results in studies exploring the relationship between FA and stress. This part not only deals with reasons as to why this

relationship may be diffuse, but also contains many constructive points. A critical examination is made of FA's strength and weaknesses in comparison with other biomarkers, and ways to improve FA as a bio-indicator are suggested.

As a whole, *Developmental Instability* is a mature and balanced compilation of an important subject in biology, which is, after all, about half a century old. Michal Polak has managed to combine excellent contributions of all the big names in the field. The overall emphasis lies on constructive criticism and a particularly attractive side of the book is that different points of view are represented alongside each other. The studies discussed are broad, dealing with animals and plants from many geographical regions (Europe, N. Americas, Russia). *Developmental Instability* gives a unifying overview of fundamental, phenomenological and applied issues of developmental instability and is relevant to both advanced students and researchers in the field.

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Evo-devo discovers morphology

A review by Christian Peter Klingenberg

The Development of Animal Form: Ontogeny, Morphology, and Evolution. By Alessandro Minelli, 2003. Cambridge University Press, Cambridge, ISBN 0-521-80851-0, xviii + 323 pp.

Evolutionary developmental biology, in the form in which it has emerged during the 1990s, has been dominated by comparative developmental genetics, which has tended to overshadow other connections between evolution and development. The explicit goal of Alessandro Minelli's book *The Development of Animal Form* is to redress this imbalance and to point out how more traditional biological disciplines such as comparative morphology can contribute to a broader synthesis.

The first few chapters set out the conceptual basis of the book. One of the principal ideas is the critique of the 'adultocentric' view of development. In other words, Minelli reminds us that a chicken is just an egg's way to make more eggs – an equally valid alternative to the more familiar 'chicken-centred' perspective. Consequently, the emphasis of the book is on the process of development *per se*, which is more than just a means to produce an adult form, and imposes its own influence on evolution.

Continuing his critique of the 'adultocentric' view of development, Minelli draws the parallel to evolution, where the notion of progress has been abandoned more and more (Ruse, 1996), and attacks as 'finalistic' any reference to the directedness of development. I think this critique is problematic because, although life cycles may have no beginning and no end, they definitely do have a direction. Because Darwinian fitness depends on the success of entire life cycles, each piece of the cycle can be expected to be under selection to ensure a smooth transition from one stage to the next. One might even dare to say that development is progressing from one stage to the next in the cycle.

An interesting aspect of the book is that many of the positions taken by Minelli reflect recent arguments by philosophers of biology against the notions of genetic programmes (Keller, 2000) and the dominant role of genes in general (Griesemer, 2000; Moss, 2003). These critiques are an interesting complement to the prevailing perspective in biology, which focuses primarily on genes as the controlling factors in development, for instance, when speaking of 'master control genes' (Gehring, 1998) and *cis*-regulatory 'hardwiring' (Davidson, 2001). Bringing these arguments to the attention of a broader audience of biologists is certainly most helpful. However, the alternatives that Minelli offers, in particular the emphasis on generic mechanisms and forms (e.g. Newman, 2003) and on developmental systems theory (a theory much more at home in philosophy than in biology; e.g. Robert, 2003), are likely to be just as controversial as the more conventional gene-based view.

Under the heading of 'periodisation' Minelli reviews work about developmental time and developmental stages. He goes into considerable detail about the problem of comparing and homologizing ontogenetic stages, about the nature of larvae and metamorphosis. Minelli discusses the important role of timing in laying down spatial patterns, for instance, the segmentation clock (Pourquié, 2003). The connection of temporal and spatial order is also inherent in the often-cited example of the *Hox* genes, where the parallelism is spatial, temporal, and the chromosomal arrangement of these genes (Kmita & Duboule, 2003). This topic leads to a further focus of the book, the division of the body into distinct regions, with particular emphasis on the tagmatization of arthropods. The author's great expertise on arthropod comparative morphology clearly manifests itself here – this chapter is a treasure trove of specific examples that demonstrate just how difficult it is to squeeze the diversity of natural forms into neat conceptual frameworks.

A lengthy chapter is devoted to the evolution of body axes. Minelli introduces the idea of the 'dual animal' that

contrasts the patterning processes in the 'somatic animal' consisting of ectodermal and mesodermal components against those in the endodermally derived 'visceral animal'. He defends this contrast with evidence on the differential evolution of body axes in the two components and with the difference in patterning genes (*Hox* vs. *ParaHox* genes). The chapter presents a number of additional hypotheses that will be controversial. For instance, Minelli argues that the tail of vertebrates is an appendage (like the paired limbs) and not a part of the main body axis, or more precisely, that the appendages (and with them the tail) are derived from the main body axis by evolutionary duplication.

A further focus is the evolution of segmentation. Minelli starts by examining the question how many times segmentation had evolved in the Bilateria and concludes, with some caveats, in favour of the hypothesis of multiple independent origins. He goes on to introduce the distinction between true segments (eosegments) and a more superficial secondary type of segments (merosegments) that may be superimposed on the true segments in the same animal. Although Minelli thinks that segmentation *per se* has evolved several times in different lineages, he applies the distinction between these types of segments throughout the Bilateria. This raises the question whether the two types of segments are a necessary outcome of some 'generic' mechanism, and whether they arose separately on the different occasions when segmentation evolved. Minelli's first-hand experience from his own studies on myriapod segmentation and its evolution is a valuable asset that enables him to illustrate the subject with many concrete examples. The examples clearly show the difficulty of applying theoretical concepts of segments consistently to concrete groups of organisms, for instance, when the dorsal and ventral sides of the same animal have different and incompatible patterns of segmentation.

A discussion of homology concludes the book. This chapter makes a courageous attempt to address homology from various perspectives including comparative morphology, the use of gene expression patterns as indicators for the homology of parts, as well as the homology of genetic networks. There are also brief reviews of related issues such as modules, germ layers, embryonic fields, among others. Accordingly, this chapter is densely packed with difficult conceptual matter, but the many examples help the reader to relate abstract notions to real organisms.

Given the author's involvement in systematics, it is perhaps surprising that the book uses very little explicit phylogenetic reasoning. For instance, the discussion of segmentation does not include a systematic examination of the distribution of the different forms of metameric structure throughout the Bilateria. Instead, there is just a comparison of segmentation in annelids, arthropods and vertebrates. In many other contexts, the reader must reconstruct phylogenetic histories from enumerations of two-taxon comparisons. At times, this makes it rather difficult to follow and evaluate the arguments about homology of parts and processes that are at the core of the book.

Minelli's emphasis on arthropods invites comparison to another book on a related subject, *Insect Development and Evolution* by Bruce S. Heming (2003). Clearly, as an overview of insect development and its evolution, Heming's book is not primarily concerned with theoretical and methodological issues, but his treatment of the subject matter embodies much of the synthesis that Minelli advocates. Heming's treatise comprehensively covers the diversity of developmental processes among the insects, using information from the 'traditional' disciplines such as comparative and experimental embryology, morphology as well as recent discoveries from molecular genetics. The book not only covers embryonic development, but also gametogenesis, post-embryonic growth and metamorphosis, and therefore produces a rich picture of the entire life cycle and can serve as an example of how to avoid the 'adultocentric' perspective criticized by Minelli. Heming makes use of model organism *Drosophila melanogaster* as a basis for comparison, which is needed to appreciate fully the diversity of information about nonmodel species from all insect orders. It is particularly noteworthy that a consistent phylogenetic approach is an organizing principle throughout his book, mapping important developmental traits onto a phylogeny of the insect orders. Overall, I think Heming's book can be a model for the type of evolutionary developmental biology for which Minelli is calling.

Integrating all the information relevant to the evolution of developmental processes will be a challenge for the sheer amount and complexity of this information, but I agree with Minelli that it is an intellectual adventure well worth undertaking. Minelli's book is a signpost, but it is not a complete map of this new area. This book will be a great basis for graduate seminars, because it is full of intriguing speculation and contentious ideas that will provoke discussion and it also offers an abundance of factual information with which those ideas can be put to the test.

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