

Cold comfort

Cold-adapted Organisms: Ecology, Physiology, Enzymology and Molecular Biology

edited by R. Margesin and F. Schinner

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If there is one feature that defines the possibility of life, it is liquid water. Perhaps it is because of the absolute requirement of life for liquid water that cold has long been viewed as an extreme environmental challenge. Once extracellular water has turned to ice, cells face an enormously restricted ability to exchange gases and nutrients, and once the cells themselves freeze death is almost inevitable. For these reasons, cold has been regarded as the fiercest enemy of life. For many years, considerable attention has been directed at unravelling the processes that enable organisms to live at low temperatures. Extreme environments represent natural experiments that test the limits of adaptation, and thus illuminate evolutionary processes and the constraints that operate on them.

Perhaps somewhat paradoxically for an extreme condition, low temperature environments are actually quite common. Given that the largest habitat on the face of the earth – the deep sea – is permanently below 4°C, low temperature might even be regarded as the norm. If one looks at the distribution of life in relation to temperature, then it is the higher temperatures that appear to set the greater challenge, because above 50°C effectively only microbes can exist. Nevertheless, cold represents a significant environmental challenge for organisms, particularly in relation to the phase change from liquid water to ice, thus the ecology and physiology of organisms living at low temperatures has attracted much attention.

Because cold is a widespread and economically significant environmental factor, it has been studied in a great many organisms and in a large number of laboratories. This heterogeneity has sometimes hindered the discovery of general trends. Thus, those interested in plant cold hardiness typically work with economically important models, whereas polar ecologists look to plants that live in Arctic or alpine locations. Physiologists use different names for the same class of protein in insects and fish, and many papers blur the distinction between short-term laboratory (acclimation) or field (acclimatization) adjustments and long-term evolutionary

adaptation. This distinction is important because what an organism does in response to a short-term challenge, such as seasonal variation, might not be the same as the outcome of evolutionary response to long-term climate change.

This volume consists of an edited collection of 21 papers, involving over 55 authors from 12 countries. There is a strong European bias, which is to be expected because the volume emanates from the work of a consortium of European labs interested in the problems of low temperature (EUROCOLD). The editors have done a valiant job of attempting to synthesize information across the whole spectrum of life. Chapters cover microbes, plants, terrestrial invertebrates, and marine and terrestrial vertebrates. These chapters also address processes at different levels of organization, and the book title is justified because there are sections on molecular biology, enzymes, whole organism physiology and ecology. There are particularly valuable chapters on the physiology of low-temperature microorganisms (Gounot and Russell), mechanisms of cold acclimation in plants (Kacperska), terrestrial invertebrate cold hardiness (Somme), the ecology of Antarctic fish (Vacchi and colleagues) and low-temperature enzymology (Gerday and colleagues). As book chapters should, these attempt to summarize the state of knowledge in a given field, and, as such, they contribute to the emergent themes in low-temperature biology.

It is interesting to contrast the scientific approach in different areas of low temperature biology, as revealed in this valuable review of the complete field. Thus, plant physiologists are tackling questions of signalling pathways and genome analysis, while invertebrate ecophysiologicalists typically are interested in the function of specific molecules. Although stress proteins are implicated in protection from short-term exposure to cold in a variety of organisms, they appear to play only a minor role in long-term or evolutionary adaptation. Or, perhaps they are just insufficiently studied in this context?

A few chapters take a more focused view of recent results and these can provide exciting glimpses into new fields. Evolutionary biologists have long asked the question of whether there are any differences between evolutionary processes in cold and warm habitats. The chapter by Tutino and colleagues opens the exciting possibility that patterns of genetic diversity and mechanisms of gene flow might be quite different in the microbial community of polar soils from those in warmer habitats.

Overall, this volume is a helpful synthesis of current knowledge in key areas of cold-adapted organisms. Its strengths are

the wide taxonomic coverage and the attempt to take a holistic view from molecules to ecology. The papers reflect the growing interest in understanding thermal biology at the molecular level, and one strong theme is the close link between dealing with cold and coping with drought. If I had one criticism it would be that insufficient consideration is given to the important influence of timescale (acclimation versus evolutionary adaptation). I enjoyed this volume, learned much and would recommend it unhesitatingly to any scientist interested in temperature.

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EDB grows up

Evolutionary Developmental Biology: Second Edition

by Brian K. Hall

Kluwer Academic Publishers, 1998.

\$280.00 hbk, \$75.00 pbk (xviii + 491 pages)

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First the bad news: this book is very expensive. At the price tag of \$280 the hardback is only affordable to an exclusive set of libraries in a handful of countries around the globe. Fortunately, the paperback edition, although still very expensive, is a must read for anyone interested in evolutionary developmental biology (EDB).

The first edition of *Evolutionary Developmental Biology* was published in 1992 and was less than half the size (previously 275 pages, now 491 pages), half the number of chapters (previously 12, now 25) and half the number of references (now over 2200) of this second edition. In terms of organization, both editions are quite similar in the way the topic is approached. It is organized roughly into eight parts. The topics covered in these eight parts include: (1) a historical placement of the discipline of EDB (as Brian Hall calls it) and the interdependent relationship between development and evolution, plus a review of extinct and extant animal phyla; (2) Achetypes, phylogenetic stages, *Baupläne* and homology; (3) embryonic and life history stages in development; (4) innovation, complexity, multicellularity, and the developmental and genomic innovations necessary for the evolution of chordates and their major steps in diversification; (5) environmental

induction, adaptations and other interactions between environmental variation, genetics and plasticity in development; (6) a return to the topics of homology and of the interconnectedness of development and evolution, and the evolutionary mechanisms that shape developmental processes; (7) heterochrony and how embryos measure time; and (8) a summary of the major ideas of the book. Laudably, all chapters have an up-to-date 'endnote' section where ideas are developed further and referenced with the most recent publications. This structure adds a lot to the readability of the book.

In 1992, when the first edition of Hall's book was published, EDB was only a budding new biological discipline. Not least because of Hall's work, it is now an established scientific field with at least three new journals exclusively devoted to it. *Genes, Development and Evolution*, *Molecular Developmental Evolution*, and *Development and Evolution* have all been launched since the publication of the first edition. During the past five years or so, many leading universities have responded to the huge renewed interest in EDB by creating new faculty positions in this area and 'evo-devo' sections were established in scientific societies and funding agencies also.

Brian Hall's scholarly work aims to be the first textbook for this maturing field of EDB. His lucid and scholarly writing, and his most impressive knowledge of the literature and the history of the field, make this book a great pleasure to read and a treasure trove of information. The book is somewhat broader in its scope, and more oriented towards history, than Raff's¹ extremely insightful and influential book *The Shape of Life*. It is also more complete in its selection of topics than Gerhard and Kirschner's² recently published *Cells, Embryos and Evolution*, but Hall covers less of his own theories of the evolution of development in his book than they did. Hall's book is a highly authoritative summary of the current state of knowledge and how we got there from an historical perspective – it is less a devo-evo textbook that deals with how developmental biology 'works'. Because of that, in a devo-evo course, this book should be used jointly with Gilbert's³ *Developmental Biology* textbook. Hall's book would have been much improved if diagrams were presented in two or even in multicolors. Because development deals with morphologically complex two- or three-dimensional relationships colored graphics are an absolute must, but this was presumably too expensive for the publisher to agree to. Unfortunately, this omission diminishes the value of the book as a textbook of development – prior knowledge of developmental biology or the concurrent usage of a developmental textbook like Gilbert's³ is required.

Hall is surely one of the foremost historians of the field of devo-evo. Not since Gould's⁴ book *Ontogeny and Phylogeny* has the field been reviewed so masterfully. Gould's⁴ book can be credited (justifiably) with having single-handedly sparked a rekindled interest in the connections of development and evolution, which lay dormant for almost a century after Ernst Haeckel, Anton Dohrn and others who thought about it then. The book was the major cause for the interest among evolutionary biologists (and less so developmental biologists) in phenotypic plasticity and heterochrony during the 1980s.

Gould's book was published more than 20 years ago and dealt with devo-evo issues almost devoid of a discussion of the molecular basis of development – and that is where most of the progress in the 1990s came from. The new comparative molecular genetic and genomic data on gene expression and gene regulation from various model systems collected by biologists, formally known as developmental biologists but now termed evolutionary developmental biologists, during the past ten years or so is what is at the basis of the reincarnation of devo-evo. Debates that date back more than 100 years, about the ancestry of vertebrates from annelid or ascidian-like ancestors, which then involved people like Geoffroy, Semper, Dohrn, Gegenbaur, Kovalevsky and Haeckel, and that centered around arguments about segmentation and dorsal-ventral axes, have now been re-addressed with novel molecular data. These new molecular developmental data are mostly similar in expression patterns of presumably homologous genes in different regions of developing embryos from different phyla. Among the most exciting new findings are expression patterns of homologous genes that specify ventral and dorsal sides of embryos in protostomes and deuterostomes, respectively, or highly conserved genes that specify the expression of optical sensors in all phyla. The extremely high degree of conservation of developmental control genes, in terms of expression and interactions with other genes during evolution, came as the major biological surprise of the 1990s. The challenge remains to explain how body plans diversify during evolution in spite of this 'laxness of evolution', which keeps genes and their interactions the same. The crucial question is where does novelty come from and how does evolution diversify morphology?

Everyone now agrees that developmental processes affect evolutionary change just as evolution selects, canalizes and directs development, but how exactly this happens (e.g. through what kind of mutation or change in regulation of genes interacting or freeing up functions of genes through duplications of genes or genomes) is

unclear. We are still in the more undirected and observing 'natural history' phase of the discipline of EDB; a coherent set of theories of development, which would permit predictions to be made, is still required. Just like the incorporation of development into the modern evolutionary synthesis is still incomplete. However, I am confident that it will emerge, not least because of the large amounts of data that are being collected currently on all kinds of genes and gene pathways in all kinds of model systems. Obviously, the ongoing genome projects are going to do their significant part in permitting the elucidation of homology relationships among genes and gene families, which are at the basis of being able to compare developmental mechanisms across species and phyla in an established phylogenetic framework. Without gene and species trees, comparative developmental data cannot be interpreted properly.

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Tower of Babel

Linguistic Diversity

by Daniel Nettle

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Different human communities speak different and, for the most part, not mutually understandable languages. This fact is a mighty challenge to all naïve functionalist and adaptationist explanations of the origins and structure of language. Had language been the result of the need to communicate, then linguistic diversity should not have been possible. Whether less naïve approaches might succeed is an open question. Another elementary fact about language defies extreme innatist explanations. Because every human newborn can learn any human language, it is inconceivable that linguistic diversity might have been caused by some sort of cumulative allelic