Evolutionary immunology?

A review by A. F. Read

Evolutionary Mechanisms of Defense Reactions. By V. Vetvièka & P. Šíma. Birkhaüser Verlag, Basel. 1998. 196 pp. Price CHF 148.00/DM 178.00 ISBN 3-7643-5813-0 (hardback).

This book has the wrong title. Better might be *Comparative Physiology of Immune Defense in Metazoans*. Imagine a two-way table, with metzoan taxa (minus tetrapods) as columns and major elements of mammalian immunity (phagocytosis, cytotoxicity, thymus, complement system, antibodies, lymphocytes, etc.) as rows. Entered in each cell is present/absent/don't know. Then write a book justifying the cell entries. This is that book.

Of course, such a table is a start towards an historical account of the origin of the diverse immune mechanisms used by animals. But what evolutionary mechanisms might explain the diversity of animal defenses? On this, Vetvièka and Šíma are largely silent. Occasional glimmerings of theory are seen but these are truly frightening. ' ... there is a lot of [insect] taxa of which representatives are very minute creatures, or live in extreme conditions. We have no information about their immunity. The morphofunctional endowment of these miniature animals did not allow the development of sufficiently potent immunocompetent structures and organs. There remained only a few evolutionary pathways of how to escape pathogens, such as the shortening of individual's life span, rapid change of generations, or numerous offsprings' (p. 56; grammar as in original).

Nevertheless, at least two of the patterns described in this book demand explanation, if real. First, ever more sophisticated defence systems have apparently been added throughout evolutionary history. Why? Relatively simple mechanisms suffice for most taxa. It is tempting to think that increasing life span - and hence pathogen challenge – led to the need for ever more elaborate search and destroy systems. But there are some very long-lived invertebrates (oh, to know more about Nautilus immunity), and trees do fine without T-cell subsets or complement-mediated immunity. Part of the answer may be boring: given that most of the dazzling complexity of our own immune system has only been revealed in the last 30 years, it may be that the two-way table has not yet been filled in correctly. Indeed, it may be that the table should be larger: the assumption cutting through all

of this is that human immunity is somehow a pinnacle, rather than a subset of what is out there.

Second, immunological mechanisms are apparently conserved within large taxa. According to Vetviècka and Šíma, it makes sense to talk about 'annelid' immunity, 'mollusc' immunity and so on. Is this really fair? Remarkably few nontetrapod species have been subjected to immunological study – typically, only those of some economic or biomedical value: carp, earthworms, snails, mosquitoes. (As an aide, why is immunology one of the very few branches of basic biology not to have sought initial understanding from organisms simpler than mammals?) Is it fair to generalize to very large taxa from single representatives? If it is, the implication is that immunological innovation occurs early in the radiation of higher taxa. Does immunological innovation *facilitate* large-scale radiation?

And what favoured particular immunological innovations? For instance, it seems that, at least to a reasonable approximation, acquired immunity (immunological memory) was itself acquired only by bony fish (and hence tetrapods). Why? Vetviècka and Šíma go with the idea that innate immunity is sufficient only for the jawless. The idea is that jawed animals exploit food that causes more physical injury in the digestive tract. While some comparative methods might consider the simultaneous origin of jaws and acquired immune systems sufficiently improbable that they must be causally linked, it is not obvious to me. Indeed, there is the very real worry that such stories will proliferate as the data get better. If immunological innovation is indeed rare, we have a major problem. Like the origin of life, we would like at least one compelling story to explain the origin of novel immune mechanisms. But I cannot imagine competing stories being easily tested with single, unrepeated events.

So what might a book with the title of this one actually be about? I see two possibilities. First, the somatic evolution of the vertebrate immune system has some remarkable parallels with the intergenerational processes evolutionary biologists more conventionally deal with. Can population genetics give a quantitatively accurate account of how mutation and selection shape, for example, the B-cell repertoire of individual humans (or mice)? Immunologists have better data on the nature of mutational variation and the strength of selection on that variation than anything evolutionary biologists have yet come up with. Second, why does the relative importance of different immune mechanisms depend on host and pathogen, infective route, dose and so on – even within a species? As with decisions made by battlefield generals, a key must be the relative costs and benefits of the particular weapons systems that can be deployed. The microeconomics of defence is bread and butter to a number of subdisciplines in evolutionary ecology. Understanding the factors underlying investment in, say, spleenic tissue and antibody production rather than hyperinflammatory responses may also help us understand why the defence systems of older taxa are apparently insufficient for bony fish and mammals.

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Scratching itches

A review by Michael Mogie

Sex and Death. An Introduction to Philosophy of Biology. By Kim Sterelny & Paul E. Griffiths. The University of Chicago Press. 1999. xvi + 440 pp. ISBN 0-226-77303-5 (hardback) \$60.00/£47.95. 0-226-77304-3 (paperback) \$22.00/£17.50.

Some 2400 years ago Plato argued that everything that could possibly exist ought to exist. Why? Because as an aspect of its perfection, the god in which he believed would want the best, which would be full existence (because to exist is better than not to exist), and would be able to create it (Lovejoy, 1936). But what might this best of all possible creations be like? Thomas Aquinas pronounced on this issue some 750 years ago (Aquinas, 1947). He observed that individuals came into existence through reproduction but he believed that species had been created directly by the god described in Genesis. He concluded that these different causes of existence meant that species were more pure than the individuals they contained. In the best possible creation, species were the category of existence that should be maximized. This could be achieved in a finite universe only if species contained sufficient individuals to ensure their survival, but no more than this: the good of the species took precedence over that of the individual; individuals did not exist for themselves but to enable species to exist.

Designing deities have no place in modern biology. Instead, we have life evolving under the hidden hand of natural selection. The concept that nature *ought* to be such and such also has no place in modern biology. Instead, we have theories, hypotheses and speculations about why and how nature *happens* to be how it is, and we have debates about whether properties common to all living systems on Earth (e.g. they are, or are built from, cells) are necessary in the sense that they must be properties of life anywhere, any time, in the universe. Kim Sterelny and Paul Griffiths offer a thought-provoking introduction to how biologists and philosophers of biology are developing and utilizing these. The book has great breadth, with discussion ranging from units of selection to the role of contingency in evolution, from epigenesis to universal biology, and from morphospace to human nature. The parts are well integrated, being organized around a central theme of how rethinking the modern synthesis has played a major role in shaping the development both of evolutionary biology and of the philosophy of biology over the last 30 or so years (the authors describe the conception of evolutionary biology that is the modern synthesis as the 'organizational spinal cord' of the book). Of particular relevance here is the challenge offered by evolutionary biology to the central claim of the modern synthesis that both diversity and adaptation are explained by selection operating at the level of the individual organism.

Given this scope, it is perhaps not surprising that some areas are covered more thoroughly than others. Detailed and informative discussions are offered of adaptation and adaptationism, of whether Mendelian genetics can be reduced to molecular genetics (probably not, at least in any simple way), and of the interconnection of ecology and evolutionary theory (they operate at different scales and use different classification schemes but are intimately connected). In contrast, meme theory, which the authors doubt will tell us much about human society and culture, is dismissed rather too briefly. However, readers wishing to know more about a particular topic are offered an authoritative introduction to relevant literature at the end of each chapter. This will be particularly useful to readers new to the debates taking place within evolutionary biology.

The text is informative and often entertainingly robust, for example in its critique of evolutionary psychology, which it accuses of having been somewhat premature in its commitment to the concept of a modular mind, and in its account of the field of artificial life, which it describes as 'over-hyped'. The writing style leads to a good read, despite the authors' concern that the book is a 'long march'. At least it will be a good read for biologists from senior undergraduate onwards, because philosophical concepts are introduced with care. But I guess that students of philosophy who wish to obtain a taste of the philosophy of biology may find it a long march, because the biology at times lacks the clarity of the philosophy. In some cases, this problem could have been avoided by the inclusion of a figure (for example, in the discussion of adaptive landscapes). In some others it could have been avoided by modifying figures that are over complicated. This is the case, for example, for Fig. 9.4, which depicts the phylogenetic species concept but whose message is in danger of being lost in a storm of arrows, and from the