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Insect Metamorphosis

Xavier Bellés
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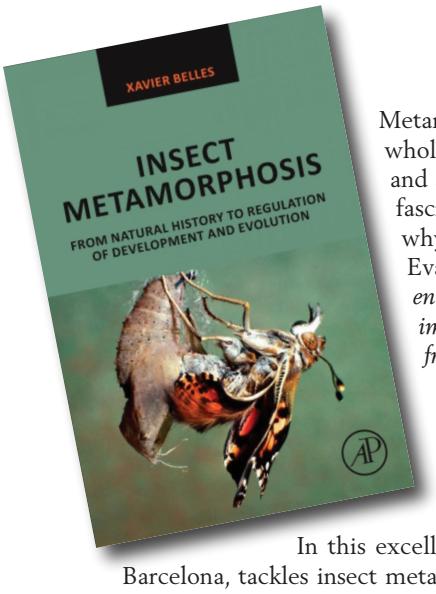

Metamorphosis, especially in its complete form, is one of the most striking phenomena in the whole of biology. It is as though a single life-form occupied two (or even three) entirely separate and alternating bodies that transformed from one to another during each generation. This has fascinated interested observers at least since the ancient Greek philosophers. To understand why metamorphosis is so strange to us, just stand back and appreciate this remark of Robert Evans Snodgrass [*Smithsonian Miscellaneous Collections*, **122** (9), 1-124 (1954)]: *"…in entomology we commonly think of metamorphosis as the transformation of a larval insect into the imago. In so doing, however, we overlook the fact, quite as extraordinary, that a caterpillar hatches from the egg of a butterfly."*

Is the caterpillar really the same individual animal as the butterfly? How is this extraordinary transformation achieved? What is the proximal reason for the change in body form? And how did the process evolve? Among other reasons for its perennial interest is the notion that metamorphosis is a larger scale, and therefore experimentally accessible, model for the development of an embryo from a fertilised animal egg.

In this excellent new book, Xavier Bellés, from the CSIC/UPF Institute of Evolutionary Biology in Barcelona, tackles insect metamorphosis with a special emphasis on molecular cell biology, but also relates this to the biological processes that are initiated and regulated by the hormonal and cell signalling pathways he describes. Bellés is an expert on this. He is one of a small number of scientists who worked out the nature of the MEKRE93 pathway, the regulatory system of three transcription factors, Met, Krüppel, and E93, which respectively direct the formation of the larval, pupal and adult stages of holometabolous insect development. A lot of the reason for writing this book was to explain how this pathway accounts for much of what is seen to occur during metamorphosis.

An important point, however, is that Bellés's own research concerns metamorphosis in hemimetabolic insects (i.e. those that undergo incomplete metamorphosis and don't have a pupal stage). This gives him a special perspective on the evolution of complete metamorphosis (i.e. that undergone by holometabolous insects). One of the take-home messages of the book is that the same signalling pathway is present in both kinds of insect and has been adopted during evolution by holometabolous insects for their own purposes with only minor adaptations. Moreover, Bellés is also an accomplished traditional entomologist with an interest in cave insects, some of which show extraordinary metamorphic adaptations. This allows him to write with authority on some of the more extraordinary variations in metamorphosis that are seen in non-model insects, and the book is particularly good on this topic, last covered with authority by Snodgrass [1954, *op. cit.*].

The resulting book is very good indeed. Its publication is an important event for entomology because it is the first attempt for many years to bring together in one place everything that is known about insect metamorphosis. It should certainly be in the library of every institution where insect science is studied. It is also an important book for all those who study animal phylogeny and evolution in general. Its publication is timely. Although there have been multi-author collections of papers about insect metamorphosis, the last major single-author scientific book about insect metamorphosis that attempted both to be comprehensive and to provide an authoritative overview was published no less than 66 years ago [Wigglesworth, V.B. (1954) *The Physiology of Insect Metamorphosis,* Cambridge University Press]. Thus, Bellés's book is now the most obvious starting point for advanced students of entomology, especially graduate students beginning to work on this topic for the first time, and also of course the authors and revisers of general textbooks of entomology.

The book is best described as a monograph, although it is much broader in its scope than most such publications. As is to be expected, Bellés gives due prominence to the work of his own group on metamorphosis, but he ranges very much wider than this, and I would say that he has been scrupulously fair in dealing with the contributions of others. This is particularly important because there are still points of significant controversy in the field.

Writing this book can have been no mean task. The sheer mass of literature on insect metamorphosis is intimidating. Weighing the importance of all those papers requires a great deal of experience. This kind of sifting, comparing the work of many individual scientists to theories which may be of long standing (and which sometimes deserve to be overturned!), is an

essential component of the collective scientific enterprise. I am firmly convinced that a book is sometimes the best way of doing this, and I am heartily glad that Bellés has attempted this task on behalf of the community of students of insect metamorphosis.

The book is not always an easy read because it is packed with detail and includes a very large number of references. This is obviously a very strong point. Its breadth and depth go much further than any available recent review paper (examples are the several papers in a special issue of *Philosophical Transactions of the Royal Society* (Vol. 374), and the excellent recent review paper in C*urrent Biology* by J.W. Truman, 2019). I'd like to tell you exactly how many references there are in Bellés's book but because they are listed at the end of each chapter and many are thus listed multiple times, they are hard to count. I confess that I would have preferred a single list for the whole book.

This raises an interesting point. The reason that the references are listed in this way is presumably because the book is also available in electronic form, one chapter at a time (each chapter has its own DOI identifier). In preparing this review, I used a real printed copy of the book. But I suspect that most readers will actually look at the electronic version, and I fear that this probably means many people will just look at one chapter. They probably won't actually read the book all the way through, as it deserves. Perhaps I am getting to be a bit of an old fogey, but I think that to appreciate the integration of a subject that a good book can achieve, you have to read the whole of it.

Stuart Reynolds