Biased Embryos and Evolution

WALLACE ARTHUR

Professor of Zoology
National University of Ireland, Galway

CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011–4211, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014 Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published 2004

Printed in the United Kingdom at the University Press, Cambridge

Typefaces Trump Mediaeval 9.5/15 pt. and Times *System* LaTeX 2$_\varepsilon$ [TB]

A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication data
Arthur, Wallace.
Biased embryos and evolution / by Wallace Arthur.
p. cm.
Includes bibliographical references (p.) and index.
ISBN 0 521 83382 5 – ISBN 0 521 54161 1 (pbk.)
1. Developmental biology. 2. Embryos. 3. Evolution (Biology) I. Title.
QH491.A768 2003
571.8 – dc22 2003062621

ISBN 0 521 83382 5 hardback
ISBN 0 521 54161 1 paperback

Contents

I The microscopic horse

You ask me to describe a horse; I answer as follows. A horse is a microscopic animal that is incapable of movement. It consists of a rather small number of cells (a few hundred, as opposed to the trillions found in a human). These cells are not organized into sophisticated organ systems. The horse is a parasite of another animal, and so acquires its resources from its host. It is entirely incapable of acquiring energy in any other way. There is no fossil record of its existence, so for all we know there may have been no such thing as a horse before the dawn of the art age in the caves of France, where our forebears drew remarkably good pictures of horses, among other things.

But wait. Their horses don't look like my description. And indeed since my description at first sight looks quite mad you might wish to agree with the cavemen and not with me. There is, however, method in my madness. My description is fine. It just refers to a time-slice in the horse life cycle that is different from the one we normally picture in our minds at the mention of the word 'horse'. We picture the adult, or if not this then perhaps a beautiful but unsteady newborn foal. What I have pictured is the horse as an early embryo, invisible to our view because it is implanted deep within its maternal host.

The point I am getting at here is that animals, and indeed all organisms, are four-dimensional things. The three dimensions of their bodies expand and change as they slide along that slippery and inevitable slope of time. Even as adults we change, albeit more slowly and often not in encouraging ways. As the American biologist John Tyler Bonner has put it, organisms do not *have* life cycles, rather they *are* life cycles.[1] We tend to picture adults in our minds for all sorts of reasons. Our brains handle three dimensions more easily than four. Adults are bigger and more visible. Even when developmental stages are big and conspicuous, like tadpoles, they are often short-lived compared with the adult. But this is not always so. In some insects, perhaps most famously mayflies, the adult lives a transient life of at most a few days, while the developmental stages through which it was produced lasted much longer. But even in these cases where the rationale for thinking in terms of life cycles is strongest, we still tend to picture the adult in our mind's eye.

The reason for this is rooted in language. Often, at least for familiar creatures, the very word we use may be adult-specific. A tadpole is, arguably, not a frog. But is a foal not a horse? And the same applies in the invertebrate world. A caterpillar is, arguably, not a butterfly (though its genes are identical); but a baby centipede is definitely a centipede.

Whether we should fall into the old familiar groove of picturing the adult, or whether we should be more mentally adventurous and try to force our lazy brains to go 4-D and 'think life cycles' depends on what we are trying to do. For our cave-painting ancestors, the adult was all that was required. But for understanding how horses evolve, this static picture just won't suffice. Every stage in a life cycle only comes into being if the previous one survives. An adult can only come into being if *all* the earlier stages survive. At the level of the individual, death is all too real an option at every single stage. Therefore at the level of the population there will be natural selection at every stage – because at each stage some individuals will live and some will die. Of course the living and the dying could be genetically identical and the difference merely a matter of chance. But the last century's accumulated knowledge of the huge amount of genetic variation present in nearly all natural populations suggests otherwise.

All this is beginning to sound very conventionally Darwinian. And in some ways, so it is. But Darwinism is all about mechanisms, and we are not quite ready to discuss those yet, or to consider the extent to which Darwinism is acceptable to those who take a developmental approach to evolution. First, we need to complete the mental shift that we have begun towards a four-dimensional view of organisms.

Let's consider a very simple evolutionary tree with just four species: ourselves, a cow, a hen and a fish. There are three ways we can picture this evolutionary tree, as can be seen from Figure 1. First there is the tree of adults; then there is the tree of embryos; finally there is the tree of life cycles. Which is best? The answer is the life-cycle tree. The others are three-dimensional shorthand. The embryo tree is a means to an end, not the end itself. Consideration of the embryo tree is meant to reveal the arbitrariness of using, as most folk do, the adult tree. In fact, since most species experience most mortality at young rather than old ages, it would seem more sensible for those intent on 3-D shorthand to use an early developmental stage as the basis for their tree. That is, they should use an embryo tree rather than an adult tree, because if we want to think in terms of some variants doing better than others in the survival game, this would seem a sensible place to start. Which has the higher mortality rate – tadpoles or frogs? Statistically speaking, there's no contest.

A tadpole, however, is not an embryo. Usually, we restrict the term embryo to those developmental stages that are protected from the elements by virtue of their location within their mother's body or, in some instances, within the casing of an egg. So our embryo tree is too simple. Science is all about generalizing (more on this in Chapter 6), and embryos are special cases of the more general concept of developmental stages. But then again, these stages, like the adult, have no clear boundaries. A life cycle does not operate in discrete stages – rather the process of development is a continuous one. This is even true in those cases, like the tadpole/frog, where major changes occur between one 'stage' and the next. Life flows. So, using the embryo tree as a means of forcing our thoughts out of old and inappropriate habits, we nevertheless end up not with this tree any more than the tree of adults. We end up with the life-cycle tree.

* * * *

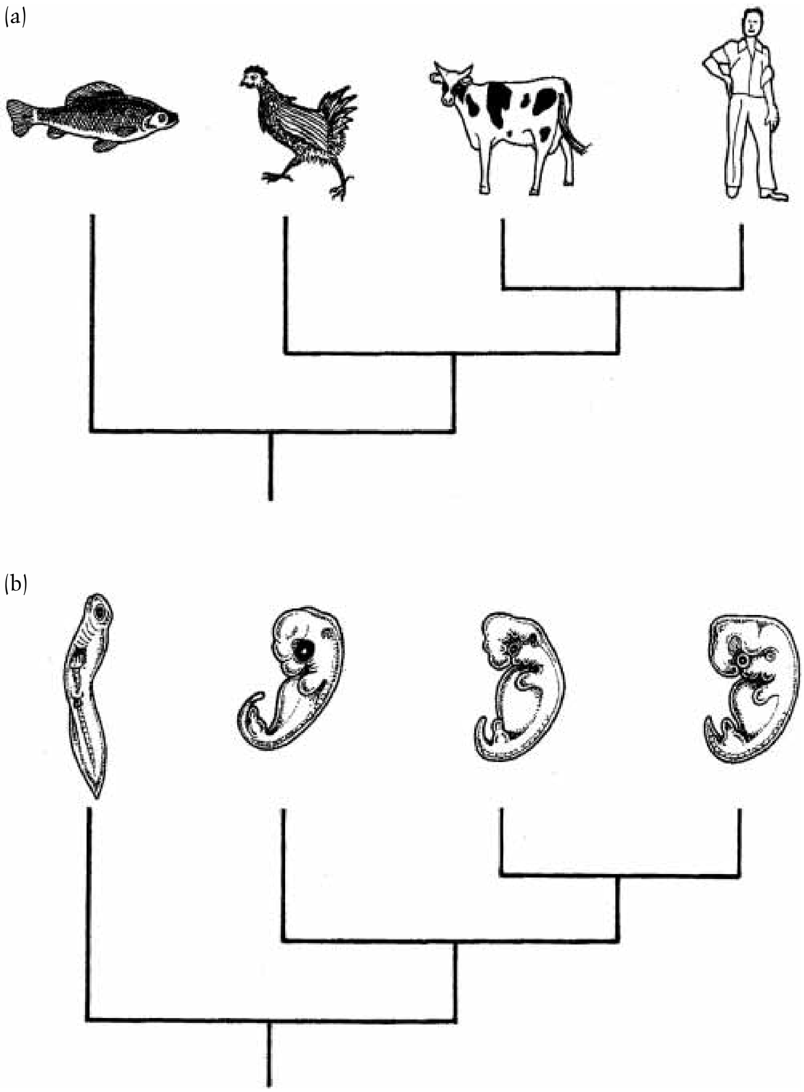

FIGURE 1 Three ways of picturing evolutionary trees: (a) adult tree; (b) embryo tree: (c) life-cycle tree.

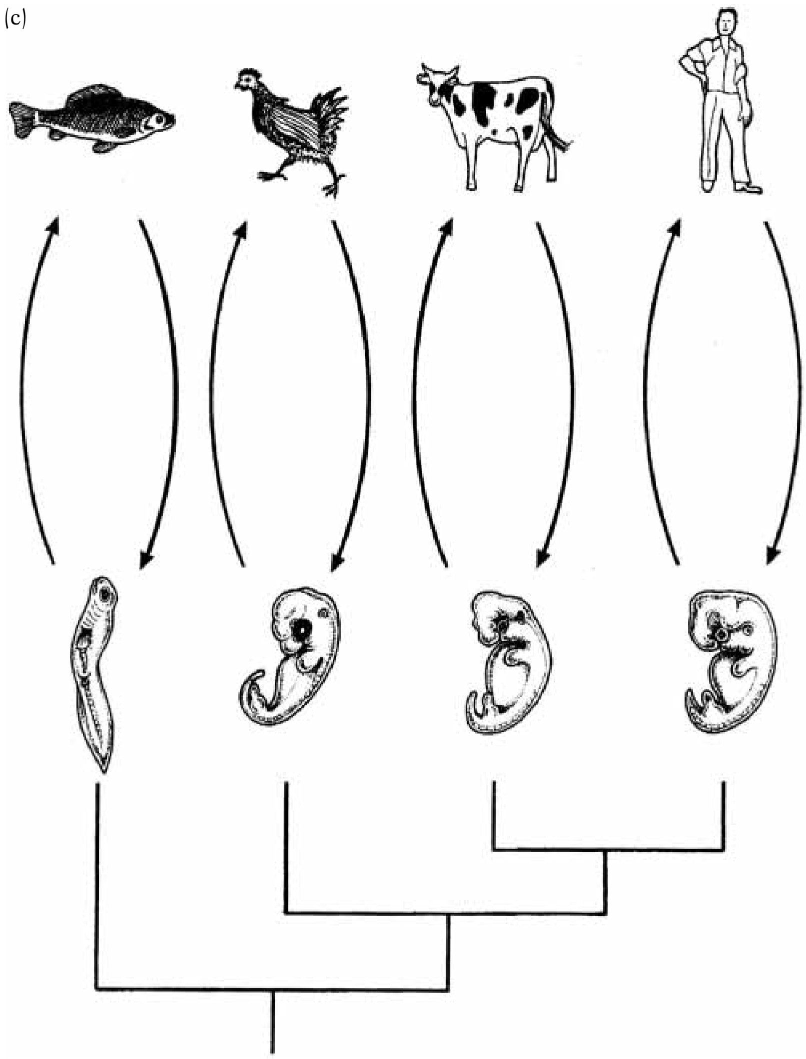

FIGURE 1 (Continued)

If we venture into the realm of imagination, it is possible to go forwards or backwards in evolutionary trees. And there is a major difference concerning time travel in these two directions. Consider yourself as an observer represented on any of the versions of Figure 1 by a bright red symbol (a monorail train is appropriate here) moving inexorably along the line of descent. If you move forward in time, you keep being faced with a series of decisions to make. Right fork or left? But if you start at the top of the tree, at the twig representing any of the four arbitrarily chosen extant species, and move backwards in time, no choices arise. Rather, you just keep going until you fall off the end into the primordial soup.

This picture of reverse-gear evolution is useful because it serves again to remind us that life flows continuously between generations as well as within them; over millions of years as well as periods of a few days. Begin with a human life cycle and start going back through the generations. Then accelerate. Eventually you are blasting back through ape-like life cycles, then through even less humanoid ones; and you might just notice the thin confines of a flatworm life cycle before you completely lose your head. (The first animals didn't have any.) Countless backward cycles have taken you close to the dawn of animals.

Notice that I said 'ape-like' rather than 'ape'. Present-day apes, like the chimp, are not our ancestors any more than we are theirs. No current species is the ancestor of any other. This is logically impeccable but frequently forgotten in careless discussions of evolution. Of course, following a lineage divergence, one line of descent may undergo much more profound changes than the other. But this does not mean that the comparative evolutionary slowcoach is standing still. In evolution, no one stands still for very long. Even when nothing much is happening on the outside, molecular changes are happening within.

What causes one life cycle to be different, even if just ever so slightly, from the one that went before? To consider this question, let's think of each life cycle as starting with a fertilized egg and ending with an adult. Although this disregards the chicken-and-egg problem, we need to have some landmarks to find our conceptual way, and these are as good as any. Indeed, there is one respect in which this particular mental picture is best. This concerns codes versus actual things. The fertilized egg is a minimal thing, as animals go. In our case, it is a tiny fraction of a trillionth of what will follow in terms of cell number. But from an information-content perspective it is just the same. The egg contains all thirty thousand or so genes of the recently revealed human genome. No new genes are created as we develop. Occasionally, as in mammalian red blood cells, genes are lost. But generally, the genes are simply copied each time a cell divides. So one way to look at development is as a means of getting from minimal form and maximal encoding to the opposite state of affairs through a complex interconnected series of code-readings and construction events (of which I give some examples in Chapter 4).

An offspring life cycle will thus be different from its parental life cycle only if something that affects the great developmental unfolding has changed. Such things can be of two rather different kinds: genetic or environmental. If you take a big fly that grew up with lots of great maggot-food and get it to lay an egg somewhere where the food supply is only just sufficient for growth, the new life cycle will produce a smaller fly with fewer and/or smaller cells. Alternatively, if the new food supply is the same as the old, we might still get a smaller fly if a gene involved in the production of a growth hormone has mutated. In general, it is the latter, genetic type of change that is of interest to those who study the evolutionary process. However, the two cannot always be so neatly separated. Sometimes they interact. For example, a gene mutation can alter the way a developmental process responds to an environmental change. But for now things are complex enough, so I will defer discussion of such matters until Chapter 12.

The American evolutionary biologist Leigh Van Valen once said[2] that 'evolution is the control of development by ecology'. This statement, which I believe captures only part of evolution's essence, would benefit from dissection. What Van Valen meant was that, over the years, as environmental conditions change (or as organisms invade new environments, which amounts to the same thing), those life cycles that are fittest for their environments prosper. Or, to put it another way, the environment is moulding life cycles through the agency of natural selection. Given genetic variation for life cycle features, those genes that produce what we can for now simply call fitter life cycles tend to spread, while those that produce less fit ones gradually die out.

If this is how evolution works, then to understand it we need to know about two things: the mechanics of natural selection (the Darwinian realm), and the mechanics of building bodies (the developmental realm). But if that were all you needed to know, I could simply refer you to two textbooks – one on population genetics and one on developmental biology – and you could read first one and then the other. If that were the answer, it would have saved me the job of writing this book. But while that way lies some of the truth, the whole truth is harder to acquire. In my view, a developmental approach to evolution is not simply a bolting-together exercise. Rather, it is a case of the whole being more than the sum of its parts.

What I mean by this is that juxtaposing the two great disciplines of evolutionary and developmental biology produces insights that do not emerge from either on its own – including an insight into what determines the direction in which evolution proceeds. These insights alter in a fundamental way both how we see embryos and how we see evolution. They collectively characterize the nascent field of Evolutionary Developmental Biology or 'evo-devo'. In the approach used by students of evo-devo, embryological (and larval) development becomes a front-line soldier in the battle to construct an elegant, accurate and complete evolutionary theory, rather than some straggler at the rear that everyone has long since forgotten. Let battle commence.