Anomalous larvae and the burning of heretics[1,2]

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Anomalies in a received conceptual framework may show the way to, or at least show the need for, a new framework. Kuhn made this the centerpiece of his theory of scientific revolutions, but despite the resulting association with supposedly mutually untranslatable paradigms and the like, the point is valid and applies at all levels. Of course, it is usually possible to modify the existing framework to accommodate the anomalies, in a natural way or with more or less adhoccery.

Williamson has given us a new set of anomalies. Mostly he does this by showing that what we know doesn't fit together as well as we thought it did. In particular, the major phylogeny of the animal kingdom as estimated from adult characters doesn't fit very well with that estimated from larvae. Such a discrepancy for different stages has occasionally been reported within families of insects, and it has an apparent resemblance to the discordance occasionally found between phylogenies inferred from morphological and molecular characters. In such cases the usual conclusion (I ignore data chauvinists) is that we should somehow use all the available information to infer the correct phylogeny. After all, there was just one real phylogeny that occurred in the past, and we want to find it as closely as we can.

For Williamson there was not just one real phylogeny. Larvae sometimes have a very different ancestry from adults. Again, this view has an apparent resemblance to the theory of the early evolution of eukaryotes by endosymbiosis, and Margulis actually provides a forward to the book, gently chiding him for being too orthodoxly neoDarwinian. And, there, Williamson is indeed orthodox. His heresies are elsewhere.

Are the anomalies real? I think so, but I would like it shown more definitively than is done in this book. I don't mean the now usual practice by cladists of plugging (often developmentally, functionally, or adaptively related) characters into somebody's program and believing what is excreted, usually without much regard for the likelihood that several or many trees are consistent with the real data at a level of belief (confidence) corresponding to a five-percent or so significance level. What I would like is a specific consideration of character complexes on a scale as broad as the apparent divergence of larval and adult phylogenies. Yes, echinoderm larvae resemble those of hemichordates, in presumably derived ways. But the details aren't here. And if adult echinoderms don't fit with hemichordates, just where do they fit? And why, exactly? Williamson does make a plausible case that to invoke larval convergence is grasping at straws. But he may be wrong. (continued)

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[1]Contribution 118, Lothlorien Laboratory of Evolutionary Biology.

[2]**Larvae and Evolution**: Toward a New Zoology.
Donald I. Williamson. 1992. Chapman and Hall. xiv + 223 pp. Acid-free paper. ISBN 0-412-03081-0. Hardbound. $40.00 (minus 5 cents).

Evolutionary Theory 10: 279-281.

Taking seriously the idea of a double phylogeny (for many groups,not just the example I gave) is one heresy. Williamson's explanation of the putative phenomenon is another. He invokes hybridization between members of distantly related groups, such as different phyla. This itself isn't as ridiculous as it seems from our experience of terrestrial animals with courtship, internal fertilization, and the like. In the sea spermatozoa often find themselves with no egg nearby but a stranger's. An egg's defenses are good but not always perfect, and sometimes a wrong sperm gets in and initiates development.

One would expect that a wide hybrid wouldn't get very far in development, having not merely unintegrated but conflicting instructions coming from its two haploid genomes after the initial phase of control by inherited maternal proteins, organelles, and mRNAs. Facts can destroy beautiful theories, though, and the frontispiece of Williamson's book is a picture of a 29-day-old hybrid larva from an ascidian egg fertilized with a sea-urchin sperm. Oddly, it expresses the paternal genotype, not the maternal one, and looks like a good pluteus larva. It isn't a unique case, and some individuals have actually metamorphosed before eventually dying. Williamson lacks the facilities for the obvious tests to make on the genotype of such hybrids; he and I hope that others will pursue this. After all, it hasn't been fully excluded that only the paternal genome remains.

A subsidiary heresy comes in Williamson's explanation for the occasional developmental success he proposes for wide hybrids. He gives evidence that in some groups metamorphosis from the larval stage involves effectively a complete formation of a new individual, which is not the case even with holometabolous insects. (The larva may persist, feed, and swim around for a while afterward!) This suggests the existence of a real double developmental program, one for the larva and one for later development. That for the larva must be switched on, and the other suppressed, initially. Thus, eureka. The larval program of the sperm's genotype is initially switched on in ther hybrid, and only later is control transferred to the egg's genotype.

I find this proposal difficult to accept. It seems to require having effectively the same control mechanism operate in different phyla. Not just the same organization of control, but the molecular details of recognition. And the backcross, to produce a population rather than an individual, doesn't have as severe problems as Goldschmidt's hopeless monster but it doesn't seem straightforward.

However, this isn't where the major heresy will founder, if it does. The existence of the proposed double ancestry is easily testable, if done appropriately, by nucleic-acid sequencing. Again, I hope that this will actually be done. A small chance, perhaps, but a large gain in knowledge if Williamson is even partly right.

Heresies, including those discussed here, usually have difficulty getting published. A new concept is, by its very nature, uncomfortable and perhaps even threatening. And most new concepts prove to be wrong anyway. For instance, Raff's direct-developing species of the sea urchin *Heliocidaris* (e.g. Bioessays 14: 211 [1992]) is clearly derived from a larvaceous ancestor, and its early development is remarkably altered. Why not evolve in this other direction sometimes, rather than invoking hypothesis piled on unproved hypothesis?

We return to the anomalies. I find the phyletic anomalies to be the most convincing, but there are others which I haven't mentioned, such as what Williamson calls cataclysmic metamorphosis. Here it is

received views which are reduced to adhoccery. So who is right? My point is that the subject seems worthy of attention rather than of reflexive ridicule.