

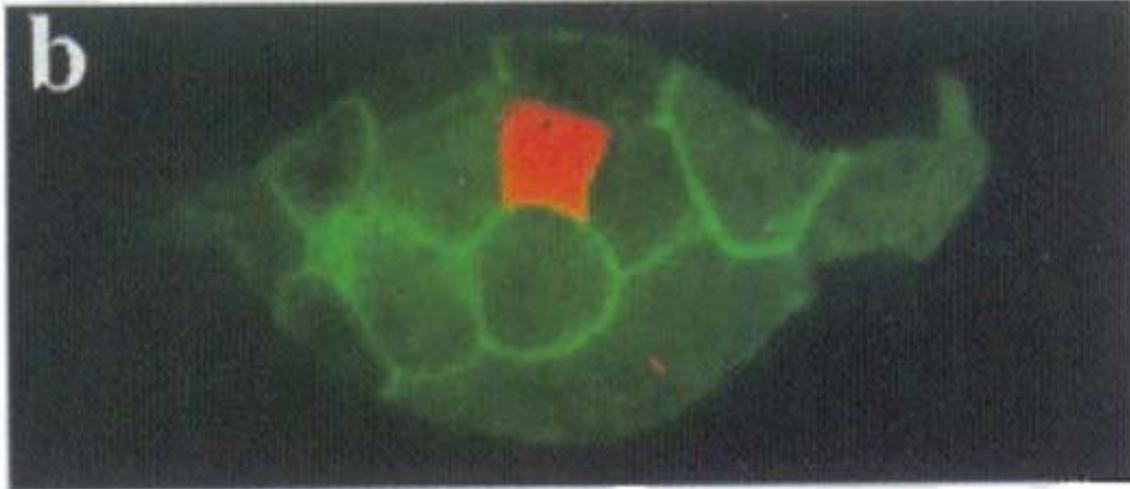
SEARCHING FOR DEEP VARIATION IN THE MODEL SYSTEMS OF EVO-DEVO

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Abstract: Evolution by natural selection requires variations that (a) exhibit fitness differences, and (b) are heritable. We use these criteria to examine what McDonald called a “great Darwinian paradox,” namely, that there is little evidence for relevant variation at “those regulatory loci set deep with the control network” (1983, 92-3) of metazoan ontogenies. Currently, the absence of heritable variation in what Wimsatt calls the “deeply-entrenched” features of ontogeny has led many investigators to argue that profound temporal asymmetries exist in evolutionary history; in short, things were different in the pre-Cambrian. Yet it is unclear how ontogenetic architectures early in metazoan history could have differed fundamentally from present-day systems. We have commenced a survey of the literature of the principal model systems of evo-devo, as well as lesser-known systems, looking for evidence of heritable mutations in such features as cleavage patterns, axis specification, or modes of gastrulation. The continued absence of such evidence suggests that it may be time to re-examine basic assumptions.

THE PROBLEM

- A. There are striking differences in the early development in animals, even within classes and orders.
- B. Assuming that these animals are descended from a common ancestor, these divergences suggest that early development evolves relatively easily.
- C. Evolution by natural selection requires heritable variation.
- D. Heritable variations in early development are not observed.*
- E. Therefore, we may be justified in questioning basic assumptions.



[figure from Grbić and Strand 1998]

This is an insect embryo, from the parasitic wasp *Aphidius ervi*. The pink cell contains a tracer dye smaller in size than *Drosophila* transcription factors. As development continues, the dye will remain in the injected blastomere. Unlike its dipteran cousins, therefore, early development in the hymenopteran *A. ervi* “proceeds in a cellularized environment” (Grbić and Strand 1998, 1099), not a syncytium. Equally remarkable examples of early ontogenetic divergence abound (e.g., in nematodes; Felix 1999; Schierenberg 2001).

Indeed, these divergences have now become a commonplace of the evo-devo literature, and are taken as *prima facie* evidence – against the widely-held neo-Darwinian conviction – that early development evolves dramatically. “It is clear that a casualty of [these comparative data],” argues Davidson (1990, 384), “is the 19th century concept that early development must be an evolutionarily conserved process” – a concept, interestingly enough, which Davidson himself advocated in 1971: “One can imagine modest alterations or additions to the early parts of the developmental program,” he wrote at the time, “but it would be very unlikely that such programs could be supplanted” (1971, 131).

The classical view of conservation of early development collapsed under the weight of comparative data. Yet there remains a striking paucity of *experimental* evidence showing heritable variation in what Wimsatt and Schank (1988) call the “deeply-entrenched” features of metazoan development. We have begun a broad survey of the developmental literature, looking for such cases, and thus far have found surprisingly few.

Why is such deep variation so hard to find?

WHAT DOES THE LOGIC OF NATURAL SELECTION REQUIRE?

For selection to occur (Endler 1986), a population requires:

A. Variation in a trait q

**B. Fitness differences in consistent relation to the presence of trait q ,
and**

C. Heritability of trait q .

The experimental literature on model systems such as *Drosophila* describes many mutations in early developmental characters and patterns. With rare exceptions, however (see note* below), such mutations are *not* heritable, in the sense that the phenotypes exhibited do not survive as stably-breeding lines. As a result, some have argued that we should not expect mutagenesis to reveal the basis of adaptive variation: “The take home message,” argues Nagy (1998, 820), “is that mutagenesis in model systems does not undo evolution or reveal, in any direct fashion, the basis of evolutionary change.”

But if the experimental literature does not provide evidence of heritable deep variation, how do we know that such changes are even possible? “Comparative embryology abounds,” argue Wray and McClay (1989, 811), “with empirical evidence of evolutionary modification of early development.” The theory of common descent, of course, underwrites the assumption. *Because* the animals are related by descent from a common ancestor, *therefore* it must be possible for early development to vary heritably. “So the dilemma is easily solved,” argues Thomson (1992, 112). “Because early stages have changed, they must be capable of change.”

What if the evidence from model systems continues to suggest that fundamental variation in early ontogeny is not heritable?

Might we have to question basic assumptions?

THE HYPOTHESIS OF TEMPORAL ASYMMETRIES IN ANIMAL EVOLUTION

Among the leading solutions to this puzzle is that proposed by Campbell and Marshall (1987), Foote and Gould (1992), Arthur (1997), and Erwin (1994, 2000), among others. ***Macroevolutionary processes acting over the history of the animals display temporal asymmetries, such that at certain critical periods – e.g., the Cambrian Explosion – adaptive changes in ontogenetic architectures were possible that are no longer accessible to selection.***

“There seems to be no alternative,” argue Campbell and Marshall (1987, 97) “but to seek some unusual feature of the primitive genome that would allow it to change in such a way that large coordinated viable morphological changes could take place over short periods of geological time.” After these critical periods, ontogenies supposedly “hardened” (McKinney and McNamara 1991, 363), and now resist fundamental perturbation.

This hypothesis places tremendous weight on the theory of common descent, at a fairly high cost to what we know from genetics and developmental experiments. The “labile” ontogenies from the hypothesized critical periods in evolutionary history are typically uncharacterized (i.e., they are unarticulated beyond the level of postulates). Furthermore, how exactly would a pre-Cambrian metazoan be free to vary in ways that it (now) could not? “One cannot ignore the fact,” argues Levinton (2001, 857), “that a stable developmental program was just as necessary for survival in the Cambrian as it is today.”

CONCLUSION

On the assumption that dramatic divergences in early development are due to evolution by natural selection from a common ancestor, we would expect to see substantial heritable variation in early development. The fact that we do not suggests that we may need to question basic assumptions.

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*The only notable exceptions involve *losses* of structures: e.g., Swalla's work on the loss of the tail in ascidian larvae. [See Swalla, B.J. and W.R. Jeffrey, 1996, "Requirement of the *Manx* gene for restoration of ancestral chordate features in a tailless ascidian larvae," *Science* 274:1205-1208.] Mutants that reverse the direction of shell coiling in gastropods are another frequently-cited exception, but their evolutionary significance is unclear.