

Did Natural Selection Construct Metazoan Developmental Sequences?

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Abstract

The necessary and sufficient conditions of the process of natural selection (Ender, *Natural Selection in the Wild*, 1986) are (1) variation, (2) selection or fitness differences, and (3) inheritance. These conditions impose evidential demands on any investigator who wishes to employ natural selection in evolutionary (i.e., historical) explanation. Data from model systems (e.g., *C. elegans*, *Drosophila*, and *Danio*), as well as theoretical analyses, raise challenges for the use of natural selection as the causal process responsible for the origin of developmental sequences. In particular, the conditions of (2) selection differences and (3) inheritance have not been adequately described in current theories of the evolution of the Metazoa.

I. The Problem: “The Paradox of Teleological Evolution”

In his classic text, *Order in Living Organisms*, evolutionary biologist Rupert Riedl described what he called the “paradox” of “teleological evolution” (1978, 219-20). He illustrated the paradox with a diagram of gastropod early cleavage stages (Figure 1), although any bilaterian developmental architecture would also make the point.

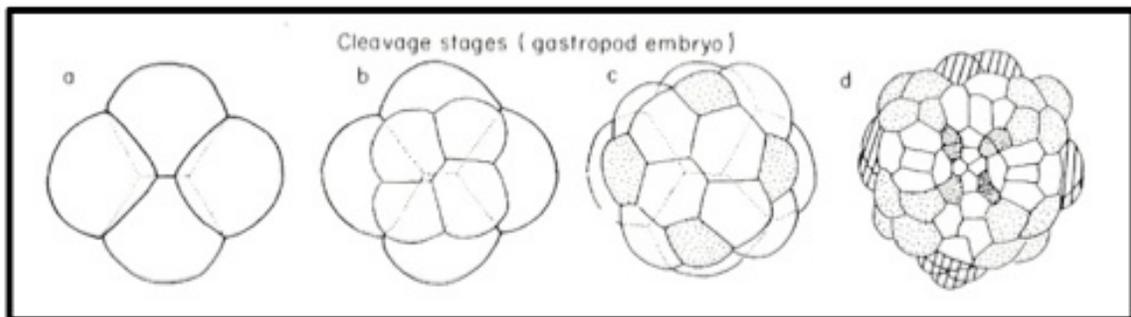


Figure 1. Riedl’s (1978, 221) illustration of the paradox of “teleological evolution” – early cleavage stages in a gastropod embryo.

These developmental stages, Riedl argued, cannot represent “functional ancestors,” because the stages are only temporary way-stations *en route* to the reproductively capable adult. The parts of embryos “always strive towards functions,” Riedl observed, “without

being able to possess them during their formation.” It would be “naïve,” he concluded, to imagine “that the Algonkian seas were populated at one time with four-cell stages, and later with eight-cell stages and that these finally decided to let cell 4d sink in, so as to form the future musculature” (1978, 220).

Any evolutionary or developmental biologist would agree. The Principle of Continuity (Orgel 1968; Wolpert 1994; Penny 2005; Sly *et al.* 2003) requires that all organisms in a lineage of descent with modification be viable and reproductively capable. A four-cell gastropod embryo could have evolved, therefore, only when it would have been viable and stably heritable.

But when was that point in the lineage of the Mollusca? Riedl does not say, and refers the historical origin of “primordial development” to “self-organization” (1978, 213), without elaborating further. We can ask, however, **whether the process of natural selection could have caused the evolution of gastropod cleavage patterns, or indeed any bilaterian developmental architecture.** This problem is currently unsolved.

II. The Process of Natural Selection and Its Evidential Requirements

The process of natural selection (Endler 1986) comprises three jointly necessary and sufficient conditions, which may be expressed by the following conditional:

If, within a species or population, the individuals

a. **vary** in some attribute or trait q -- *the conditions of **variation**;*

b. **leave different numbers of offspring** in consistent relation to the presence or absence of trait q -- *the condition of **selection differences**;*

c. **transmit** the trait q *faithfully between parents and offspring* -- *the condition of **heredity**;*

then the frequency of trait q will differ predictably between the population of all parents and the population of all offspring.

Endler (1986) notes that one must provide evidence for the conditions of (a) variation, (b) selection differences, and (c) heredity to infer the action of natural selection in explaining the origin of any trait (Figure 2 – the “three legs” of the stool).

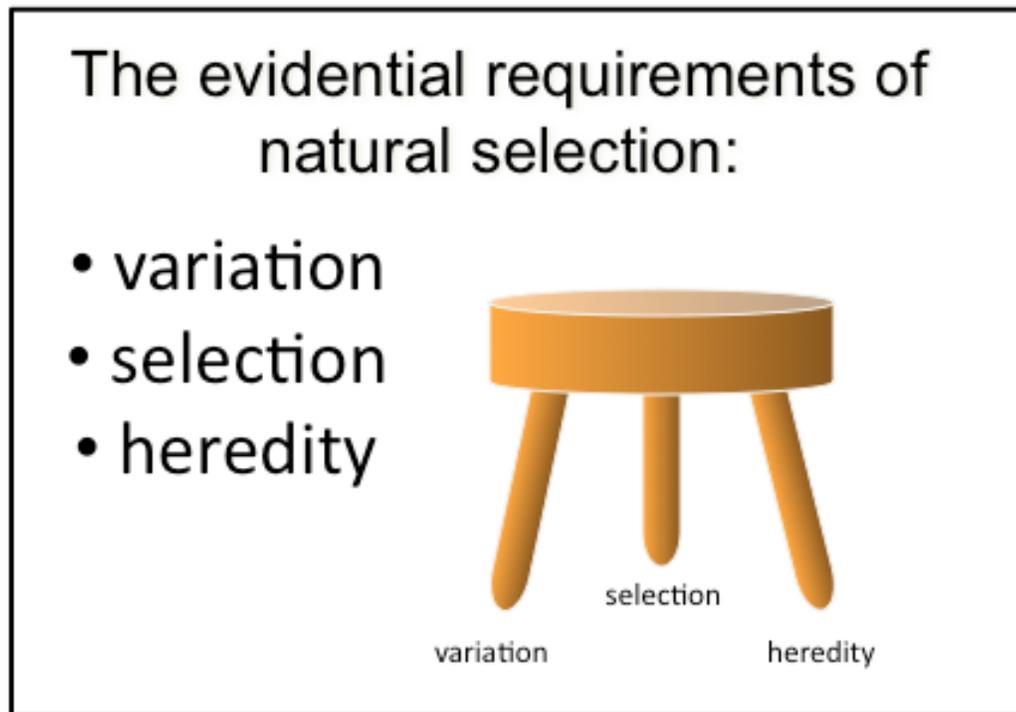


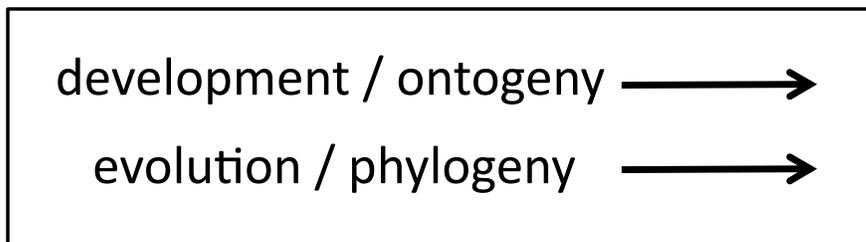
Figure 2. The necessary evidential requirements to infer the role of natural selection in the origin of any trait.

With this formulation of natural selection in hand, we can turn to the question of the origin of bilaterian developmental architectures. We wish to know if the first appearances of the molecular, cellular, and systems-level features found in the

developmental pathways of groups such as nematodes (*Caenorhabditis elegans*), arthropods (e.g., *Drosophila melanogaster*), or vertebrates (*Danio rerio*), are best explained by natural selection. For this, we may in each case employ the following schema, a **Developmental Characters Evolutionary Timeline (DCET)**.

III. Locating the Embryonic Characters to be Explained in Evolutionary History: Developmental Characters on an Origins Timeline

Even before Darwin, naturalists had noted striking parallels between the “unfolding” of animal development in each new generation, and hypotheses about the evolutionary history of the animals.



Although the empirical generalization “ontogeny recapitulates phylogeny” was known to be false in the late 19th century (Gould 1977),

developmental and evolutionary biologists still seek clues about the origin of embryonic characters by broadly comparative analyses. We may ask a related question: ***when, in the history of any taxon, did its specific developmental characters first appear?*** Consider, as an example, Riedl's own question about the first appearance of the four-cell stage in gastropods. (See Figure 3.)

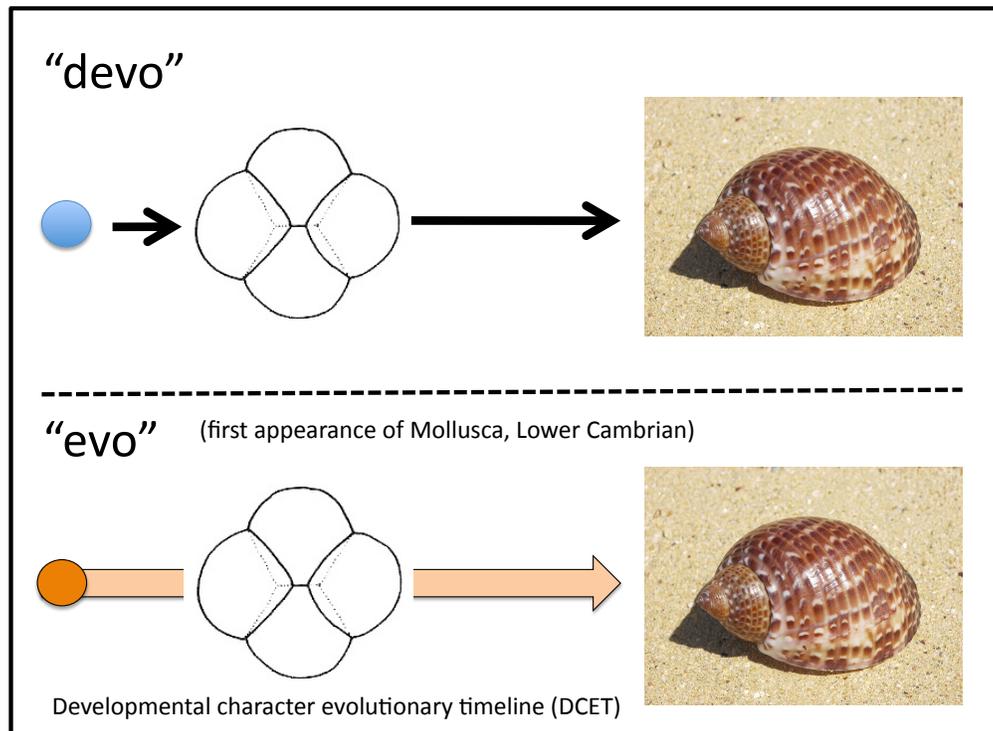


Figure 3. When and by what process did the four-cell stage, now observed in gastropod embryogenesis, first appear? The character may be located as a point on a developmental character evolutionary timeline (DCET).

The “evo” answer is unknown – and we face the problem that macroscopic form of Mollusca (that is, as body fossils in the Cambrian) requires us to postulate the co-existence of some embryonic architecture capable of building the organisms in each generation. **Thus, we must presuppose the existence of the very feature, the four-cell stage, whose origin we want to explain.**

The same difficulty recurs when we consider the origin of other key embryonic characters in well-studied model systems, such as the two-cell stage in *C. elegans* (see Figure 4).

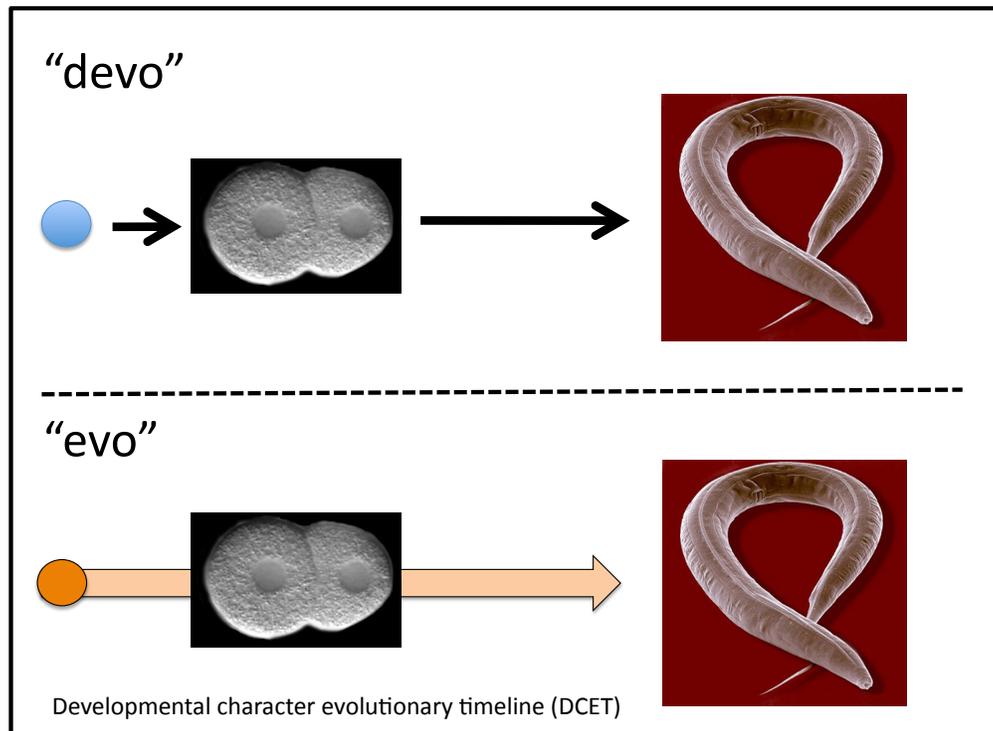


Figure 4. When and by what process did the two-cell stage in *Caenorhabditis elegans* first appear?

But it is when we try to deploy natural selection to explain the origin of these characters that we face the gravest difficulties:

- **The condition of variation (a, above) is not satisfied**, because mutations to deeply-entrenched developmental characters such as primary cleavage patterns “are always catastrophically bad” (Davidson 2011, 6). The reason is straightforward: “system level output,” such as follows from mutations to early embryonic characters, “is very impervious to change, except for catastrophic loss of the body part or loss of viability altogether” (Davidson 2011, 4).
- Given that (a) is not satisfied, conditions (b) and (c) of the process of natural selection, *which are conditional on (a)*, cannot be satisfied either. No species can stably transmit a developmentally catastrophic mutation, and no positive fitness difference obtains with such mutations.

Thus, there is no evidence that natural selection caused the origin of early-arising developmental characters in the bilaterians.

IV. When Devo and Evo Conflict

In 1987, on the basis of Wimsatt's "developmental lock" model for the causal structure of animal development (see Figure 5) and the comparative genetic data available, Rasmussen predicted that early-acting key embryonic regulators in *Drosophila*, such as *bicoid*, should be widely conserved in the Arthropoda.

William Wimsatt's "developmental lock" model for the causal structure of animal development

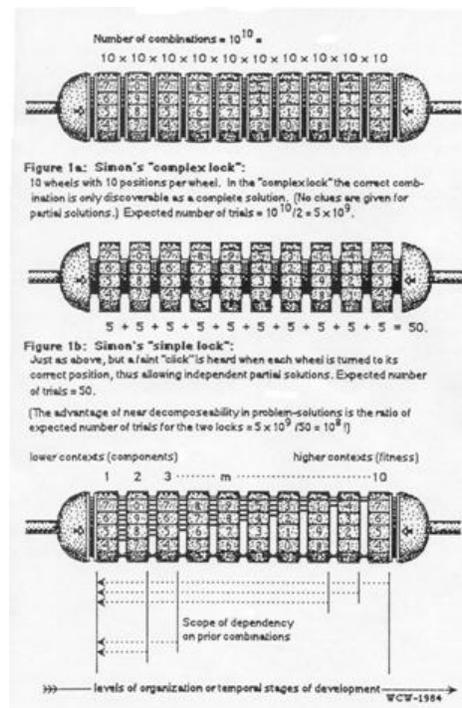


Figure 5. Wimsatt's developmental lock.

Rasmussen's reasoning was compelling: given that mutations to *bicoid* were known to be catastrophic (embryonic lethals) in *Drosophila*, these genes and their protein products (diffusing morphogens) should be conserved, not just in the Diptera, but throughout the Insecta and indeed the Arthropoda. (See Figure 6.)

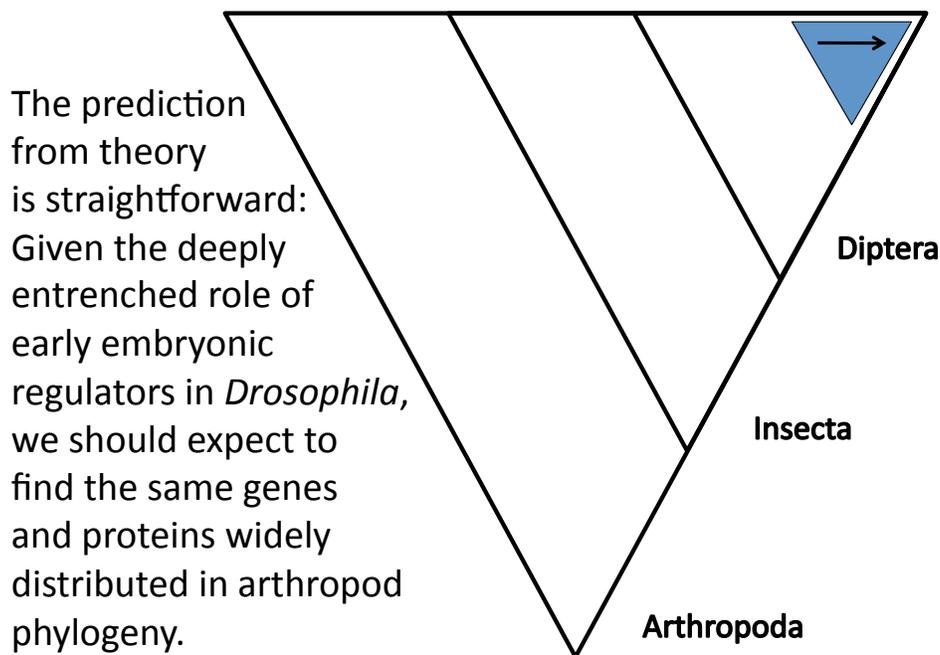


Figure 6. Rasmussen's (1987) prediction concerning the distribution of *bicoid* in the phylum Arthropoda (blue triangle indicates observed data from *Drosophila*).

As Rasmussen expressed the prediction, “the gene functions in the positions of greatest generative entrenchment in the hierarchy must

be among the oldest, since it should be virtually impossible for a new gene function to appear very far upstream in the causal structure of ontogeny” (1987, 275).

Yet, remarkably (Rudel & Sommer 2003, 25):

Phylogenetic evidence suggests that *bcd* may be a new innovation in the anterior positional information gene network during the evolution of Dipterans. Despite repeated attempts, it has not been possible to clone *bcd* homologues outside of the Cyclorraphan flies (Stauber et al., 1999). Additionally, *bcd* is not present in the Antennapedia complex of the flour beetle *Tribolium castaneum* (Brown et al., 2002). This has caused speculation that *bcd* may have evolved late in the evolution of the Dipterans.

Here, our knowledge derived from *Drosophila*, when coupled with a theory about the causal structure of development and the hypothesis of common ancestry (“evo”), led to an admirably

clear, but erroneous prediction (Figure 7).

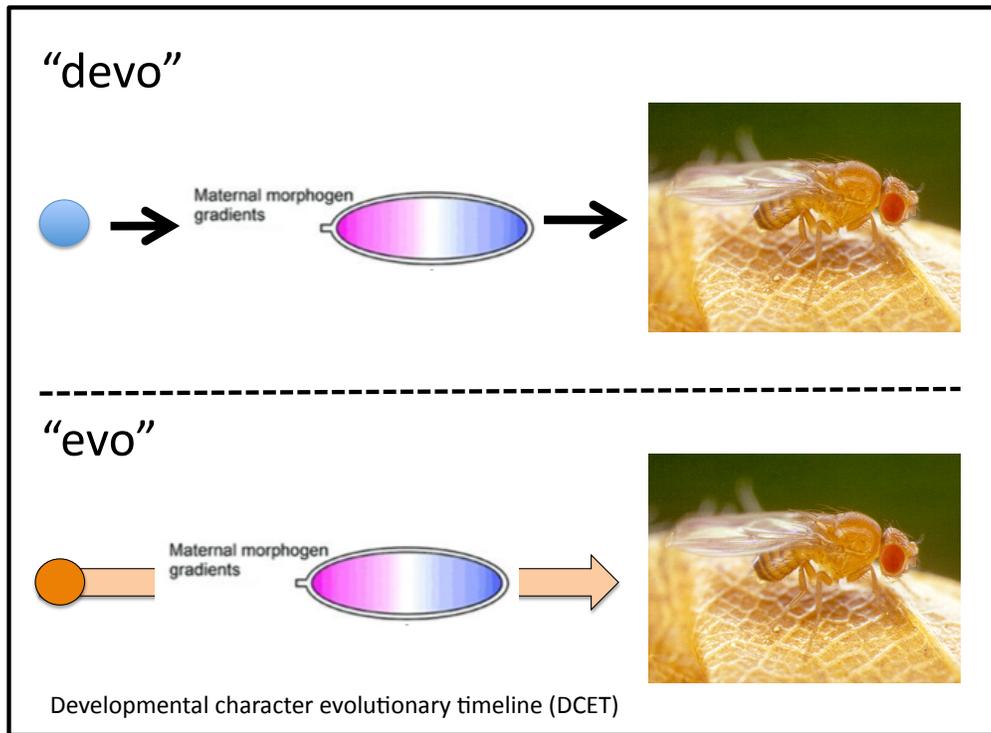


Figure 7. Observational expectations from the theory of common descent, and data from model systems, are often in conflict.

V. Conclusions

- There is no evidence that the process of natural selection caused the origin of primary embryonic characters in the Bilateria.

- Data from the model systems of evo-devo, and expectations based on the theory of common descent, are frequently in conflict.

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