PROBLEMS WITH CHARACTERIZING THE PROTOSTOME-DEUTEROSTOME ANCESTOR

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Paul A. Nelson
Discovery Institute
Center for Science & Culture
1511 Third Avenue
Suite 808
Seattle, WA 98101
nelsonpa@alumni.uchicago.edu

Marcus R. Ross
Department of Geosciences
University of Rhode Island
317 Woodward Hall
9 East Alumni Avenue
Kingston, RI 02881-2019
mross1106@postoffice.uri.edu

Abstract

Since Darwin's time, the origins and relationships of the bilaterian animals have remained unsolved problems in historical biology (Conway Morris 2000). One of the central difficulties is characterizing the common ancestor of the protostomes and deuterostomes. We argue that an unresolved conceptual puzzle has plagued the many attempts to describe this Urbilaterian, or, in Erwin and Davidson's (2002) terminology, the protostome-deuterostome ancestor (PDA). Any organism sophisticated enough to be a realistic candidate for the PDA, with such characters as an anterior-posterior axis, gut, and sensory organs, must itself have been constructed by a developmental process, or by what we term an ontogenetic network (Ross and Nelson 2002). But the more biologically plausible the PDA becomes, as a functioning organism within a population of other such organisms, the more it will tend to "pull" (in its characters) towards one or another of the known bilaterian groups. As this happens, and the organism loses its descriptive generality, it will cease to be a good candidate Urbilaterian.

1. THE PROBLEM

Since Darwin's time, the origins and relationships of the bilaterian animals have remained unsolved problems in historical biology (Conway Morris 2000; Valentine 2004). The intractable nature of these problems has been variously explained by

- Few (and equivocal) shared anatomical characters among the phyla – "clearly identifiable, informative homologs are rare" (Collins and Valentine 2001, 432);

- Missing fossil evidence – "the most striking features of large-scale evolution are the extremely rapid divergence of lineages near the time of their origin...what is missing are the many intermediate forms hypothesized by Darwin" (Carroll 2000, 27); and

- The neo-Darwinian explanatory emphases on allelic variation and speciation – "the evolution of major complexities in the history of life has had very little to do with the origin of species" (Miklos 1993, 34; see also Valentine and Erwin 1987, 96-7; Ohno 1996, 8475; Jablonski 2000, 26; and Davidson 2001, 19-20).

The salient event in the bilaterian puzzle is, of course, the Cambrian Explosion: "The most striking burst of evolutionary creativity in the animal fossil record comes early in the Phanerozoic, with the Cambrian Explosion of metazoan body plans. This extraordinary interval...saw the first appearance of all but one of the present-day skeletonized phyla (along with an array of less familiar forms)" (Jablonski 2000, 22; Valentine 2004; see also Valentine, Awramik, Signor, and Sadler 1991).

But with the emergence of the research field of "evo-devo" over the past twenty years, in parallel with the rapid growth of molecular phylogenetics, many workers have tried new approaches to attacking the long-standing puzzle of the origin of the bilaterians. "Amazing as it might have seemed only 10 or 15 years ago," note Peterson *et al.* (2000, 1), "the great problem of animal origins has become both the source and object of experimental inquiry." It may seem that the puzzle is soon to yield its answer.

We argue, however, that the problem of the origin of the Bilateria is likely to remain unsolved, at least within the current monophyletic framework, because of two closely-related difficulties – one **conceptual** and the other **evidential**:

A Conceptual Difficulty

Any organism sophisticated enough to be a candidate for the common ancestor of the protostomes and deuterostomes, with such characters as an anterior-posterior (AP) axis, gut, nervous system, and sensory organs, must itself have been constructed by a developmental process, or by what can be termed an *ontogenetic network* (see below). The more realistic this common ancestor becomes, as a functioning organism within a population of other such organisms, the more it will tend to "pull" (in its characters, both developmental and anatomical) towards one or another of the known bilaterian groups. As this happens, and the organism loses its descriptive generality, it will cease to be a good candidate Urbilaterian.

An Evidential Difficulty

To derive disparate body plans (*sensu* Gould) from this common ancestor would require modifying its early development (Miklos 1993; Arthur 1997; Davidson 2001). In all known bilaterians, body plan characteristics have their developmental roots in the earliest stages of ontogeny. Yet the evidence from the model systems of developmental biology also strongly indicates that *Bauplan*-disrupting mutations are inevitably deleterious. Known ontogenetic networks are constrained in their range of variation. This anomaly has led to proposals of non-uniformitarian temporal asymmetries in evolutionary processes (e.g., Erwin 1999, Shubin and Marshall 2000). In short, evolution was different in the past. But different how?

The purpose of this poster is thus two-fold:

1. To encourage reflection about a neglected puzzle of evolutionary theory – neglected, that is, not in lacking for hypotheses (there are plenty of those), but rather in a deeper sense. *What does it mean, biologically speaking, to be a non-specific ancestral form?* Can we really describe a bilaterian common ancestor that escapes the constraints we know obtain for the model systems of developmental biology?

2. To ask, Where is the deep variation required by macroevolution? There is a striking paucity of *experimental* evidence showing heritable variation in what Wimsatt and Schank (1988) call the "deeply-entrenched" features of development – i.e., those processes specifying body plan formation. While the classical neo-Darwinian view of the conservation of early development has collapsed under the weight of comparative data, the neo-Darwinian skepticism of macromutations is still amply justified by the signals returning from current model systems.

2. THE DIFFICULTY OF TRYING TO BRING A HYPOTHETICAL COMMON ANCESTOR INTO FOCUS

The bilaterians we actually know are constructed (in each new generation) by an ontogenetic network that commences with the fertilized egg. Although it may seem paradoxical to say so, this 'if-you're-an-animal-you-develop' requirement goes for hypothetical bilaterians as well, including the postulated common ancestor of the protostomes and deuterostomes. And therein lies the difficulty.

"Trying to imagine the morphological attributes of ancestral stem-group bilaterians," note Peterson *et al*., "is something of a project for the 'X-files'" (Peterson *et al*. 2000, 11). Nevertheless, X-file scripts can be written, and hypothetical common ancestors can (and indeed need to) be specified. Based on a survey of genetic regulatory homologies across the bilaterian phyla, Erwin and Davidson (2002, 3029) give their approximation of the protostome-deuterostome ancestor (PDA) as follows:

"It had an AP axis, a two-ended gut, mesodermal layers and a central and peripheral nervous system with sensory cell types."

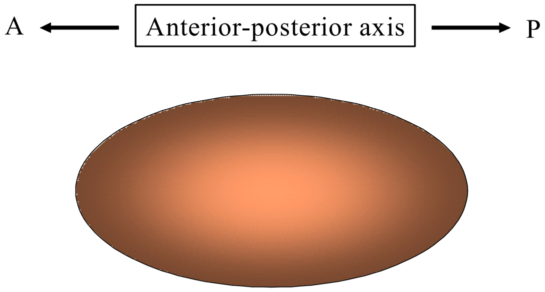
Now it is likely that even if this hypothetical metazoan were very small – on the scale of *C. elegans*, perhaps – it possessed no fewer than several hundred cells in its adult phenotype, of several distinct cell types (digestive, nervous & sensory, cuticular, germ line, and so forth). And if it were a developing organism, these differentiated cell states would have arisen from a single cell. Is there any reason to think that the process of specification and differentiation, from egg to adult in the PDA, would differ fundamentally from known bilaterians in its regulatory complexity?

Significantly, Erwin and Davidson (2002) omit one character from their PDA "parts list" that functional logic suggests must have been present – namely, the formation of gametes. Was the PDA reproducing by generating eggs and sperm? If the answer is Yes (probably), then we invite the reader to try a simple thought experiment, the first of two on this poster.

Let's suppose the cell depicted in Figure 1 represents a fertilized PDA egg, about to commence cleavage. Where is this egg going? – i.e., what specific morphology lies at the adult (reproductively capable) end of its ontogenetic network?

The answer, of course, depends on how the structure of the egg was specified maternally – i.e., on Mom. Was Mom, as Valentine argued recently, "a small, soft-bodied worm," with "about fifteen to twenty cell morphotypes" (2004, 483)?

However one answers this question, it is clear that the functioning bilaterian ontogenetic networks that we know are specified in remarkable detail.



Thought experiment #1:
What will this PDA egg become?

Figure 1

Here a parallel with *C. elegans* is instructive. “It has been estimated,” notes Golden (2000, 418), “that 100-400 maternal gene products could be involved in cell-division processes in the 1-cell embryo” of *C. elegans*. While it is unreasonable to expect that one could give anything close to that level of detail for the developmental architecture of the PDA, as one sketches more of its particulars, the organism will fall into one or another specific ontogenetic network. And such networks, in our experience, are constrained in their range of possible (viable) variation.

A generalized PDA is useful as a phylogenetic placeholder, anchoring the historical relationships (cladograms) of what are very different types of organisms. But real animals, such as those depicted below (see Figures 2-4), develop via ontogenetic networks of remarkable specificity.

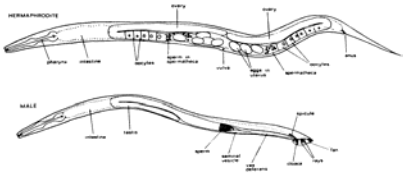
This brings us to our second simple thought experiment, to bring this evidential difficulty home. **Think of how – in particular, *when during development* – the body plan begins to be specified in the model system you know best.** Now ask yourself which mutations are tolerated least well by that same model system, when those mutations are expressed, and which morphological features they mainly affect.

Is there any reason to think that the body plan specification processes in the PDA would be any different? If so, why? And how would its ontogenetic network function?

Drosophila melanogaster

(Lawrence 1992)

Figure 2



Caenorhabditis elegans

(figure after Hodgkin 1987, 135)

Figure 3

Halocynthia papillosa

(Burton 1980)

Figure 4

The plain fact is that we do not now observe viable changes to body plan characters (with the possible exception of *losses* of structures, e.g., the frequent loss of the tail in ascidian larvae). This has led to the hypothesis of profound temporal asymmetries in evolutionary processes.

3. THE HYPOTHESIS OF TEMPORAL ASYMMETRIES IN ANIMAL EVOLUTION

In light of the absence of viable macromutants today, some evolutionary theorists contend that "patterns of intraspecific variation in modern phyla are qualitatively different from those that must have existed in the taxa that lived during Neoproterozoic and probably Early Cambrian times" (Shubin and Marshall 2000, 335). Many workers have argued that (in effect) had evolutionary biologists been present at the Neoproterozoic-Cambrian boundary, they would have seen events in populations then evolving that could not be replicated in laboratories or the field today; see, for instance, Campbell and Marshall (1987), Foote and Gould (1992), Arthur (1997) and Erwin (1994, 2000), among others. We may summarize this thesis as follows:

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 (networks) were possible that are no longer accessible to selection.

"Many of the characters that evolved during the origin of phyla," argue Shubin and Marshall (2000, 335), "are no longer able to change." Thus, "there seems to be no alternative 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" (Campbell and Marshall 1987, 97). After these critical periods, ontogenetic networks 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 high cost to what we know from genetics and developmental biology. 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, such as the PDA, 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."

4. CONCLUSIONS

It is likely that the ontogenetic complexity of Cambrian bilaterians was as great as developing animals today. Indeed this would be the case for the hypothetical common ancestor of the protostomes and deuterostomes (PDA). It is unclear, however, how the ontogenetic network of this organism would have varied to allow it to give rise to the disparate ontogenetic networks of the extant bilaterian phyla. That it did so vary seems to be an inference supported, not by what we know from developmental biology or genetics, but rather by the theory of common descent.

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