

Ontogenetic Depth and the Origin of Animals
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This ISCID informal discussion paper represents work in progress that I am undertaking in collaboration with Marcus Ross, a paleontology graduate student in the Department of Geosciences, University of Rhode Island (317 Woodward Hall, 9 East Alumni Avenue, Kingston, RI, 02881-2019; E-mail: mros1106@postoffice.uri.edu). Marcus presented the first part of our joint project as a poster, "Ontogenetic Depth as a Complexity Metric for the Cambrian Explosion," Paper No. 187-34, at the 2002 Annual Meeting of the Geological Society of America (30 October 2002). We will be submitting a follow-up paper on the concept of ontogenetic depth to the 62nd (2003) Annual Meeting of the Society of Developmental Biology, to be held July 30 to August 3 in Boston, MA (where, incidentally, the poster Jonathan Wells and I had planned to present at the 2002 SDB meeting in Madison will also be available as a paper for anyone who is interested).

1. THE PROBLEM

No scientist sets out (consciously, anyway) to become the butt of jokes in the future. Thus, when we now read Ernst Haeckel's statement that a cell is a "simple little lump of albuminous combination of carbon," we smile to ourselves – perhaps saving the passage for a humorous Powerpoint interlude – but we may also add, "Well, actually, in the late 19th century – could Haeckel or anyone else have foreseen just how complicated the cell would turn out to be?" The guy got it wrong.

The deeper point, of course, is that one cannot explain the origin of something when one does not understand *what that thing really is*. Haeckel failed to explain the origin of cells because he profoundly misunderstood, or mischaracterized, his explanatory target. As the historian and philosopher of science Harmke Kamminga (1986) has observed, "At the heart of the origin-of-life problem lies a fundamental question: What is it that we are trying to explain the origin of?" In 2003, we know that the ultimate target of abiogenesis research – the object whose origin we are trying to explain – is *not* an "albuminous combination of carbon." Therefore any historical explanation that aims to generate "simple lumps," instead of a real cell, will miss the mark by a long distance.

The same problem of accurately characterizing the explanatory target arises later in the history of life, with the origin of the bilaterian animals. The origin of the animals has remained a puzzle in historical biology from Darwin's time to the present. As with any

scientific problem, understanding what needs to be explained stands as the first task. The motivating question can be framed as follows: What sort of *biological event* does the geological first appearance of forms such as arthropods (e.g., *Anomalocaris*) or molluscs (e.g., *Scenella*) represent?

Intuitively most workers respond that these events represent a significant increase in biological complexity. As McShea (1996, 477) notes, however, although “the notion that complexity increases in evolution is widely accepted...the best-known evidence is highly impressionistic.” Various measures have been proposed to quantify complexity increases in evolution, notable among them genome size (Britten and Davidson 1969), gene number, and cell type (Valentine 1994).

But genome size is vulnerable to the so-called “C-value paradox,” i.e., the lack of correlation between genome size (measured as DNA content) and apparent morphological complexity. Gene number estimates can vary widely (see, e.g., Ewing and Green 2000 versus Liang et al. 2000, whose estimates for gene number in humans differ by a factor of 4), and cell type counts may be skewed by the use of intensively studied model taxa, possibly leading to higher counts (McShea 1996, 483). These difficulties suggest that a more comprehensive measure, relating more of the data of interest – body plans, organ systems, cell and tissue types, etc. – may be needed. Valentine (1994, 406) notes that “the ultimate measure of body-plan complexity would presumably be one that reflects the information required to specify the entire body, involving both gene number and the organization of gene expression.” We suggest that a measure of **ontogenetic depth** may bring together many (if not most) of the key biological parameters, and help investigators focus on what really needs to be explained in such events as the Cambrian Explosion.

2. A PROPOSAL

Consider Figure 1, which shows several of the salient biological levels employed in assessing the complexity increases exhibited by the Cambrian Explosion. **Gene number** is the sum of all functional sequences in a taxon’s genome (whether those loci are classical protein-coding genes or regulatory sequences). **Cell number** is the total count of discrete cells, of any type, possessed by an adult organism capable of reproduction. **Cell type** describes the total number of histologically differentiated cellular morphologies (e.g., gut epithelium, nerve, muscle, blood cell). **Tissue type** describes the organization of cell types into functional units such as sheets or epithelia, connective materials, skeletal parts, and so on. **Organ systems** are the higher-level anatomical relationships responsible for major organismal functions (e.g., sensory, locomotory, digestive, reproductive), while **Body plans** represent the major architectural features characteristic of groups such as Arthropoda, Mollusca, Brachiopoda, and the other bilaterian phyla.

It might seem that the natural way to illuminate the relationship between these levels would begin “bottom up,” with the genes. We argue, however, that for the problem of the origin of the phyla, the concept of an **ontogenetic network** best integrates these levels (see Figure 2). An example of one aspect of an ontogenetic network can be seen in

Figure 3, depicting the beginning of the cell lineage of the nematode *Caenorhabditis elegans*. Ontogenetic networks in all animals commence with a single cell, the fertilized egg. Then an unfolding arborescence of developmental decisions begins, whose complexity and overall architecture varies by taxon. In all animals, however, a point in the adult phenotype arrives when *reproduction* – the generation of gametes capable of fertilization – is possible. This distance, from the egg to the adult capable of reproduction, is what we term **ontogenetic depth** (see Figure 4). Somewhat more formally, ontogenetic depth may be defined as *the distance, in terms of cell division and differentiation, between a unicellular condition and a macroscopic adult metazoan able to reproduce itself* (i.e., generate gametes).

The ontogenetic depth of a handful of extant animals (from the model systems of developmental biology) is known with precision. In the nematode *Caenorhabditis elegans*, for instance, a relatively small animal only 1.5 mm in length, 7 to 9 rounds of cell division lie between the fertilized egg and any cell in the adult: 959 somatic cells in the hermaphrodite (with a variable number of germ cells), and 1031 cells in the male (with its distinctive tail). For larger metazoans, of course, such as the dipteran *Drosophila melanogaster*, ontogenetic depth is much greater, as total cell number, degree of cellular differentiation, and time to reproductive capability increase accordingly. The value of ontogenetic depth as a complexity metric lies in its relationship to *all* the parameters listed in Figures 1 and 2.

Of course, the ontogenetic depth of any *extinct* organism cannot be determined with complete exactitude. However, it should be possible, using modern analogues for fossil taxa – e.g., the extant monoplacophoran *Neopilina* for the extinct mollusc *Scenella* – to obtain good estimates on the ontogenetic depth requirements of many Cambrian forms. This is research we are now conducting. It is likely that reasonable estimates of the ontogenetic networks, and depth, required to specify such organisms as *Anomalocaris* or *Opabinia*, will require no less complexity than that of modern animals.

3. OK, SO WHAT? THE MARCHING BAND PROBLEM

To a skeptic, the concept of ontogenetic depth may seem to be little more than a roundabout way of expressing the already-familiar problem of how animals originally evolved from unicellular or colonial ancestors. We think, however, that focusing on ontogenetic depth helps to illuminate the central challenge that standard evolutionary theory faces when confronted with phenomena such as the geological first appearance of forms such like *Anomalocaris*. One of us (Nelson 1999) has called this challenge “the marching band problem.”

The cells of an adult metazoan are specialized for particular functional roles (as gametes, nerves, gut epithelia, skin, skeleton or exoskeleton, sensory organs, and so on). “The production of [these] differentiated cell types,” writes Carl Schlichting (2003), “is a hallmark of multicellular organisms.” The production *process* is an ontogenetic network, commencing with the fertilized egg. “A function [one might say *the* function] of

developmental processes,” notes Strathmann (2000), “is putting the right kind of cells in the right places at the right times. The criterion for ‘right’ is survival and reproduction.”

One can conceive this process of differentiation (or cellular specialization) very much on the model of an American university marching band (see Figure 5, where a 140-member marching band is depicted as orange dots, arrayed at the sideline of a football field). In one sense, of course, any marching band is strongly disanalogous to a developing animal. A nematode or fruit fly commences its existence as a single cell (the fertilized egg), and will then construct its cell populations during development, whereas the marching band begins its maneuvers with all of its members already present.

But in another sense – the one that we’ll focus on – the two processes share many parallels. The band will move, through a series of intermediate maneuvers, toward its functional endpoint – say, spelling “CAL STATE” on the field (see Figure 6). In its development, an animal also moves from the fertilized egg, through a series of intermediate “maneuvers,” towards its functional endpoint, namely, an organism capable of reproduction. The latter process, of course, is vastly more complex: “This temporally ordered sequence of morphological heterogeneities that we call development,” writes Arthur (1997), “generates adult tissue patterns that, in some taxa, can be highly complex, involving very precise and repeatable arrangements of billions, even trillions, of cells.” Now, if the band is going to spell “CAL STATE” successfully, it should be intuitively obvious that the members must have their instructions in place before they venture onto the field. The trumpet player, for instance, standing in the front row on the sideline, who will eventually become the tip of the serif at the bottom of the “L” (see Figure 7), must know how to execute the series of turns and motions that will carry him to his endpoint on the field.

The same is the case with a developing organism. “Development is possible,” writes Arthur (2000), “only if cells ‘know’ what to do in all these respects,” i.e., assign their planes of division, tendencies to move, directions and rates of movement, modes of differentiation into particular cell types, and cell death (apoptosis). “So the key question,” Arthur continues, “becomes ‘how *do* they know?’, and the whole of developmental biology could be regarded as an attempt to answer this question.” If the question “How do cells know?” is to be answered by developmental biology, its sister (and far more difficult) question “How did cells learn what they know?” must be addressed by evolutionary (or historical) biology.

And here serious, and currently unanswered, questions arise. “How cell types of multicellular organisms came to be differentiated,” notes Schlichting (2003), “is still an open issue...the origins of differentiation remain unclear.” Given that the origin of animals – organisms defined by differentiated structures – is thought by most scientists to have been a problem solved, at least in outline, by Charles Darwin, this is not a minor difficulty. Some authors have recently noted this explicitly; e.g., Davidson 2001:

...classical Darwinian evolution could not have provided an explanation, in a mechanistically relevant way, of how the diverse forms of animal life actually

arose during evolution, because it matured before molecular biology provided explanations of the developmental process. To be very brief, the evolutionary theory that grew up before the advent of regulatory molecular biology dealt with the problem of the origin of novel organismal structures in two ways. The first has been to treat the mechanisms generating novel morphological structures as a black box. New forms were considered to arise “because” the environment changed. But while changes in Precambrian or Ordovician weather, continental shifts, or temperature may have contributed crucial selective forces, they do not generate heads or appendicular forms; only genes do that.

Or, we might say, genes *plus* (the three-dimensional localization of their protein products, et cetera – nucleic acid alone an organism never made). Davidson goes on to argue that “stepwise, adaptive changes in protein sequence...is probably largely irrelevant to the evolution of any salient features of animal morphology,” but we will focus on a more general difficulty, involving the process of natural selection itself, and its (probable) impotence for constructing ontogenetic networks.

Suppose we interrupt a marching band midway through its maneuvers, at some stage before “CAL STATE” appears on the field. Suppose, furthermore, that we cause this interruption at a marching band competition where “success” is defined (at least in part) by actually reaching the endpoint where the name of the band’s home institution is spelled. It should again be intuitively obvious that the functional reason for the band’s intermediate maneuvers is not the maneuvers themselves, *but rather the distant endpoint that those maneuvers enable or bring about.*

Now look again at Figure 3, showing the early cell lineage of *C. elegans*. One cannot interrupt this canonical cell division pattern and obtain a viable organism. Viability, and, in particular, reproductive capability – the only outcome “visible” to natural selection – lie in the distance, after several rounds of cell division and differentiation.

How then did natural selection construct the ontogenetic network of *C. elegans*? Figure 8 represents this problem in schematic form, using a very shallow network to make the point. Reproductive capability arises only in the square on the right, when its five cells are in place.

Discuss amongst yourselves.

Figure 1

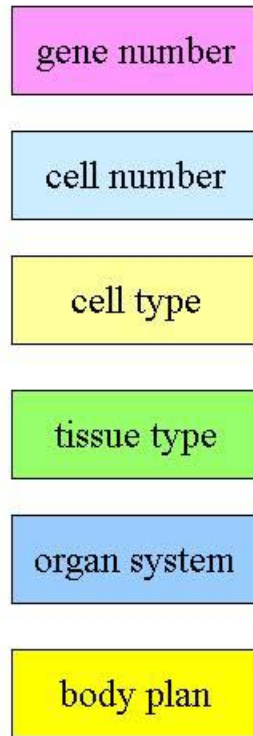


Figure 2

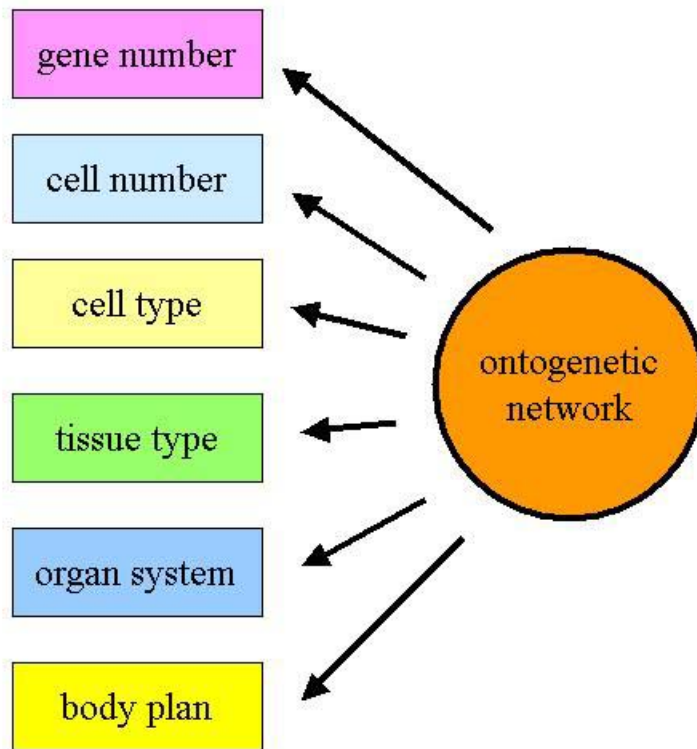
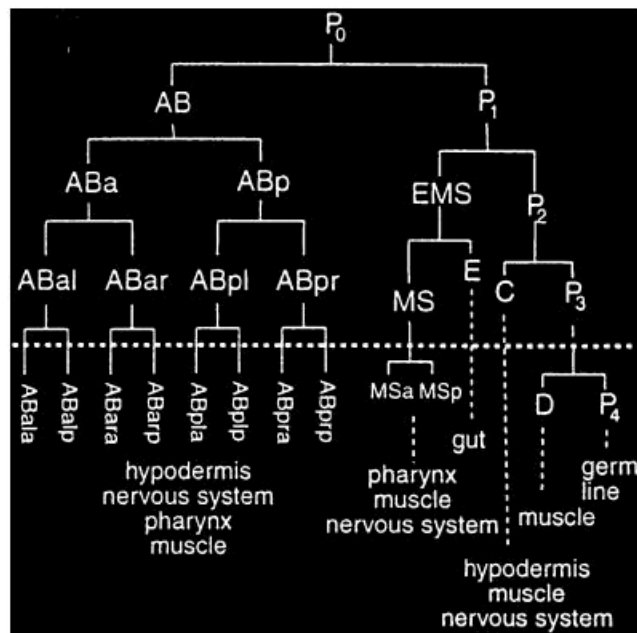


Figure 3: The early cell lineage of *Caenorhabditis elegans*



(figure after Schnabel 1997, 342)

Figure 4

Ontogenetic Depth

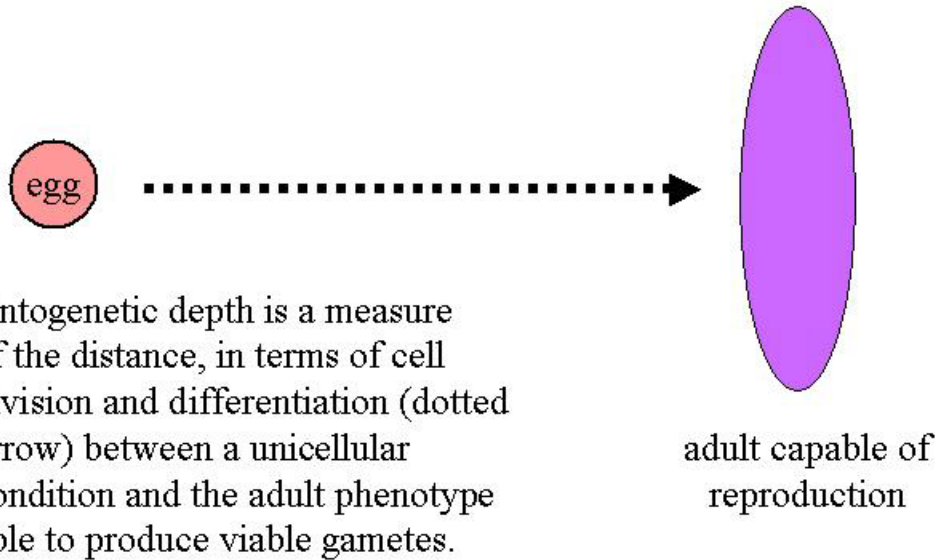


Figure 5: The marching band problem

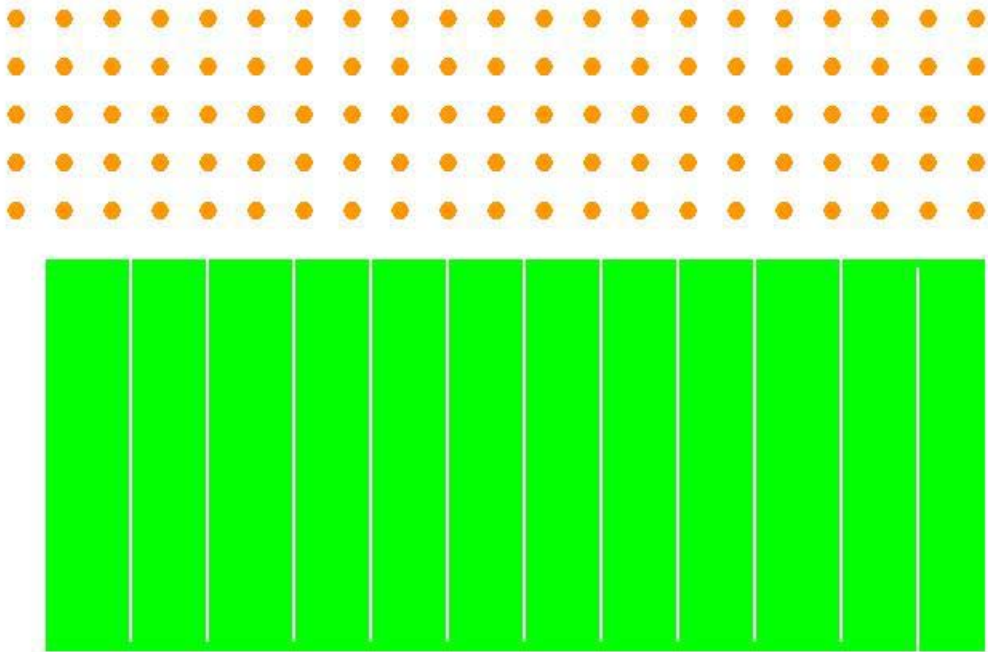


Figure 6: The marching band problem

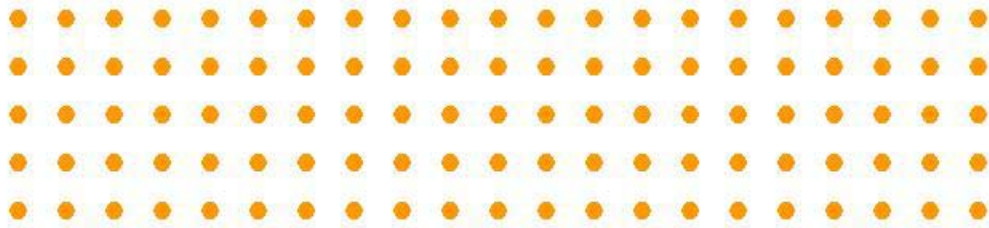


Figure 7: The marching band problem

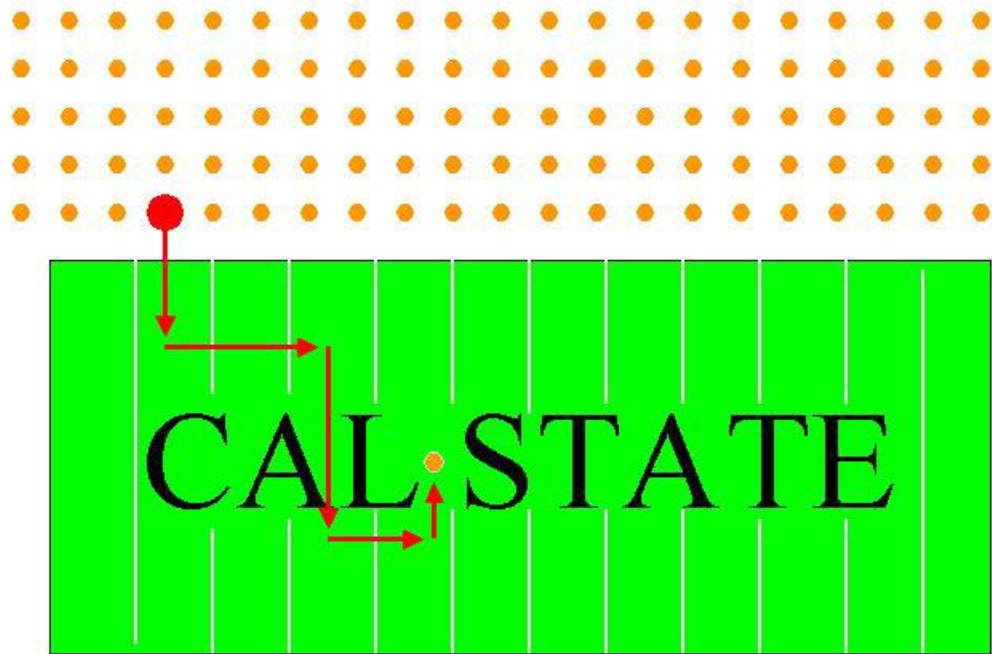
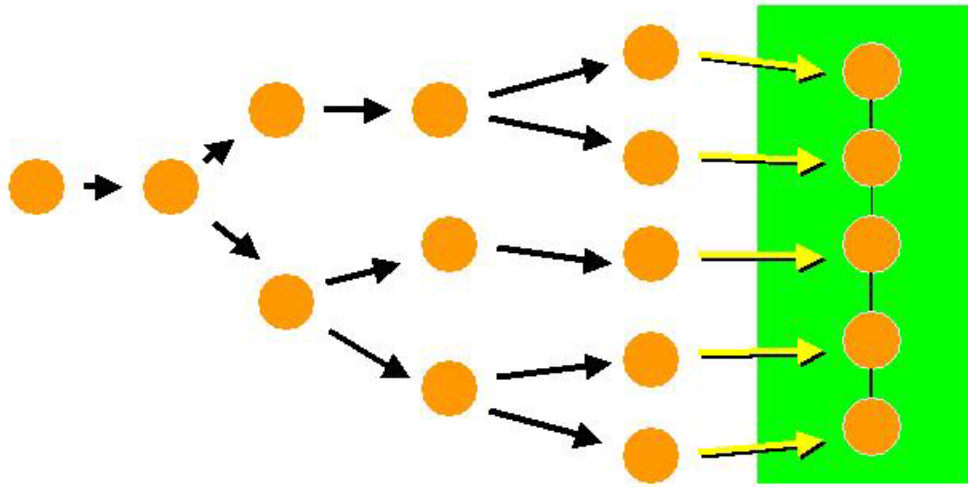


Figure 8: The causal inefficacy of natural selection for constructing ontogenetic networks



Natural selection only “sees” reproductive output

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