



The Target Problem in Characterizing Early Metazoan Developmental Sequences

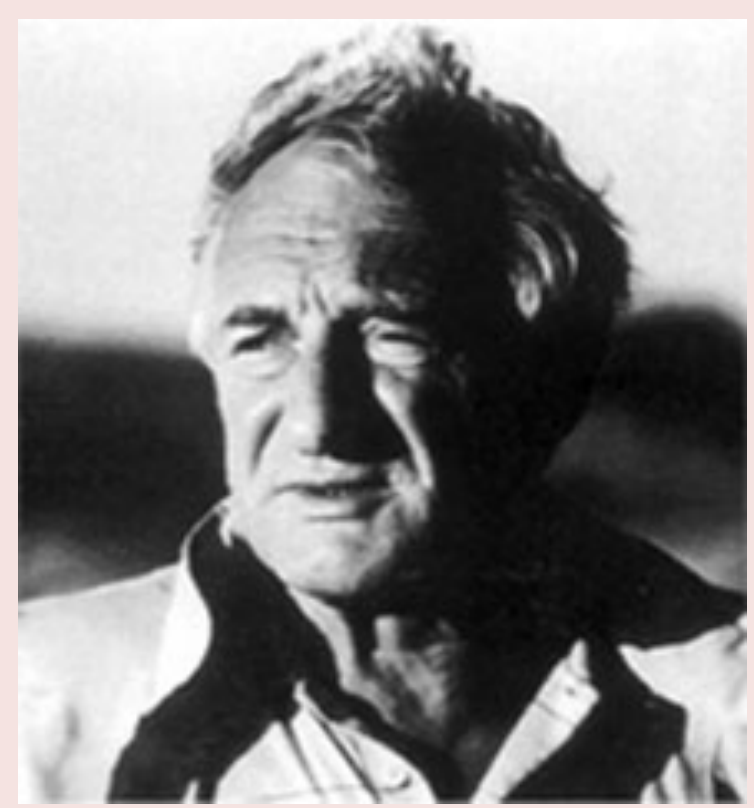


Paul A. Nelson, Biola University, 13800 Biola Avenue, La Mirada, CA 90639
nelsonpa@alumni.uchicago.edu, paul.alfredp@gmail.com

Abstract

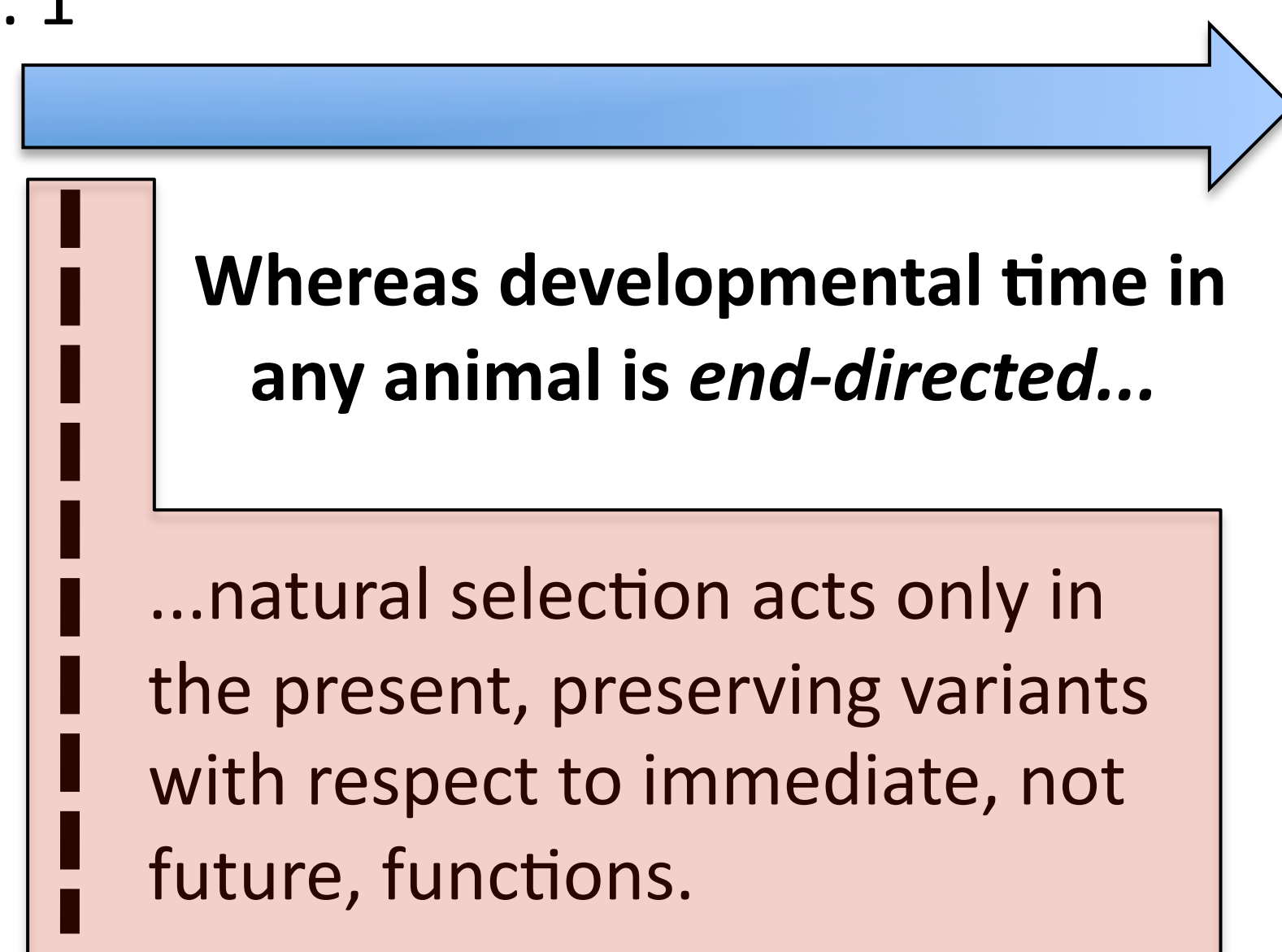
In 1978, Riedl described what he called “the paradox of teleological evolution.” Today the paradox remains unsolved. Evolution by natural selection is not an end-directed process, but metazoan development is. Normally developing embryos “head towards” functional targets (e.g., differentiated cell, tissue, organ, and body plan states) lying temporally in the distance. The paradox arises when one employs an undirected process such as evolution to explain the step-by-step acquisition of developmental stages, such as initial cleavage patterns, which, while not themselves viable endpoints, are necessary to reach distant functional states. This is the target problem: **characterizing and explaining the origin of developmental stages required for organismal viability and reproductive capability, where the selectable consequence is a future (developmentally remote) state.**

1. The Puzzle



In his classic 1978 text, *Order in Living Organisms*, which addressed the causal relations between developmental and evolutionary biology, Austrian zoologist Rupert Riedl described what he called “the paradox of teleological evolution” (1978, 219). Embryos, he wrote, while they are clearly necessary to build reproductively capable adult organisms, do not themselves represent “functional ancestors.” Their parts “strive towards functions,” so to speak, “without being able to possess them during their formation.” Riedl then draws an analogy to the uninhabitability of a building during its construction process. This puzzle can be expressed more formally as follows: **What were the selectable functions of the variants that increased cell number and differentiation along the pathway from unicellular eukaryotes to (for instance) the origin of *C. elegans*? The current function of initial cleavage stages in *C. elegans* – e.g., zygote to founder cells AB and P1 – is to partition the regulatory elements that will specify the various outcomes of their daughter lineages. But those functions could not have been selected for when the initial cleavage first evolved, as the daughter lineages did not yet exist. Natural selection has no foresight (Fig. 1).**

Fig. 1

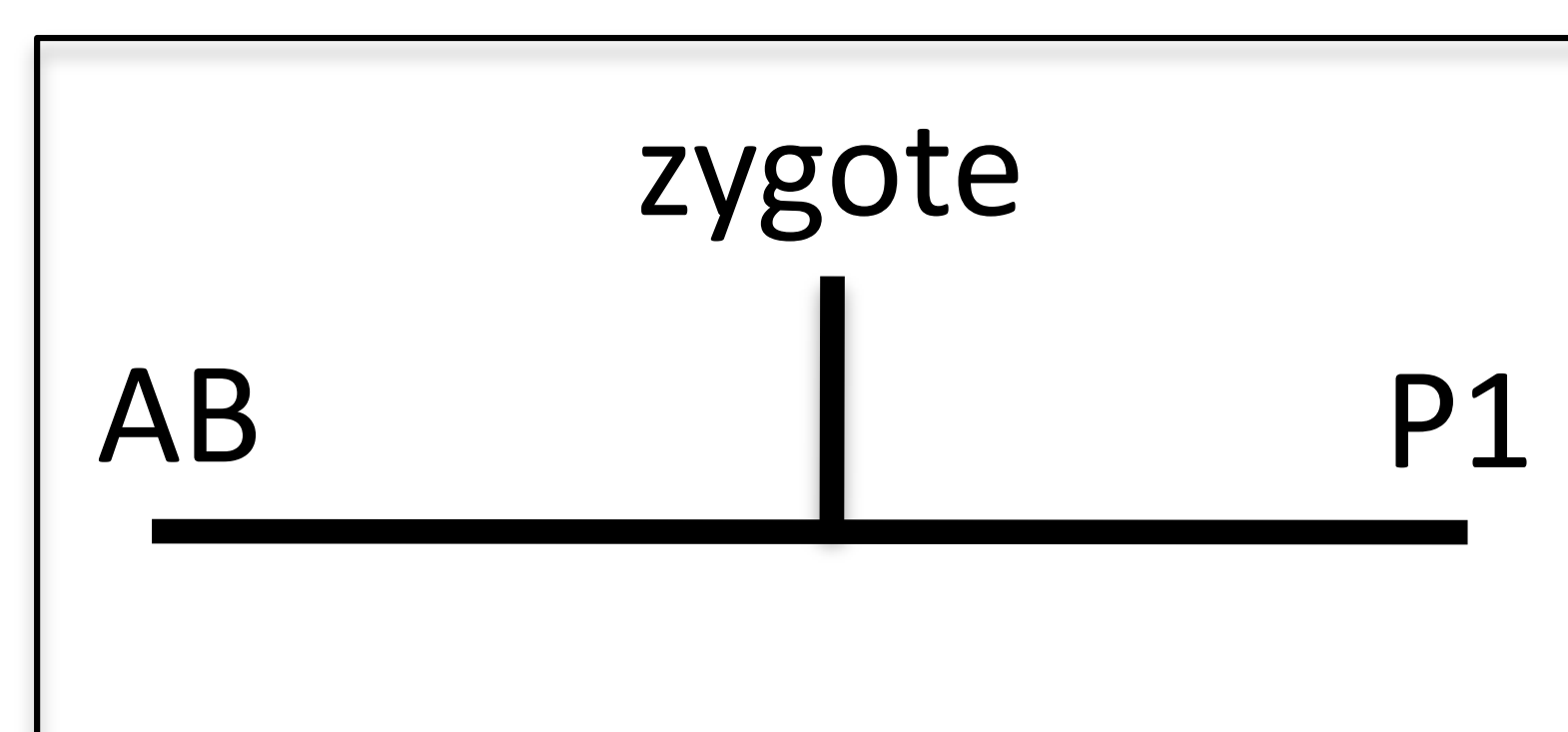
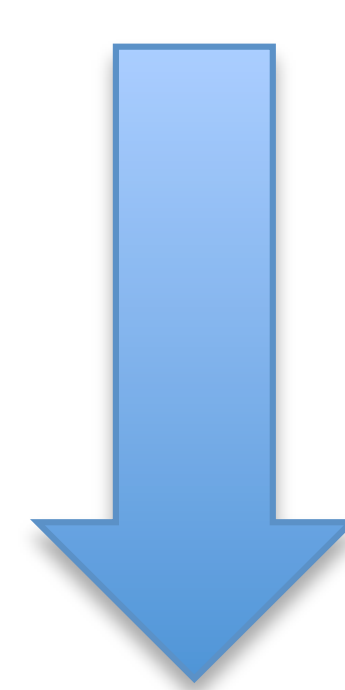


2. Visualizing the Puzzle

The obvious answer to the difficulty is to propose functions that could have been selected in the ancestral forms lying on the evolutionary pathways to the metazoan phyla. But, as Fig. 2 illustrates, this move only forestalls the problem, it does not solve it. (Data from Sulston *et al.* 1983)

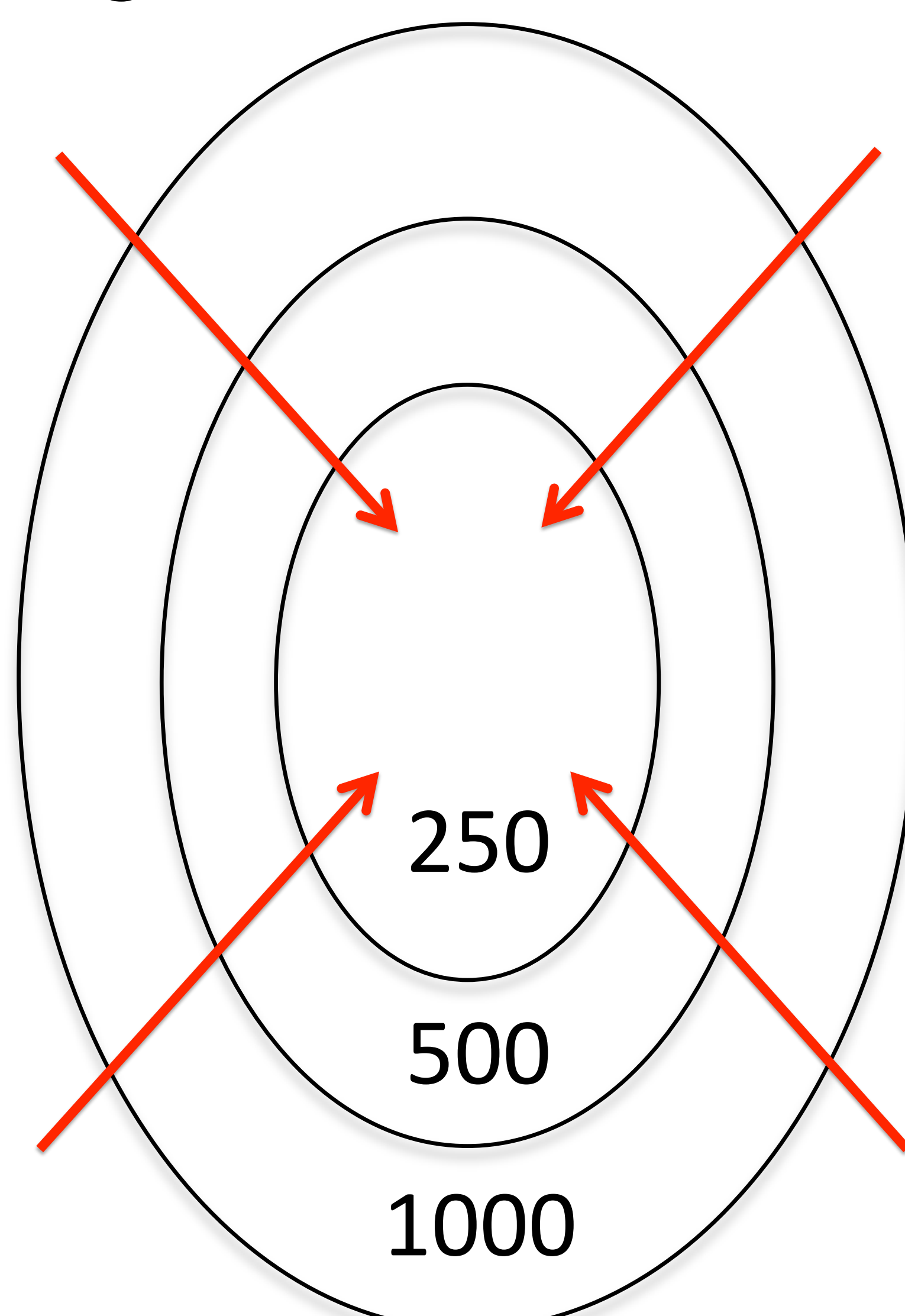
Fig. 2

Whatever the antecedent functions may have been, at some point in the origin of *C. elegans*, this developmental state must arise.



The puzzle can also be visualized by “counting back” cell number and modes of differentiation from wild-type *C. elegans* to what must have been its ancestral forms, leading back ultimately to unicellular eukaryotes. In this case, however, the cleavages that occur in normal development are lost, because the termini of any cell lineage in a reduced ancestral form must function as adult tissues in a reproductively capable animal. Again, the problem of evolving developmental stages that are not themselves functional endpoints is not solved, only forestalled.

Fig. 3



3. Could A Non-Selective Evolutionary Process Solve the Puzzle?

One might respond that the difficulty flows from employing natural selection as the causal process explaining the origin of developmental stages where they didn’t exist before. However, no evolutionary process – selection, drift, recombination, etc. – possesses foresight (see Rodin *et al.* 2011). The explanatory advantage of natural selection is plainly that the process biases the otherwise random walk of undirected variation towards functional states. But, as noted earlier, selection cannot bias towards any functional state that exists in the future – and metazoan development, characterized by long decisions chains where the end state (reproductive capability of adult morphology) is some distance from its starting point in the zygote, is just such a “future-directed” state. Mechanisms such as drift are correspondingly even weaker as causal solutions, due to inherent randomness.

4. Conclusion

The evolutionary puzzle described in this poster uses *C. elegans* as an example, but the general difficulty extends to any metazoan ontogeny. Key events in the history of life, such as the Cambrian Explosion, are marked by the appearance of novel macroscopic anatomies significantly greater in size and complexity than any nematode. Those species were constructed by developmental stages where – akin to the relatively simple example of *C. elegans* above – the intermediate “building” stages were only ephemeral but necessary transformational points along a trajectory towards the reproductively capable adult. The mystery posed by Rupert Riedl in 1978 still awaits its solution.

References

- Rupert Riedl, *Order in Living Organisms* (New York: John Wiley, 1978).
- Andrei S. Rodin, Eörs Szathmáry, and Sergei N. Rodin, “On the origin of the genetic code and tRNA before translation,” *Biology Direct* 6 (2011), p. 14.
- J.E. Sulston et al., “The Embryonic Cell Lineage of the Nematode *Caenorhabditis elegans*,” *Developmental Biology* 100 (1983):64-119.