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Framing causal questions about the past: The Cambrian explosion as case study

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ABSTRACT

About 540 million years ago, a rapid radiation of animal phyla radically changed the Earth's biota in a geological eye-blink. What caused this "Cambrian explosion"? Over the years, paleontologists have pointed to a wide array of different physical mechanisms as the causal "trigger" for the explosion. More recently, some paleontologists have proposed complex causal pathways to which multiple physical mechanisms are said to have contributed. Despite their variety, these answers share an assumption that a single explanation can in principle be constructed that identifies some factor or confluence of factors as the cause of the Cambrian explosion. That assumption is unjustifiable. The Cambrian explosion had multiple causes, and different aspects of the event are best explained by different causes. These different causes cannot, even in principle, be integrated into a single causal explanation. We can learn much about the causes of the Cambrian explosion—or for that matter about any historical event—but only by attending more carefully to how we frame our causal questions about the past.

1. Introduction

Life on Earth before the Cambrian period was predominantly unicellular and homogeneous. The advent of the Cambrian was dramatic. In a geological blink of an eye, entirely new body plans appeared, many representing stem groups of modern forms of life. The "Cambrian explosion" was probably the single most significant radiation in evolutionary history. What caused it? In the past, most answers to this question have focused in on a single physical mechanism as the "trigger" primarily responsible for the radiation. More recently, some paleontologists have rejected the search for a single triggering cause, instead seeking to integrate an array of different physical processes into a single, complex causal explanation. Despite their differences, all these essayed explanations share a common assumption that a single explanation can in principle be constructed that identifies some factor or confluence of factors as the cause of the Cambrian explosion. That assumption is unjustifiable. Different aspects of the radiation are best explained by different causes. These different causes cannot, even in principle, be integrated into a single causal explanation. We can learn much about the causes of the Cambrian explosion. The search for a single, integrated causal explanation of the radiation, however, is chimerical. Pluralism in our explanations of the causes of historical events is ineliminable.[1] An approach that embraces this fact offers the best prospect of knowledge of the causes of the Cambrian explosion, or indeed of any historical event.

2. The search for a primary physical mechanism

Most paleontologists who have analyzed the cause of the Cambrian explosion have searched for the single physical mechanism most directly responsible for the radiation. The candidate causes that scientists have proposed fall into three categories: environmental, developmental and ecological. Environmental explanations for the Cambrian explosion focus on developments in the earth's climate, chemistry or other similar factors. Developmental explanations point to changes affecting the ontogeny of individual animals. Ecological explanations privilege interactions among organisms, such as predation or parasitism.

Environmental mechanisms proposed as causes of the Cambrian explosion include: increased atmospheric oxygen made possible a range of new body types (Frei et al., 2009); a "snowball earth"

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[1] My concern in this paper is causal explanations of historical events. I am not concerned with causal explanations of robust and repeating processes or with non-causal (e.g., statistical) explanations.

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developed, with isolated ice-free refuges where new forms of life evolved (Runnegar, 2000); and tectonic movements released methane into the atmosphere, resulting in warming that enabled new forms to evolve (Kirschvink & Raub, 2003). Developmental mechanisms credited with setting off the Cambrian explosion include: key gene duplications allowed more complex animals to develop (Lundin, 1999); the evolution of neural cells enabled complex central nervous systems, driving the radiation (Stanley, 1992); and the increasing complexity of the "developmental toolkit" of regulatory genes opened up a much wider set of possibilities in ontogeny (Valentine et al., 1999). Ecological mechanisms credited with setting off the Cambrian radiation include: increases in phytoplankton provided food for an array of new herbivores (Butterfield, 1997); new herbivores created ecological space for the development of a range of predators (Stanley, 1973); and the evolution of predators' ability to prey upon larger animals put pressure on prey, and in turn on predators, to evolve rapidly (Peterson et al., 2005).

Despite their variety, the proponents of these alternative mechanisms share a similarity of approach. The scientists identifying developmental factors as primary do not deny the action of environmental factors (such as the presence of sufficient oxygen in the atmosphere to support large animals) or ecological factors (such as the availability of new ways of making a living that developmental mechanisms could seize on). And the same is true of the proponents of environmental and ecological explanations. Notwithstanding that a wide array of factors must have played a role in the causal sequence, however, they all identify one as primary. None of these scientists offer (nor, not being philosophers, should they be expected to offer) an explicit philosophical account of causation, and all are aware that a number of different forces cooperated in order to bring about the Cambrian explosion. Yet all, in one way or another, emphasize a single cause. Thus, Kirschvink and Raub (2003) identify methane as the "fuse" that set off the Cambrian explosion. And Peterson et al. (2005) review an array of possible "triggers" and conclude that the evolution of predators that could prey on larger animals was "the ultimate cause" (50) of the Cambrian explosion.

We might best understand what these scientists have in mind by recourse to the concept of relative significance. A relative significance analysis conceives of each physical mechanism as a separable cause, responsible for some determinable part of the outcome. (For a fuller discussion of relative significance, see Beatty (1997).) The idea can be likened to vector addition of forces in physics. The analogy is not a perfect one: the relative contributions of environmental, developmental and ecological factors to the Cambrian explosion are not supposed to be ascertainable with mathematical precision, but in principle, the contributions are considered to be separable and additive. On this reading, a number of factors are understood to be operating, but one is identified as being of predominant significance relative to the other cooperating causes.

This way of thinking about how physical processes interacted to bring about the Cambrian explosion is an error. In vector addition, if one force were to stop operating, the others would continue unaffected. In contrast, the various physical processes that cooperated to produce the Cambrian explosion are not separable causes. Each of these processes are aspects of a single explanation that cannot even in principle be disaggregated so that their respective contributions to the outcome can be compared. They are inextricably complementary in their explanatory role.

Consider the following thought experiment (borrowed from Keller, 2010, 7–9): Billy and Suzy want to fill a 100-L bucket with water. Each holds a hose over the bucket, and each turns on their tap. The water flows from Suzy's hose more quickly—in the time it takes for 40 L to flow from Billy's hose, 60 L have flowed from Suzy's hose. This is an additive system, and it makes perfect sense to say that Suzy is "the cause" of 60 percent of the water in the bucket, and Billy is "the cause" of 40 percent. Now imagine that the children dump out the water and start over, but this time they use one hose; Suzy holds the hose over the bucket, and Billy turns on the tap. In this latter case, it is impossible to attribute any particular percentage of the water to either child. We no longer have a system with two independent variables the effects of which can simply be added together, and to the extent additivity has been lost, our ability to assess the relative significance of Suzy's and Billy's respective contributions has been compromised. To generalize, when an event has multiple causes, we can only apportion responsibility among the various causes if the causes are separable and additive. Keller (2010, 38). There is nothing particularly new about this insight. The basic intuition dates back to Mill (2006 [1843], 327–28), who asked his readers to suppose that a man had eaten a particular food and died. The cause of his death included the eating of the food, but also his bodily constitution, state of health and other factors: we might reasonably suppose that he would not have died had he not eaten the food, but also if he had not been susceptible to the particular poison. There is no secure philosophical basis, argued Mill, for singling out one cause as most important, or for any determination of the relative significance among the network of cooperating causes.

Keller's and Mill's logic applies to the causes of the Cambrian explosion. Even if we could successfully identify all of the causes of the radiation, the various causes are not independent. Within any one category of causes (environmental, developmental and ecological), the interactions are bound to have been plentiful and significant. At least some changes in the environmental conditions facing a particular Cambrian predator species must also have affected its prey and/or its parasites, with those changes feeding back on the predator, and so on. Any gene duplication in a Cambrian herbivore must have interacted with other changes in the animal's genome in significant ways. And ecological changes by definition have interacting effects: the notion of predation presupposes interacting predator and prey species, just as parasitism presupposes interacting hosts and parasites.

The interactions *between* the environmental, developmental and ecological causes of the Cambrian explosion must have been even greater. Organisms do not just respond to their environments; they create them through what evolutionary biologists call "niche construction" (see, e.g., Odling-Smee et al., 2003) and ecologists call "ecosystem engineering" (see, e.g., Jones, et al., 1994), with the resulting environmental changes feeding back on the niche constructing organisms, and also on other species. Moreover, how new toolkit genes affected the development of any particular lineage must have been strongly influenced by the ecological dynamics affecting that lineage.

In short, the interactions between the various environmental, developmental and ecological variables that constitute the physical mechanisms underlying the Cambrian explosion are themselves central to the causal story. Attempting to "disentangle" the causes entirely misses the point that their entanglement is central to their causal power. Environmental, developmental and ecological factors are not alternative explanations, but elements in a cooperating network of causes. As with Mill's poisoned man and Keller's children filling a bucket, we have no secure philosophical basis to determine the relative significance of the various causes of the Cambrian explosion. The causes cannot be disentangled.

When I argue that the causes of the Cambrian explosion are inextricably intertwined, I do not contend that no meaningful distinctions can be drawn among the event's causes. Different aspects of an event may have different causes, such that which cause strikes us as primary depends on what aspect of the event we are