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Narratives and/or Mechanisms in the Explanation of the Origin of Eukaryotes

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Abstract

The arrival of eukaryotic cells, cells with a nucleus, is considered a major evolutionary event. Explaining the emergence of eukaryotes has been a subject of interest amongst biologists from the early 20th century to the present. This paper explores the form, rather than the content, of these explanations. I focus on two representative hypotheses: the phagotrophic theory from Tom Cavalier-Smith (first formulated in 1975) and the hydrogen hypothesis from Bill Martin (first formulated in 1998). I argue that these two explanations contain a combination of contingency, order, and sketchiness. I confront this state of affairs with epistemological tools that have been identified as useful for the explanation of unique events, namely "narrative explanations" and "ephemeral mechanisms". From my case study, I argue that elements of each explanation can coexist at different stages of a given explanation. I also argue that both narratives and mechanistic explanations are unable to account for the sketchiness present in both Cavalier-Smith and Martin's explanations. This paper, then, sheds light on the work needed to refine our understanding of (a) the relation between narrative and mechanistic explanations and (b) the explanation of unique events in historical sciences.

1. Introduction

The origin of eukaryotic cells on Earth is a momentous event. Beforehand, the Earth was populated with prokaryotic cells, unicellular organisms with limited internal compartmentation. Eukaryotes, on the contrary, are structurally and functionally compartmentalized cells. The genetic material, in the form of DNA, is localized in the cell nucleus. The maturation of proteins is shared, at different stages, between the endoplasmic reticulum and the Golgi apparatus. The production of cellular energy, in the form of adenosine triphosphate (ATP), takes place in the mitochondria. Internal and surface movements, as well as exchanges with the environment, are mediated by the reshufflings of the cytoskeleton. While it is possible to find precursors of all of these features in prokaryotes, their full evolution and articulation happened in eukaryotic cells. It is also within these organisms that multicellular life arose: plants, fungi, animals are eukaryotes.

A task for evolutionary biologists is thus to explain the evolution of eukaryotic cells from prokaryotic cells. This has been a topic of scientific interest from the 20th century onwards.[1] The debates have revolved around matters of timing and the associated causal relations: when did this event happen? Which cellular innovations appeared first? How did they appear? Did they cause the origin of the other innovations, or did these other structures evolve independently? In this paper, I propose to address a different, epistemological, question: *What kind of theory is this?*

Section 2 presents two representative hypotheses about the evolution of eukaryotes. The *hydrogen hypothesis*, first formulated in 1998, has been chiefly defended by Bill Martin. It claims that the origin of mitochondria by the acquisition of a foreign organism, a process also called "endosymbiosis" or "symbiogenesis", is the central event and main trigger of the evolution of eukaryotes. The *phagotrophic hypothesis* was first formulated in 1975 and has since been defended mainly by Tom Cavalier-Smith. It claims that the origins of the endomembrane system, the internal network of cellular compartments, and in particular phagocytosis, the ability to engulf foreign bodies, have paved the way to the origin of eukaryotes.

While sharply divergent in terms of contents, *Section 3* proposes an epistemological analysis of the shared formal features of Cavalier-Smith and Martin's theories. In both cases, the origin of eukaryotic cells is explained with a unique and contextually anchored causal story. While the conjunction of all these events is indeed unique and argued to be improbable, these hypotheses are mainly composed of "normal" cellular behaviours, analogous to those found in contemporary organisms. Each hypothesis, however, also invokes some physiologically "unprecedented" behaviours, unknown (or merely suspected) to occur in contemporary organisms. Moreover, Cavalier-Smith and Martin's hypotheses are sketchy: some parts are spatiotemporally unordered, or left unexplained. Each thus contains a mixture of ordered and unordered, familiar and

[1] See Sapp 1994; Archibald 2014 for historical reviews.

unusual. I argue that this state of affairs has remained present throughout the development of both hypotheses. This excludes the idea that my analysis only pertains to immature theories, and that progress occurs by tidying up such hypotheses.

Section 4 confronts this description with how the explanation of unique events has been conceptualized in the philosophical literature. In particular, my case study is mobilized to assess the relevance of *ephemeral mechanisms* and *narrative explanations*, the two main epistemological tools devised to address unique events. Ephemeral mechanisms are subsets of mechanistic explanations. The uniqueness of events is explained by the "ephemerality" – understood either as fragility or rarity – of the initial configuration triggering this event. When the initial configuration is obtained, the rest of the events are argued to follow from normal interactions. Narrative explanations, on the contrary, account for pervasively contingent sequences of action, where events do not necessarily follow from the initial conditions. Both types of explanations have been considered mutually exclusive. I argue, instead, that narrative and mechanistic elements are together present in Cavalier-Smith and Martin's hypotheses. I also argue that ephemeral mechanisms and narrative explanations do not account for the sketchiness found in these hypotheses.

On the whole, this paper argues for further studies on (a) the relation between narrative and mechanistic explanations and (b) the explanation of unique events in historical sciences.

2. Cavalier-Smith and Martin on the Origin of Eukaryotes

2.A *Martin's Hydrogen Hypothesis*

Martin's hypothesis for the origin of eukaryotes has kept the majority of its main steps unchanged since its initial formulation, in collaboration with Müller (Martin and Müller 1998).

It begins, about 1.5 billion years ago, in the anoxic depths of the ocean. In the absence of oxygen, dissolved hydrogen gas is an aliment of choice to some prokaryotes. Hydrogen plays a central role in bringing together the two main actors in the emergence of eukaryotes. It is "the bond that forges eukaryotes out of prokaryotes" (Martin and Müller 1998, 40). Hydrogen is a waste product of the anoxic metabolism of some alphaproteobacteria. This waste product attracts some methanogens, who "live by reacting hydrogen gas with carbon dioxide, and evanescing methane gas as a waste product" (Lane 2005, 52).

In the hydrogen hypothesis, the origin of eukaryotes began with an incident induced by this increased physical proximity. Methanogens, feeding off the hydrogen-producing alphaproteobacteria, started changing shape. They progressively surrounded their source of food. This tight embrace eventually turned into a physical encapsulation. Alphaproteobacteria became engulfed organisms within methanogens. The following steps in Martin's hypothesis are a sequence of problem-solving episodes mobilized to transform this accidental, and initially ill-functioning, collaboration into a fully-functioning host/endosymbiont association.

Confined within a host, metabolic rearrangements are needed for the newly symbiotic alphaproteobacteria to thrive in its new environment. Similarly, the methanogen host needs to find ways to survive the presence of a foreign cell living within it. Martin describes a series of genetic transfers from the symbiont to the host required both for the survival of the association and for some of the features of the purported first eukaryotic cell to emerge. This includes the acquisition by the host of the symbiont's genes for some membrane proteins, as well as the ones coding for the whole of a metabolic pathway. These genetic transfers are facilitated by the death of many symbiotic cells which did not successfully adapt to their new cellular environment. These deaths released genetic material in the cytoplasm of the host, which then can be acquired and incorporated in the host cell's DNA.

The rearrangements cause drastic changes in the metabolism of both the methanogen host and the alphaproteobacteria symbiont. It creates a metabolically versatile entity, capable of living in aerobic and anaerobic conditions. The initially autonomous and free-living hydrogen-producing alphaproteobacteria have now been stripped down of anything that does not contribute directly to the functioning of the symbiosis. They have become cellular compartments specialized in a restricted set of functions. These engulfed alphaproteobacteria are the common ancestors of mitochondria in eukaryotes.

In parallel to the metabolic rearrangements linked to genetic transfers, Martin also postulates a membrane changeover in the methanogen host. The membrane lipids went from being archaea-like (like the host) to being bacteria-like (like the symbiont). This, according to Martin, is an indirect consequence of bringing an initially free-living organism within the cytoplasm of another: it continues to behave "inside" as it would have if it was "outside". Alphaproteobacteria secrete lipid vesicles to the environment. Inside the host, the becoming of these vesicles is twofold:

> They can fuse, either with themselves to generate larger vesicular compartments, or with the plasma membrane to export their contents to the cell exterior. The former generates a basic [endoplasmic reticulum (ER)] topology. The latter constitutes, we propose, the ancestral outward state of eukaryotic membrane flux, and furthermore converts the chemical composition of the host's plasma membrane from isoprene ethers to bacterial fatty acid esters (Gould *et al*. 2016, 3).

In other words, the continued secretion of lipid vesicles by the engulfed alphaproteobacteria is at the origin of two major evolutionary changes. Firstly, the membrane lipids of the host are progressively replaced by the secreted lipids of the symbionts. Secondly, the secreted lipids constitute, within the cell, the basic system of internal cellular compartments known as the endomembrane system.

This accidental engulfment and the following series of metabolic and membrane rearrangements has turned an initially ill-functioning prokaryote-prokaryote symbiosis into the first fully-fledged eukaryotic cells. In this view, this radical series of events has made accessible a whole space of new evolutionary possibilities:

> That cell has time, energy and ample genetic starting material (two highly divergent and partially merged prokaryotic genomes) to evolve cytological and genetic traits that are specific to the eukaryotic lineage (Martin and Müller 1998, 41).

Martin argues that it is, in particular, the acquisition of mitochondria that greatly increased the energetic efficiency of eukaryotes. The compartmentation of energy production within the former free-living alphaproteobacteria has been calculated to make these cells afford a "roughly 200,000-fold rise in genome size" (Lane and Martin 2010, 929). That is all that is required for eukaryotes to "evolve, explore and express massive numbers of new proteins in combinations and at levels energetically unattainable for its prokaryotic contemporaries" (Lane and Martin 2010, 933). In sum, the origin of mitochondria paved the way for the rest of the eukaryotic innovations.

2.B *Cavalier-Smith's Phagotrophic Hypothesis*

Cavalier-Smith's hypothesis, initially formulated more than forty years ago (Cavalier-Smith 1975), has been regularly amended ever since (Cavalier-Smith 2014 is the latest version). His origin of eukaryotes is woven around different threads. It is not two organisms that merge into one, as in the hydrogen hypothesis, but one organism, an actinobacterium, from which stems two domains of life: archaea and eukaryotes. This summary focuses only on the emergence of the latter.

The hypothesis starts with the loss of the cell wall by an actinobacterium. The sudden absence of this structural key component of prokaryote cell, producing

"naked L-forms" (Cavalier-Smith 2014) is usually followed by death. This time, the wall-less cells and some of their descendants recovered thanks to the evolution of a new, more flexible, way to link the glycoproteins on the outside membrane.[2] From this emerged two new lineages. Archaea developed a new type of lipids adapted to the colonization of extremely hot environments. Eukaryotes further exploited the newly-gained flexibility to evolve phagotrophy, the ability to feed off engulfed foreign substances. In sum, the exceptional recovery from a usually catastrophic cellular event led, in eukaryotes, to the evolution of a new mode of feeding.

The acquisition of phagotrophy came with an upheaval of the rest of the organization of the cell. From these changes came most of the eukaryotic innovations. The newfound flexibility of phagotrophic cells is underpinned by the evolution of the cytoskeleton.

The cytoskeleton, as a network of assembling and disassembling proteins, is a shifting cellular infrastructure that poses new constraints in the cellular environment. Cavalier-Smith argues that the emergence of the cytoskeleton exposes the cell's DNA to potential structural damages. This provides grounds to the origin of the nucleus, as a protective membrane to the genetic material. Cavalier-Smith argues that this relocation of genetic material, in turn, drastically shifted the selective pressures on genome size. In particular, it partially freed eukaryotic genomes from the tight grip of the selection for small and streamlined genome present in prokaryotes. Thus, the origin of phagocytosis is defended as a key cause for the increased size of eukaryotic genomes (Cavalier-Smith 2006), the exact opposite of what Martin's hydrogen hypothesis claims.

In parallel to these events, mitochondria emerged as the result of incomplete phagocytosis. The proto-eukaryote ingested but failed to digest an aerobic alphaproteobacterium. Once accidentally inside another cell, the

[2] This is why the whole sequence has been dubbed the "neomuran revolution" (the Latin for "new walls").

alphaproteobacteria have been progressively reduced, and "enslaved" as energy-producing cellular structures. While Martin argues that the origin of mitochondria is the main trigger to the origin of eukaryotes, Cavalier-Smith sees it as a byproduct of the main event, which is the origin of phagotrophy. According to the latter, the evolution of mitochondria provides improvements in the "aerobic utilization of intracellular digestion products" (Cavalier-Smith 2014, 51). Mitochondria together make for a better yield in the digestion of foreign substances. It enables eukaryotes to fully enjoy the spoils of the phagotrophic mode of feeding.

The evolutionary importance of mitochondria, in this view, is also to be understood in a broader cellular context. Cavalier-Smith argues that the addition of mitochondria is part of the co-evolution of a new, eukaryote-specific, division of energetic labour. The mitochondria, endoplasmic reticulum (ER) and peroxisomes together constitute a cellular "energy belt" argued to have originated more or less simultaneously. Peroxisomes create breakdown products of the lipid metabolism, that are sent to mitochondria which produce ATP, and this ATP is in turn exploited by the ER to synthesize novel proteins and cellular components. In sum, the origin of phagotrophy paved the way for a period of cellular coevolution, which includes the acquisition of mitochondria, at the origin of fully-fledged eukaryotic cells.

3. Analysis

The previous section makes clear that Cavalier-Smith and Martin's hypotheses are sharply divergent in terms of content. They postulate different types of organisms and give unequal evolutionary importance to certain events. For instance, the origin of mitochondria is central to the origin of eukaryotes for Martin, while it is given an important, but secondary, role by Cavalier-Smith. I will not dwell on the divergent theoretical and evidential bases of both hypotheses (see Bonnin accepted). In this section, I focus on the shared formal features possessed by both hypotheses.

It is clear that both explanations of the origin of eukaryotes consist of purportedly unique sequences of events. Cavalier-Smith and Martin are not fitting an existing abstract explanatory pattern to this particular context. Instead, they both provide explanations that are thoroughly tailored to the event in question.[3] This appears in the fact that both explanations postulate "abnormal" events. Martin, for instance, postulates a prokaryote-prokaryote engulfment for which there is currently no known mechanism and seldom, if any, evidence. Cavalier-Smith builds on an improbable recovery from a cell that has lost its cellular wall.

The presence of "abnormal" events is linked to the contingency of the events postulated by each hypothesis. By "contingent event", I mean what Sterelny states as "a change in a system [that] could not be predicted from information about the prior state of that system" (Sterelny 2016, 522). Contingency pervades both of the postulated events. The unfolding of events, in both cases, could not have been predicted from the initial conditions. It requires highly unusual events and the "right sequence" to occur. It is thus implicit that, at each step, most cells die and very few of them manage to adapt and survive.

Moreover, Cavalier-Smith and Martin insist on the pioneering, and unprecedented changes that their events brought about. Martin talks about the substantial shifts in energetic abilities that mitochondria brought, and from which the rest of the eukaryotic innovations were made possible. Cavalier-Smith's hypothesis articulates the co-evolution of most of the eukaryotic traits from the radical structural changes brought with the origin of phagotrophy. Both hypotheses, therefore, postulate a unique sequence of events that radically shifted the space of evolutionary possibility for life on Earth.

On one hand, thus, Cavalier-Smith and Martin's hypotheses postulate sequences of unique, contingent, abnormal and groundbreaking events. As we will see, these are the narrative-like properties of these explanations.

[3] In other words, these explanations are not "embedded", in Currie's sense (2019).

But these are not the only components. One can argue that Martin's team has been working to reduce the degree of contingency in the hydrogen hypothesis. The initial motive for the rapprochement between the alphaproteobacteria and the methanogen is driven by the rather mundane process of an organism getting closer to a food source. This can also be seen in the recent explanation of how the membrane changeover and emergence of the endomembrane system was an expected consequence of the secretion of vesicles by the bacterial symbiont (Gould *et al*. 2016). Efforts were also made about to elucidate the so-far mysterious initial engulfment of a prokaryote by another. Martin's team has been trying to find examples of similar situations in contemporary organisms (Martin *et al*. 2017). This is done in order to make the postulated engulfment appear less abnormal.

Attempts by Cavalier-Smith to "tidy up" the hypothesis he defends are visible, for instance, in the transition from a prokaryote to a "neomuran", the cell at the origin of the eukaryote and archaea lineages. Over time, Cavalier-Smith has drawn increasingly detailed diagrams that specify the steps in the making of the main cellular innovations in eukaryotes. The origin of phagocytosis is a good example of this increased specificity. Compare the relatively minimalist 1975 figure (Cavalier-Smith 1975, 464, figure 1) with the already caption-heavy 1987 version (Cavalier-Smith 1987, 44-45, figure 8) with the visually complex and even more descriptively generous latest version (Cavalier-Smith 2014, 6-7, figure 2). More details are added over time. They concern the specific proteins involved in the apparition of phagocytosis as well as how this event is coordinated with the emergence of other eukaryotic structures.

Both scientists seek to increase the ordering of some aspects of their explanations, each in their own way. Martin does so by reducing the contingency of the events he postulates, by transforming "abnormal events" into recognizable cellular behaviours. Cavalier-Smith aims to clarify the continuity between prokaryotes and the neomuran cell at the origin of both eukaryotes and archaea.

These examples display another side to both of these hypotheses: they can also postulate necessary (i.e. non-contingent) events deriving from mundane cellular behaviors (Martin). They can also increasingly emphasize the increased continuity between organisms before and after the evolutionary events, and somewhat decrease (and make more precise) the novelty brought forth by the event in question. These features, as we will see, are more *mechanistic-like*.

Beyond these *narrative* and *mechanistic-like* elements, Cavalier-Smith and Martin's hypotheses also display an explicit degree of *sketchiness*. By this, I mean:

(1) that they contain events that occur in parallel.
(2) that some of the events occur at spatio-temporal scales that cannot be sequentially brought together
(3) that, while causally related, the relative timing of some events are left unspecified or
(4) that the details of some events are left unspecified.

In Martin's hydrogen hypothesis there are two sequences of events clearly running parallel occurring after the initial engulfment has been done. On one side there are the genetic and metabolic rearrangements required to turn the initially dysfunctional association into a metabolically viable symbiosis. Roughly simultaneously, there is the continuous secretion of lipid vesicles by the symbiont alphaproteobacteria, which trigger a membrane changeover and the emergence of the endomembrane system. Because of the importance of membrane exchanges and internal transport to cellular metabolism, one can assume that these two parallel processes are linked. In the current state of Martin's hypothesis, however, their relations are left unspecified.

It is also interesting to note that sketchiness extends within each of these parallel events. In the genetic rearrangements, the sequence of genetic transfer is sketchy in two ways. While there are hints in the timing and nature of the genetic material transferred (the transfer of the glycolysis pathway precedes the transfer of the

membrane "taps", for instance), it is neither strictly ordered or the nature strictly specified. Martin also leaves room for sketchiness in the formation of the membrane compartments from the secretion of lipid vesicles. The readers do not know the relative timing of apparition of the nucleus, endoplasmic reticulum, and the changeover of membrane material. These parallel series of events therefore combine different types of sketchiness within them.

Sketchiness also pervades Cavalier-Smith's phagotrophic hypothesis. A clear instance of this is the co-evolution of peroxisomes, mitochondria and the endoplasmic reticulum. In earlier formulations, the evolutions of the three entities were given separate explanations. Now, the apparition of these structures has been evolutionarily linked and pictured as the emergence of an "energy belt" in the cell. However, the relative timing of the origin of these structures is left unspecified. It is just assumed that their contemporary functions are related in a way that necessitates a roughly simultaneous, and coordinated, evolution. This temporally unspecified sequence of events is vindicated by Cavalier-Smith as an epistemological necessity. He states that the acquisition of phagotrophy triggered a rapid sequence of coevolution that led to the origin of fully-fledged eukaryote (Cavalier-Smith 2006, 29).

To summarize, the composition and maturation of both hypotheses gathers different types of components. The more *narrative-like* features emphasize uniqueness, contingency, abnormality and the groundbreaking nature of the event. The more *mechanistic-like* features emphasize embeddedness, necessity, normality and evolutionary continuity. In addition to this, *sketchiness* in different forms pervades both hypotheses. In Cavalier-Smith and Martin's hypotheses, one finds events running in parallel, or occurring in an unspecified timing, or simply only roughly specified. The continued presence of these sketchy areas points to the fact that it is not a temporary feature of such hypotheses. Instead, it rather seems a constitutive element that needs to be accounted for.

In light of the present case study, I use the next section to further specify the narrative and mechanistic nature of these hypotheses, and expand on how sketchiness is left unaccounted by these two epistemological tools.

4. Narrative Explanations and Ephemeral Mechanisms

4.A *Narrative Explanations*

Narratives are traditionally associated with the activity of telling stories. A narrative is often perceived as an entertaining product of our imagination, or as an organized display of a collection of facts as someone in the course of a conversation recalls them. To distinguish this everyday and literary usage of narratives from its usage in scientific theories, the latter are described as *narrative explanations*. Three shared features seem to stand out from conceptualizations of narrative explanations (see Danto 1962; Beatty 2016; Currie and Sterelny 2017; Morgan 2017). Narrative explanations are weaved, or configured, around a thread, whether temporal, spatial or conceptual. They track the development of this subject in a series of events that develop over time. The series of events are internally consistent.

The subject of the narrative is what provides the ordering. It provides the thread that enables picking up, in the diversity of available things, the relevant features to the explanation. This has been conceptualized as the *central subject*, "the main strand around which the historical narrative is woven." (Hull 1975 255). As said above, the nature of the thread can be extremely varied, as long as it has a form of continuity across the explanation. Continuity, here, is not to be confused with identity. Central subjects either "persist unchanged or develop continuously through time" (Hull 1975, 255). Narrative explanations, in this view, track the events and factors behind the stability or changes of central subjects.

Narrative explanations are claimed to be particularly adapted to the explanation of unique events because they could track contingent events.[4] Beatty, in

[4] Gould has famously defended that the (biological) past is pervasively contingent (Gould 1989), giving ontological grounds to the use of narrative explanations. The present argument remains

particular, insists that narrative explanations are necessary to the description of turning points, events where "we need to be told what will happen next because we wouldn't know otherwise" (Beatty 2017, 35). On this view, narrative explanations track "the causal trajectory of [something's] origin and subsequent history" (Currie and Sterelny 2017, 1) by signposting the various points at which this trajectory could have taken many different ways, and telling which path was taken. The explanatory load, in these cases, lies on the ability to establish the existence of these events and to explain how a given path was taken in contrast to the other possible ones.

These main features of narrative explanations - the contingent becoming of a central subject – are found in Cavalier-Smith and Martin's theories. Both explanations are organized around the lineage of prokaryotic cells from which eukaryotes appear. This is what, in both cases, justifies the foregrounding of some facts and constitutes a thread that is followed from the beginning (marked by the initial abnormal event) to the final resolution (the existence of fully-fledged eukaryotes). The presence of each event in their explanations is motivated by its importance in the alteration and subsequent stabilization of the lineage of cells. Narrative explanations thus conceptualize well the constitution of the subject.

Concerning contingency, it can also be said that narrative explanations capture well an aspect of Cavalier-Smith and Martin's explanations. It has already been underlined, in Section 3, that both accounts relate contingent events: the recovery from the loss of the cell wall, in Cavalier-Smith's hypothesis, could not have been predicted; the initial prokaryote-prokaryote engulfment, in Martin's hypothesis, is also not predictable from the initial conditions. These explanations for the origin of eukaryotes contain contingent events.

In that sense, this case study confirms the suitability of narrative explanations to the explanation of unique events. But this suitability is only partial. I now turn to

epistemological. It focuses on how narrative explanations can account for events *explained as* contingent.

how ephemeral mechanisms account other features of Cavalier-Smith and Martin's explanations.

4.B *Ephemeral Mechanisms*

Ephemeral mechanisms are a subset of "mechanistic explanations", a set of conceptual tools argued to be pervasive in contemporary biology (see Nicholson 2012 for a review). Mechanistic explanations account for the behaviour of systems.[5] Systems are composed of *organized* and *interacting* parts that together bring about behaviours of interest. In other words, mechanistic explanations aim at an epistemic *decomposition* of the system of interest into its salient components and identifying the relevant interactions between these components. By doing this, it also unravels how the spatial and temporal organization of these *activities* and *entities* enable the occurrence of the behaviour of interest. To explain, here, is thus to identify the right entities and activities within the system of interest, and to explain how the organization of these components successfully brings about the behaviour of interest.

Mechanistic explanations follow a sequential start-to-end causal sequence that centres on a given system. The steps in these explanations are predictable consequences of the antecedent conditions, provided one identifies the right interactions between the right entities. Traditionally, this epistemological tool has been developed to explain *types* of behaviours. Machamer, Darden and Craver argue that "mechanisms are regular in that they work always or for the most part in the same way under the same conditions" (Machamer et al. 2000, 3).

Glennan, however, has defended the relevance of mechanistic explanations for unique events, by bringing forward the concept of *ephemeral mechanism*. The nuance with "classical" mechanistic explanations is that the initial configuration of the system "is short-lived and non-stable, and is not an instance of a multiply-

[5] In this paper I emulate Nicholson's point that mechanistic explanations are best conceived *epistemologically*, as "heuristic models which target specific causal relations and thereby facilitate the explanation of the particular phenomena scientists investigate" (Nicholson 2012, 154) and not *ontologically*.

realized type" (Glennan 2010, 260). In other words, the initial conditions, by their rarity, instability or improbability, are the points at which Glennan allows contingency to occur. An example Glennan gives is the explanation of the death of French philosopher Roland Barthes after being hit by a laundry truck while crossing the streets, in Paris (Glennan 2010, 260). An ephemeral mechanism is invoked, here, since the initial conditions contain individualized elements (Barthes, Paris) set in a rare and unstable configuration (the unlucky spatial contiguity of a street crossing pedestrian and a launched vehicle).

What remains traditionally mechanistic about ephemeral mechanisms, however, is that once that contingent configuration is obtained, the other events follow by necessity. In Barthes' case, Glennan states that "we can describe the interaction between Barthes and the laundry truck as an instance of change-relating generalization involving persons and laundry trucks, or persons and large vehicles" (Glennan 2010, 261). Ephemeral mechanisms, more generally, then explain unique events by delineating a system in which contingent initial circumstances are followed by a rather normal unfolding of events. In Glennan's words, "[t]he same sorts of generalizations which characterize the interactions between parts of ordinary mechanisms also characterize interactions between the parts of ephemeral mechanisms" (Glennan 2010, 261).

The main features of ephemeral mechanisms are the focus on a system with entities and activities, and the combination of an initial "ephemeral" state with a mechanistic sequence of events which brings about a unique event.

I argue that ephemeral mechanisms capture the more orderly aspects of Martin's hypothesis. For instance, the secretion of vesicles by the alphaproteobacteria symbiont can be seen as an instance of a mechanistic behaviour occurring in ephemeral conditions (the inside of a prokaryotic cell). The consequences, namely the constitution of a system of internal vesicles and the changeover of membrane lipids in the host, can be explained by merely invoking the lipid vesicle secretion.

In that case, Glennan could argue that what appears to be a unique event is in fact just the result of a very improbable starting point.

The fit between ephemeral mechanisms and Cavalier-Smith's hypothesis is less obvious. The origin of phagocytosis, for instance, is depicted as a series of diagrams of cells tracing the origin and coming together of the various components of this cellular process. Here, Cavalier-Smith indeed decomposes its system into its salient entities and activities. But the transition between the various steps is not explicitly filled in with mechanistic interactions.[6] They can, instead, be the result of heavily contingent steps, such as the recovery from the loss of the cell wall, which would be better captured by narrative explanations.

Ephemeral mechanisms, on the whole, are not pervasive across Cavalier-Smith and Martin's explanations. It is however interesting to point out that the search for such mechanisms seems to be used as a heuristic strategy. It appears to be the case for how Martin developed the combined explanation for the membrane changeover and the origin of the endomembrane system (Gould et al. 2016). The initial explanations were relying heavily on highly contingent gene transfers to occur. Developing ephemeral mechanisms also seems a probable heuristic for the explanation of the prokaryote-prokaryote engulfment, for which so far nobody has postulated a process.

What this analysis also shows is that narrative explanations and ephemeral mechanisms are not mutually exclusive explanatory strategies. As contingent and ordered elements coexist in a given hypothesis, this implies that the latter can encompass both mechanistic and narrative aspects within it.

4.C *Unaccounted Aspects*

While narrative explanations seem suited to account for the contingency and the ephemeral mechanisms for the more orderly aspects and of Cavalier-Smith and Martin's hypotheses, as well as possible heuristic strategies for them, none of these

[6] This makes these diagrams more akin to "lineage explanations" (see Calcott 2009).

tools successfully account for the sketchiness. It is not possible to include spatiotemporally unordered elements in ephemeral mechanisms. The whole point of mobilizing this epistemic resource is to provide orderly explanations which follow from the organized interactions of entities.

Could they be in a narrative? It depends on how strongly one takes Beatty's characterization of narratives. According to him, narrative explanations' legitimate use is for events with turning points, contingent events where we need to be told the path taken as it could not otherwise be predicted. I argue that a strong interpretation of this view sets strong constraints on the form of narrative explanations. They would need to conform to a temporally unfolding sequence, like a path along a branching tree of possibilities, where each turning point follows the other in time. This is not what we find in Martin and Cavalier-Smith's explanations. Instead, we have seen that both scientists unapologetically invoke sketchy events. It would seem difficult to translate their hypotheses into a strict series of turning points.

Therefore, in order to fit with the case at hand, narrative explanations would need to include the possibility of a sketchy ordering of events. This is something that would distinguish this type of explanation further from the strict organization of ephemeral mechanisms.

5. Conclusion

In this paper, I focused on the form of Cavalier-Smith and Martin's explanations for the origin of eukaryotes in order to extract the salient aspects of their explanations. I found that both explanations contained a mix of contingent, ordered and sketchy elements. I then compared these features with the way narrative explanations and ephemeral mechanisms were conceptualized. While narratives seem to successfully account for the contingent aspects, and mechanisms for the more ordered ones, it is debatable whether narratives can account for the more sketchy aspects identified in Cavalier-Smith and Martin's works. What was also apparent is that aspects of narrative and mechanistic

explanations can coexist within a given explanation, particularly in Martin's hypothesis. This case thus calls for further conceptual studies of the scopes, possibilities and limits of narrative and mechanistic explanations. These studies would need to focus not only on these tools' intrinsic properties but also on their heuristic aspects. This latter aspect has only been briefly evoked in the present discussion. With this paper, I also wish to emphasize the need for more case-based, whether synchronic or diachronic, studies of the form of explanations of unique events, as the current conceptualizations do not seem to be flexible enough to successfully embrace relevant examples of scientific practice.

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