

Re-understanding evolution: the Information Continuum Model

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Abstract

Evolution is contingent on inherited information shaped by natural selection. Few biologists familiar with evolution would object to this description. This apparent consensus could be taken to indicate agreement on the forces shaping evolution, but vivid discussions reveal profound divergences on how evolution is perceived. The predominant paradigm of the Modern Synthesis (MS) holds the position that evolution occurs through random changes and natural selection acting on genomic inheritance. However, studies from recent decades have revealed that evolutionary inheritance also includes epigenetic methylation, RNA, symbionts, and culture, among other factors. This has led to voices rising in demand of a broader evolutionary perspective, for example from the proponents of the Extended Evolutionary Synthesis (EES). Despite disagreements on how evolution should be conceived, the different views agree that natural selection happens through dissimilar perpetuation of inheritable information. Yet, neither the MS, nor the ESS dwell on the nature of hereditary information. We do - and find that information in and of itself is immaterial. We then argue that the quality upon which natural selection acts henceforth is also immaterial. Based on these notions, we arrive at the information-centric *Information Continuum Model* (ICM) of evolution, which asserts that hereditary information is embedded in diverse physical forms (DNA, RNA, epigenetic markers, symbionts etc.) with a combined continuum of evolutionary qualities, and that information may migrate between these physical forms. The ICM is advantageous in that it leaves exploration of evolution unrestricted by the limitations imposed by the inherent properties of the physical forms, wherein the hereditary information is embedded (for example the genome). We argue that ICM bestows us with a simple heuristic model that adds explanatory dimensions to be considered in the evolution of biological systems, and in more practical terms, in the planning and interpretation of studies and experiments.

Introduction

Evolution of life is contingent on changing hereditary information relayed through time. For a generation of biologists trained under the neo-Darwinian Modern Synthesis (MS) paradigm, the basic heuristic model of evolution maintains that the hereditary information is found in the genome¹⁻³. The genome, in turn, is shaped by natural selection among a collection of genomes created by random mutations, recombinations, integrations, and reorganizations. Furthermore, according to the MS, while the genome dictates which phenotypes an organism can display, adaptive information is not transferred to the germline other than through differential survival. This means that adaptations are not transferred to the offspring and that the changing information, on which evolution is contingent, arises by random changes in the germline. Hence, the prevailing conception is that evolutionary adaptation takes place during the transition of generations, and since the *genome* is the *hereditary information*, interchanging the two terms would not matter much. The above may rightfully be

argued to be a caricature of MS¹ - but this caricature describes our applied heuristic MS model of evolution too well to be ignored³⁻⁷. The fallacies of a simplified gene-centric model of evolution have become evident in light of the cumulative evidence that inheritance is more than just genomes, and includes epigenetic methylation, RNA, proteins, and culture, among other factors^{3,4,7-9}. These emergent weaknesses of a monolithic gene-centric model of evolution has brought in its wake a demand for a widening of the gaze, and it has been contended that the dominating gene-centric MS has been an obstacle to progress, by ousting proponents of MS-deviant views and curbing the financing of MS-conflicting research⁴⁻⁹. In a sense, the MS's singular focus on genes and genomes has since its rise served as the "one ring to rule them all", to cite J.R.R. Tolkien. Among the contenders of emerging approaches, the advocates of the Extended Evolutionary Synthesis (EES) argue that to understand evolution one should put less emphasis on natural selection and genetic inheritance, and attain a broader focus that includes *developmental bias* (the propensity of particular forms to emerge among the forms possible), *developmental plasticity* (the range of forms an organism can acquire), *niche construction* (the modifications of environmental states), and *inclusive inheritance* (heredity defined to comprise all factors leading to resemblance between offspring and their peers, including genomes)³. Despite disagreements, the different views of evolution agree that natural selection happens through dissimilar perpetuation of inherited information^{1,2,7}. However, neither the Modern Synthesis, nor the Extended Evolutionary Synthesis, dwell extensively on the nature of the substrate of natural selection: inherited information. We investigate the qualities of inherited information that render it amenable to natural selection, and formulate the findings and their consequences into a coherent heuristic model – the information continuum model of evolution. After introducing the model, we investigate its inherent conceptual, practical, and philosophical implications.

The Information Continuum Model of Evolution

All scholars and laymen familiar with evolution would agree that natural selection acting on inheritable information in genomes is a key process in evolution. However, it is important to recognize that the genome *is* not hereditary information. If a string of bacterial DNA comprising a gene is placed in a eukaryotic cell, it will not be translated into protein because bacteria use different combinations of A, T, C, and G to code for amino acids and protein termination than eukaryotic cells. But if the exact same string of DNA is placed in the mitochondria of a eukaryotic cell, it *can* be translated into protein, because the mitochondria uses the prokaryotic code to interpret the sequence. The material string of DNA is unchanged, yet in one situation it enshrines information and in another it does not. This demonstrates that while the genome is *material*, information is *immaterial*. The immateriality is further illustrated by information's ability to change its physical representation. This article, for instance, has changed from biochemical representations in the minds of the authors, to electronic representation in a computer, to physical form on a printed page, and all the way back – many times. Likewise, the information underlying a digestive proteolytic enzyme migrates from DNA via transcription into mRNA and then through translation into a protein. The information hence is physically transformed twice, before the resulting protein is finally secreted and activated to perform its function, securing energy to perpetuate the 'Dance to the tune of life', to quote the title of a remarkable book by D. Noble⁹. The above encompass the first assertion of the *Information Continuum Model of Evolution* (ICM): **Information is immaterial by nature.**

Information, by virtue of its immaterial nature, may be conceptually illusive. In an evolutionary context, it makes sense to define inheritable information as the inherited quality required to materialize as a phenotypic trait. This quality may be embedded in single or multiple genes (or, as we shall see later, in other physical carriers of information). The immaterial nature of information does not imply that ICM resorts to supernatural explanations of evolution; information depends on a

physical representation for its existence, and natural selection acts through differential propagation of immaterial information mediated by differential survival of the physical form(s) wherein the information resides (e.g. genomes). To reiterate: The genome *is* not information, just as a book *is* not a story but a representation of language that may be interpreted as a story. The genome contains a representation of hereditary information, and the information inferred depends on the living system in which the representations are interpreted by the cellular machinery⁴. This may seem an unimportant distinction to some. But consider the weight of its significance: a vital mitochondrial gene is non-sensical to the cytosolic ribosomal machinery only micrometers away; the same genome produces cells as different as those found in brains and muscles; or the fact that when transferring the nucleus of one fish species to the enucleated egg of another, the resulting fish is not representative of the species from which the nucleus originated¹⁰. The living world is rife with examples illustrating that genomes contain *representations* of information that may be read in very different ways, just as religious texts are interpreted in very different ways by scholars.

Genomes are important repositories of inheritable information – but they are not the sole repositories^{6,9}: Information embedded in epigenetic methylation is inheritable and affects genome organization and gene expression¹¹⁻¹⁴. In *Daphnia magna*, for instance, exposure to increased salinity induces a stress gene-related epigenetic DNA methylation response that persists in generations of asexual formation after exposure¹⁴. Mitochondria also harbor information that is passed, primarily maternally, through generations. The mitochondrial information interacts with the information in the nuclear genome, and combining a mitochondria with a ‘host’ cell containing an unsuitable nuclear genome can have deleterious effects. This is nicely illustrated in studies of the intertidal rock-pool copepod *Tigriopus californicus*, where hybridization between rock-pools can lead to paternal nuclear alleles occurring in combinations with less compatible maternally-derived mitochondria, resulting in reduced viability, development, and fecundity in later generations¹⁵. Inheritable information may also be conveyed by RNA molecules with no corresponding representation in the nuclear genome. Such RNA molecules may be acquired from pathogens, as seen with nodavirus-derived viRNAs that can confer non-mendelian inheritance of viral resistance in *Caenorhabditis elegans*¹⁶. The viRNAs can be amplified by RNA dependent RNA-polymerases and persist for generations, and they can be transferred between generations via both sperm and oocytes¹⁶. Information may also be relayed by proteins. For instance, inheritable conformation change in one prion-like element in unicellular bakers’ yeast can induce transgenerational obligate multicellularity¹⁷, while conformation change in another prion-like element governs transition from being a metabolic specialist to a generalist strategy¹⁸. The latter trait can persist for hundreds of generations and interestingly, is induced by bacteria with mutual benefits for both bacteria and yeast^{18,19}. Furthermore, inherited information does not need to rely on a single physical representation for its transmission between generations. Epigenetic methylation patterns are mirrored in the pattern of DNA binding proteins. While methylation is lost during post-zygotic demethylation, it is apparently reinstated based on protein binding patterns, hence upholding the general methylation pattern – an intriguing example of information being relayed via alternating routes of methylation and protein binding²⁰. While the examples above all concern information embedded in molecules transmitted via germ cells, symbionts may also serve as living carriers of inherited information. An example of this is seen in the microbial flora of termites, which demonstrate colony-to-offspring inheritance (among other modes of inheritance) and is vital for the symbionts’ joint digestion of plant biomass^{21,22}. Another example is the fetal colonization of maternal bacteria found in humans, that have lifelong effects on children’s health^{23,24}. Information may also be inherited through routes of hitherto less clearly defined physical bodies. Culture, for instance, is a source of evolutionary important information affecting the fitness, and the evolution of those sharing it^{25,26}. An elegant non-human example of this stems from

archeological excavations revealing culturally-transmitted use of nut cracking stone tools over millennia in west African chimpanzees^{26,27}. One point should be very clear from above examples; hereditary information of evolutionary importance has *numerous* representations and sometimes travel along alternating routes. The *combined* inherited representations embody the total information available for evolutionary tinkering. Strangely, we lack a word for the full gamut of physical carriers and their embedded hereditary information; we propose here the term '*hereditome*', which we adopt and use from here. The above is the basis for the second assertion of the *ICM*: **Hereditary information is embedded in diverse physical representations that collectively constitutes the hereditome.**

The hereditome compartments have distinct properties and this affects the evolutionary dynamics for the embedded information. Some hereditome compartments are stable while other are more dynamic; some are readily modified by external cues while other are more static; some may cross species boundaries with relative ease whereas others do not^{11,18,28}. The genomic hereditome, for instance, is usually inherited from both parents and remarkably constant, while crucial variability is ensured by mutations, reconfigurations, and recombinations. In contrast, the mitochondrial hereditome is generally maternally inherited and does not exhibit recombination, which renders it with different evolutionary properties²⁹. While both the nuclear and mitochondrial genetic hereditomes are quite stable across generations, the epigenetic methylation hereditome is more dynamic with potential for rapid modifications within both generations and cell types³⁰. Where the epigenetic methylation hereditome relay heritable differences associated with the genome, the RNA hereditome and protein hereditome may be equally dynamic, but are able to confer information *not* represented in the genome^{16,18}. In addition, the RNA and protein hereditomes are inherited in a non-mendelian manner, as is the maternally inherited bacterial flora^{16,18,21}. While their physical representations are less defined, cultural and knowledge-based inheritance also have adaptive significances and therefore are compartments of the hereditome – compartments with capacity for very rapid evolution affecting all sharing members. The above examples are not exhaustive and additional hereditome compartments, with yet different evolutionary characteristics, exist. Further hereditome compartments likely remain to be identified. It should be noted that dynamic parts of the hereditome and the embedded information may change very rapidly, and evolution should therefore be considered a continuous process, not a dotted line of events occurring at the transition of generations^{14,16,18,31}. The above frames the third assertion of the *ICM*: **Hereditome compartments are diverse and encompass a continuum of evolutionary properties.**

Sometimes hereditary information switches between hereditome compartments on the journey through time, as previously exemplified by information alternating between representation through epigenetic methylation and representation through the pattern of DNA binding proteins²⁰. At other times, information more permanently moves from one hereditome compartment to another, a point well illustrated by the migration of mitochondrial genes to the nuclear genome³². Another good example of this is the migration of viral *envelope* genes into the genomes of placental mammals happening through permanent retroviral inhabitation of becoming placental mammal genomes. The Envelope protein is required for the formation of the placental interface between the mother and the developing fetus, and migration of the underlying information therefore represented a vital stepping stone in the evolution of mammals^{33,34}. Information may also be assisted in its migration between hereditome compartments as illustrated by information underlying human insulin production travelling from its original position in the human genome via human intervention into yeast – only to be purified and injected into the bodies of humans in need. These examples illustrate the fourth assertion of the *ICM*: **Information can migrate between hereditome compartments.**

The information in the hereditome compartments do not act in isolation. For instance, the almost absent consequences of bubonic plague in the 21st century, contrasted to its devastating effects earlier in history, cannot be explained based on the human genetic hereditome alone – it is only understandable when taking also into consideration the human knowledge-based and cultural hereditomes. This illustrates that traits are manifestations of information conveyed by multiple hereditome compartments, and it makes sense to conceptually think of immaterial information as a quality, rather than as parcels behaving as we expect singular physical entities to. In reality, this is not much different from how eukaryote evolution is conceived under the Modern Synthesis; after all, the expression of *any* gene is dependent on the products of multitudes of genes scattered on separate chromosomes with divergent evolutionary characteristics⁵ (e.g. autosomes, sex chromosomes, and chromosomes with different recombination rates). While we generally consider organisms as separate entities, information underpinning vital traits may be embedded in the combined hereditomes of more than one organism. This may be exemplified by obligate symbionts, where the participants are mutual repositories of hereditary information bestowing traits depending on their intertwined hereditomes^{33,35}. This fits nicely into the concept of biological relativity captured by the statement that ‘biology has no privileged level of causality’^{3,9}, in that obligate symbionts may be considered to have a collective hereditome. For instance, the success of termites is best, if not only, understood by considering both information embodied in the microbial and genetic hereditome compartments²¹. The above is the basis of the fifth assertion of the *ICM*: **Information in the hereditome compartments interact.**

There is widespread agreement that cellular life originated about four billion years ago, that it originated only once, and that it was likely preceded by primitive noncellular ‘life’ in the form of replicating RNA molecules^{36,37}. It is also generally agreed that evolution is the process that, through continuous proliferation and modification, has propagated life from its earliest forms to the living systems we are part of today. It thus appears undisputed that there is an unbroken continuity from the dawn of life to present day - but a continuity of *what*? While a body of information may constantly be found in the same hereditome compartment as it descends through time (e.g. in the genome), information oftentimes moves from one representation to another. This can be exemplified by the HIV virus that, during its proliferation, alternates between having its hereditome embedded in a retroviral HIV *RNA* genome and in the human host’s nuclear *DNA* genome³⁸. Such discontinuity in physical inheritance show that it is not the physical representations of inherited information the constitutes the continuous *what* (although the predominance of DNA in our present understanding of inheritance can make it seem so). Indeed, if the cellular world of today was preceded by an RNA-world, the very earliest steps in the evolution of life likely represent a giant discontinuity of material inheritance. This argument is echoed in the observation that the physical hereditome compartments are composed of atoms and elementary particles that are unable to replicate themselves - and that the physical compartments therefore are discontinuous by nature. When a chromosome is copied it is not the physical chromosome that proliferates - it is the embedded information that does so by the reorganization of matter into a copy of the molecule. Hence it appears that although the information is contingent on a physical form for its existence, it is only the immaterial information that transcends through time, leaving behind a trail of physical representations to wither and perish. Thus, natural selection determines if information persists or not by regulating information proliferation, based on the differential survival of the physical hereditome compartment wherein the information resides. The above frames the sixth and final assertion of the *ICM*: **The substrate of natural selection is immaterial information.** This does not mean that *ICM* promotes the view that natural selection alone explains evolution; propagating information constrains the possible forms and actions of living

systems, but this does not entail that inheritance *governs* the forms and actions *within* the set constraints^{3,5,9}.

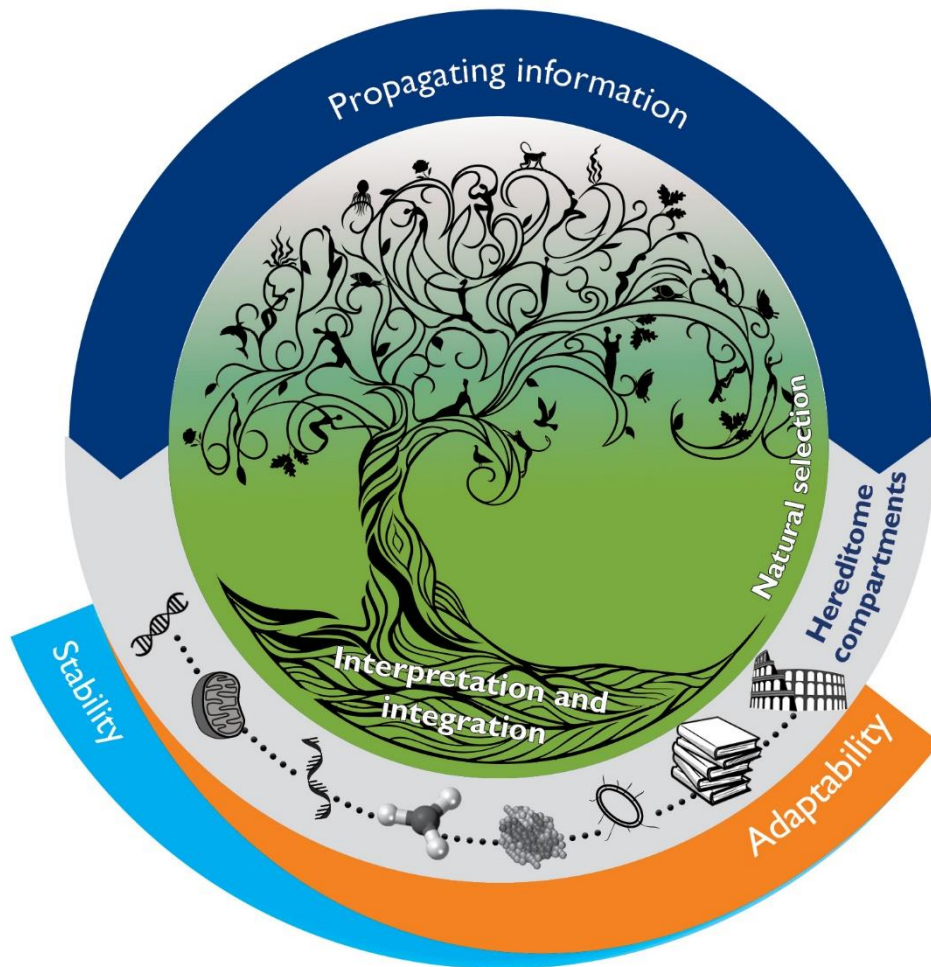


Figure 1. A conceptual representation of the Information Continuum Model. Hereditary immaterial information is represented in the hereditome compartments. The represented information is expressed through interpretation and integration by the system the hereditome compartment is part of. Natural selection acts on the manifested integrated expression and governs the continuous propagation of information in the hereditome compartments. The hereditome compartments illustrated here are, from left (most stable) to right (most adaptable): DNA, mitochondrion, RNA, epigenetic methylation, proteins, microbiome, knowledge, and culture. The compartments list is not exhaustive, and the localizations along the stability-adaptability axis are tentative.

In summary ICM contends that: hereditary information is immaterial. The hereditary information is embedded in physical hereditome compartments as illustrated in Figure 1. The hereditome compartments have divergent evolutionary properties and thereby strongly influence the possible evolutionary trajectories of the embedded information. The adaptive capacity of the hereditome ranges from relatively low, for genes residing on regularly recombining autosomes for example, to very high, such as by cultural adaptation or acquisition of symbiotic bacteria through fecal microbiota transplants³⁹. Information can migrate between hereditome compartments, for instance from genomic Y chromosome region that never recombines to an autosome that regularly do, and thereby

alter its hereditome dependent evolutionary properties. The information in the various hereditome compartments interacts with information in other compartments as it is interpreted and integrated. It is the immaterial information that replicates and diversifies and thereby is the substrate for natural selection.

Implications of ICM

The implications of ICM are conceptual, practical, and to those so inclined, philosophical. ICM regards living systems as the physical manifestation of immaterial information propagating, in essence, by reorganizing matter. Furthermore, ICM states that evolution through natural selection acts by differential propagation of immaterial information that descends with modification. The immaterial information 'substrate' of ICM alleviates the conceptual need for scales and units. Hereditary information can emerge, persist, and disappear at any timescale – it may emerge by acquiring an information-carrying molecule (e.g. viRNA) at one point in time and disappear by the discontinued proliferation of molecules harboring the information seconds or eons later. Hereditary information can also exist at any physical scale – it can be represented by a single molecule proliferating at the same rate as it degrades, or it can be imbedded in the culture of millions of organisms. The traits underpinned by the inheritable information may manifest itself at any organizational level, from resistance against antiviral pharmaceuticals in a single virion⁴⁰ to the collaborative knowledge-based problem solving in multicellular primates⁴¹. A conceptual implication of ICM is therefore that evolution is continuous and that it takes place at the level (cell, tissue, individual, population, species etc.) which forms the base of the proliferating information.

There is a tendency for heuristic conceptual models to gravitate towards single-factor explanations: to understand global warming - look to CO₂; to understand author importance – look to their H-index; to assess a legal entity's successfulness – look to their monetary income; to assess the importance of a paper – look to the citation number; to deem a person's intelligence – look to their grades; to understand evolution – look to the genomes. While the predominant singular focus on genomes in the Modern Synthesis (MS) is one of its most criticized qualities³⁻⁷, it is probably also among the qualities that has made it successful: it is both elegant and conceptually tractable. ICM offers the same conceptual heuristic simplicity as the MS because it allows interpreters to concern themselves only with "information". Nonetheless, ICM's multiple hereditome compartments, and the continuity of evolutionary properties they bestow on the hereditary information, will hopefully allow a nuanced consideration of inheritance in biology and serve to avoid monotheistic tendencies.

In practical terms the ICM brings forth a concept that encompasses all inherited information existing at any scale, which affects how we should design studies and interpret scientific data. For example, experimental organisms collected in the field are prone to have dissimilar histories and divergent hereditomes that may affect the results. Potential influence from all hereditome compartments should therefore be considered in biological studies. This is not necessarily straightforward and ICM may initially appear unappealing, as deciphering the potential contribution from a multitude of hereditome compartments interacting at all temporal scales can seem intractable. However, while the interactions in multifaceted hereditomes can yield an indefinite number of phenotypes, the *range* of the phenotypes is not indefinite. In fact, since the various hereditome compartments contribute cumulative delimitations to the possible phenotypes, unravelling the individual hereditome compartments' contributions will likely simplify matters, and allow for explanation of a proportion of the hitherto inexplicable phenotypic variation and developmental bias. As such, ICM may partly bridge the apparent gap between MS and EES. Furthermore, in an age of rapid environmental change, understanding the temporal aspect of adaptive potential is of crucial importance^{8,42} and likely requires systematic identification and study of the more adaptable hereditome compartments (residing on the

right side in Figure 1). ICM offers a conceptual framework that promotes identification of the more dynamic quarters of information residence.

Beyond the direct instrumental value, ICM also bestows us with a framework for generating hypotheses about the role of hereditary information based on the hereditome compartment wherein it resides – and a tool for identifying probable hereditome compartments carrying the information underpinning a certain trait. For instance, information related to traits under recurrent adaptational pressure, such as recurrent environmental stress, are expected to reside in more adaptable parts of the hereditome, such as in the DNA-methylation hereditome^{6,43}. Since natural selection is the result of the dissimilar ability of information to propagate itself, introduction of variation in the hereditome during propagation is indispensable for adaptation. So, in contrast to the common notion that natural selection should promote fidelity², ICM predicts that evolution must promote mechanisms that strikes the degree of information replication *infidelity* just right.

This section shows how ICM may affect the academic approaches to biological systems. We contest that ICM also have countless philosophical implications and find that the most fundamental question the model rises is: what defines life? According to ICM, living systems are manifestations of immaterial information propagating through time, in essence, by reorganizing matter. Also, according to ICM, evolution of life happens through differential propagation of diversifying immaterial information. We argue that the implication of this is that information that propagates *is* life and that reserving the quality of life for a subset of information embedded in physical forms with certain arbitrary, anthropogenically-defined attributes is inconsistent. However, discussions regarding the definitions of the interconnected conceptions of life, free will, and the nature of the self, have always thrived within the branches of Philosophy. Accordingly, we recognize that one may disagree with our definition of life, but defend the view that the concept of life has connotations related to values and rights and that it should therefore at least be defined consistently. In this respect ICM offers a platform for further transdisciplinary discussions between what C.P. Snow identified as “The Two Cultures” represented by human and natural sciences⁴⁴. That would seem befitting as this paper sprouted from conversations between a biologist (RSM) and a science philosopher (TNM). However, additional discussions of these aspects are beyond the intentions of the present paper and we will therefore here refrain from further exploration of the relationship between matter, information and the self.

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