Historical contingency and the purported uniqueness of evolutionary innovations

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Many events in the history of life are thought to be singular, that is, without parallels, analogs, or homologs in time and space. These claims imply that history is profoundly contingent in that independent origins of life in the universe will spawn radically different histories. If, however, most innovations arose more than once on Earth, histories would be predictable and replicable at the scale of functional roles and directions of adaptive change. Times of origin of 23 purportedly unique evolutionary innovations are significantly more ancient than the times of first instantiation of 55 innovations that evolved more than once, implying that the early phases of life's history were less replicable than later phases or that the appearance of singularity results from information loss through time. Indirect support for information loss comes from the distribution of sizes of clades in which the same minor, geologically recent innovation has arisen multiple times. For three repeated molluscan innovations, 28–71% of instantiations are represented by clades of five or fewer species. Such small clades would be undetectable in the early history of life. Purportedly unique innovations either arose from the union and integration of previously independent components or belong to classes of functionally similar innovations. Claims of singularity are therefore not well supported by the available evidence. Details of initial conditions, evolutionary pathways, phenotypes, and timing are contingent, but important ecological, functional, and directional aspects of the history of life are replicable and predictable.

adaptation | history | self-organization | symbiosis

History, we are told, often repeats itself. In the history of life, for example, there are multiple, sequential episodes of diversification, invasion, extinction and recovery. Functional types and adaptive innovations, including mineralized skeletons, warm-bloodedness, complex life cycles, venom injection, suspension feeding, and herbivory, among many others, arose multiple times in separate lineages. Points of departure, evolutionary pathways, and economic players vary among clades, from place to place, and over time, but the physical and economic principles of emergence, competition, feedback, and evolution governing historical change are timeless. Beneath the details of time and place, there are repeated structures and patterns in history. Selection and regulation imposed by powerful members of emerging systems of life favor some adaptations and directions of change over others and therefore make history in both the human and nonhuman realm predictable (1).

But history is also profoundly contingent. All of history's events, pathways, and participants arise from particular initial conditions or antecedent states and are therefore unique. In Gould's words, "As these antecedent states are, themselves, particulars of history rather than necessary expectations of law, . . . we regard these subsequent outcomes as unpredictable in principle" (ref. 2, p. 1333). Given that participants, such as molecules, organisms, species, and ecosystems, can interact in far more ways than can ever be realized, future states cannot be predicted even one step away from the present (3). The much larger set of potential states than of realized states ensures that contingency is an essentially universal property of dynamic systems. As Chaisson notes, "Contingency—randomness,

chance, stochasticity—pervades all of dynamic change on every spatial and temporal scale" (ref. 4, p. 7).

No reputable historian would question the pivotal role of initial conditions in setting the courses of history, but important issues concerning the nature and scope of contingency remain unresolved. Of particular interest are the existence and potential effects of truly unique phenomena, which resist categorization and that have no parallels, analogs, or homologs in time and space. From the Big Bang to the origin of life on Earth to the establishment of the genetic code, claims of uniqueness have, with few exceptions (5, 6), attracted little attention. The principle of parsimony, which in history mandates the simplest explanation of events and the fewest possible steps from initial state to observed outcomes, has made historical singularity both acceptable and expected. The metaphor of the evolutionary tree, with its single root and its many branches issuing from distinct, single nodes, further strengthens the expectation of unique phylogenetic events. But is uniqueness real, or is the appearance of historical singularity an artifact of retrospection and of sampling the inadequately preserved historical record? What evidence can be brought to bear on the frequencies and circumstances of extremely rare phenomena? What is the temporal distribution of apparently unique historical events and outcomes? What does that distribution imply about the contingency of history and about the role of physical principles and economically based selection in fashioning unprecedented states?

Answers to these questions have profound implications for how we view history and our place in the universe. If history flows from singularities, the unique "frozen accidents" of Kauffman (3) and Crick (7), then all events, interactions, players, and outcomes subsequent to the unique initial state are likewise unreplicable, meaning that we should expect life's properties and deployment elsewhere in the universe to be utterly unlike those on Earth. If, on the other hand, even very rare phenomena can be shown to be iterative and replicable, and if certain pathways and outcomes are strongly favored over others, then similar phenotypes and interactions of life should emerge wherever conditions suitable for life exist. History therefore would be predictable at the scale of phenotypes, ecological roles, and directions of change, but it would be contingent in the details of initial conditions, pathways, players, and timing.

I concentrate here on evolutionary innovations and major transitions. Not only have these breakthroughs led to diversification and ecological expansions of life (1, 8, 9), but they also represent important functional achievements in power and performance. My aim is to evaluate claims of singularity for evolutionary innovations and to test hypotheses that potentially account for cases of uniqueness.

One or more of the following four hypotheses can explain cases of purportedly unique evolutionary innovation: (*i*) the

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innovation is truly singular; (*ii*) uniqueness is an artifact arising from information loss with time or from our inability to discriminate among independently evolved similar states occurring among close phylogenetic relatives or during a very brief interval of time; (*iii*) the innovation is not unique, but the same pathway from initial to final state is followed because of self-organization governing interactions among components to form a new whole; and (*iv*) the innovation is not unique, but selection, based on economic principles of competition for locally limited resources (1), has eliminated, or prevented the subsequent recurrence of, many potentially similar innovations or strongly favored the same pathways and outcomes that cannot be identified as independent.

I suggest that few historical states are truly singular and that the second, third, and fourth hypotheses above explain or justify this absence of uniqueness. Historical sequences and outcomes flow from particular evolutionary points of departure; but these points, sequences, and outcomes are iterative or replicable in the sense that they can be classified and categorized. The laws of physics, economics, and evolution make even rare innovations likely in the long run because these innovations are either thermodynamically favored or because they provide benefits that are applicable under a wide variety of circumstances, including new conditions created by organisms themselves.

Characterizing Innovations

I define an evolutionary innovation as a newly evolved structure or condition that enables its phylogenetically derived bearer to perform a new function or that improves its bearer's performance materially in an already established function. This definition therefore excludes the reduction or loss of structures, changes in the number of iterated parts such as segments and appendages, and changes in body size or proportions (10).

To establish the number and timing of instantiations of a given type of innovation, I surveyed the paleontological and phylogenetic literature and assessed the published evidence and plausibility of claims for singularity or repeated evolution. I accepted an innovation as repeated if the same functional outcome was achieved either convergently (following different pathways) or by parallel evolution (following the same pathway) in separate clades. Some authors consider the separate elaborations of structures such as mineralized skeletons, eyes, and muscularized appendages as nonindependent, because multiple instantiations arise from a common genetic foundation (2, 11–13). The genetic instructions, however, only predispose the organism toward development of the structure and do not ensure its expression. I therefore consider these structures as phylogenetically independent, repeated innovations.

For each type of innovation, I determined the time of origin on the basis of the first observed appearance in the geological record. Times of origin of unique innovations were compared with the dates of first instantiation of repeated innovations in two-by-two contingency tests, in which the division between ancient and more recent origins was drawn at either of two points in time: 1.0 giga-annum (Ga) (the beginning of the Neoproterozoic eon) and 543 mega-annum (Ma) (the beginning of the Phanerozoic eon). Many innovations cannot arise until other innovations have evolved. For example, there can be no primary symbiosis between a cyanobacterium and a eukaryotic cell before the evolution of both eukaryotic organization and cyanobacterial oxygenic photosynthesis. These sequential dependencies, however, imply nothing about the number of instantiations of a given innovation. There is thus no inherent evolutionary bias for either ancient or more recent innovations to be either singular or repeated, except perhaps that some very recent innovations could be unique if they are so advanced that there has been insufficient time for subsequent instantiations to have evolved.

Table 1. Times of origin of purportedly singular innovations

Innovation	Time of origin	Ref.
Origin of Earth's life	Before 3.5 Ga	8
Compartments (protocells)	Before 3.5 Ga	8
Universal genetic code	Before 3.5 Ga	6, 8
Coordinated chromosomal replication	Before 3.5 Ga	8
Oxygenic photosynthesis	3.5 Ga	17, 18
Formation of eukaryote	2.7 Ga	8, 19–21
Primary symbiosis between cyanobacterium and eukaryote	2.7 Ga	22
Sexual populations	1.2 Ga	23
Eumetazoan nervous system	600 Ma	24
Eumetazoan extracellular digestion	600 Ma	24
Bilaterian pattern formation	600 Ma	24
Cnidarian nematocysts	550 Ma	24
Triploblastian three-layered construction	550 Ma	24
Ecdysozoan molting	550 Ma	25
Echinoderm water-vascular system	550 Ma	26, 27
Brachiopod cyrtomatodont hinge	450 Ma	28
Land-plant seed	370 Ma	29
Amniote amnion	340 Ma	30
Arthropod wings	340 Ma	7, 31, 32
Chelonian turtle construction	225 Ma	11, 33
Theropod feathers	160 Ma	34, 35
Angiosperm endosperm	140 Ma	36
Human language	1 Ma	8

I tested the second hypothesis (information loss with time) indirectly by examining clade sizes of each instantiation of minor, relatively recent, repeated innovations for which estimates of the total number of living as well as fossil species are available. Three innovations were analyzed as follows: (*i*) the labral tooth (a protrusion on the shell's outer lip, enabling some predatory gastropods to speed up predation on hard-shelled victims; see ref. 14, data emended from subsequently published taxonomic works); (*ii*) left-handed shell coiling in marine Cenozoic gastropods (15); and (*iii*) envelopment of the shell by extensions of the mantle or foot in marine and freshwater noncephalopod molluscs (16). If many of these instantiations occur in very small clades (five species or fewer), many very ancient, repeated innovations should appear to be unique because such small clades would be undetectable as fossils or phylogenetically.

Results and Discussion

Timing of Innovations. I consider 23 innovations that have been claimed as unique either in the history of life as a whole or within the context of kingdom-level or smaller clades (see Table 1) and 55 repeated innovations (see Table 2). Even without considering the merits of cases of purported singularity, it is clear that these unique innovations are significantly more ancient than first instantiations of repeated innovations ($P < 0.01$ for the test separating ancient from more recent innovations at 1.0 Ga; $P < 0.02$ for the test using 543 Ma). Of 23 singular innovations, 8 (35%) occur before 1 Ga and 14 (61%) occur before 543 Ma. Among first instantiations of repeated innovations, only 4 (7.3%) and 9 (16%) occur before 1 Ga and 543 Ma, respectively. Only 4 of 23 innovations (17%) arising after 250 Ma (the end of the Paleozoic era) are purportedly singular.

If these inferences are correct, they would imply that history during its early phases was substantially more contingent, that is, more dependent on singular circumstances, than are more recent historical episodes. In other words, unique "frozen accidents" were more common in the very distant past than in more recent times.

Two kinds of evidence have been advanced in support of these

Table 2. Times of first instantiation of repeated innovations

Innovation	Time	Ref.
Fixation of CO_2 into organic compounds	Before 3.5 Ga	17
Nitrogen fixation	3.5 Ma	37
Aerobic respiration	2.7 Ma	17
Multicellularity	1.7 Ga	38, 39
Plant apical growth	650 Ma or earlier	23
Animal coloniality	550 Ma	40–42
Mineralized skeleton	550	13, 43
Planktotrophic larvae	550 Ma	44
Secondary symbiosis between plastids and eukaryotes	550 Ma	18, 45
Venom injection	540 Ma	1
Animal muscularized appendages	540 Ma	12
Molluscan operculum	520 Ma	46
Image-forming eyes	520 Ma	30, 47
Bivalved accretionary shell	520 Ma	46, 48
Arthropod conglobation	490 Ma	49
Gastropod siphonal indentation	450 Ma	46
Vertebrate teeth	435 Ma	50
Vertebrate mineralized endoskeleton	430 Ma	51
Plant vascular structure	435 Ma	52
Cemented bivalved shell	400 Ma	53
Arthropod silk production	390 Ma	54, 55
Plant differentiated megaspores	390 Ma	56
Plant leaves	390 Ma	57, 58
Trees and secondary growth	390 Ma	59
Insect stylet	390 Ma	60
Tetrapod ear	370 Ma	30, 61, 62
Land-plant vines	300 Ma	63, 64
Network leaf venation	300 Ma	57, 65, 66
C4 photosynthesis by land plants	300 Ma	30, 67
Insect asynchronous flight muscles	300 Ma	31
Tetrapod jaw propaliny	290 Ma	68
Tetrapod bipedalism	290 Ma	69
Tetrapod turbinates	260 Ma	70
Tetrapod secondary palate	260 Ma	70
Vertebrate gliding	260 Ma	71
Vertebrate endothermy	225 Ma	70
Tetrapod fully erect posture	225 Ma	72
Tetrapod wings	225 Ma	1
Crustacean crab form	180 Ma	73, 74
Mammalian middle earbones	180 Ma	75–77
Animal eusociality	125 Ma	78
Plant heat production	125 Ma	79
Plant alkaloids	125 Ma	80
Vertebrate placenta	125 Ma	30
Plant basal growth	90 Ma	1
Free-floating aquatic multicellular plants	80 Ma	1
Gastropod labral tooth	80 Ma	14
Excretion of molecular oxygen by fishes	80 Ma	81
Stereoscopic vision in tetrapods	80 Ma	82
Electrical sensation by fishes	80 Ma	30
Mammalian hypsodonty	60 Ma	83
Crab heterochely	60 Ma	49
Burrowing ratchet sculpture in bivalves	55 Ma	84
Sand-dollar eccentricity	10 Ma	85

claims of uniqueness. For events in the early stages of life as a whole, the universal or near-universal and uniform architecture of cells, the genetic code, and the composition of eukaryotic cells point to unity of type and singularity of origin. For more clade-specific events, the most persuasive evidence comes from post hoc reconstruction of phylogenetic trees based on the characters of living organisms and sometimes of extinct species as well in the case of morphological states. For the most part, therefore, inferences of singularity are founded on backward extrapolation from phenomena observable among currently living organisms.

Information Loss with Time. The ancient character of nearly all purported singularities in the history of life raises grave doubts about the validity of truly unique antecedent states. Sober and Steel (5) have drawn attention to the rapid loss of information as time recedes and have argued that origins are almost impossible to specify from current states if those origins are very ancient. Phylogenetic and other evidence based solely on the phenomenology of living organisms is by itself insufficient to argue for or against unique, ancient states. The loss of information is of two kinds. First, many basal lineages are not sampled, because they have left no living descendants. Second, our ability to discriminate among closely related ancient lineages that each evolved the same innovation independently is compromised because, as Sober and Steel (5) note, differences between molecular sequences among living descendants become saturated, meaning that they cannot be temporally constrained or even identified; the independent lineages would look like just one lineage.

Indirect support for the hypothesis that information decay through time accounts for the apparent singularity of ancient innovations comes from the size distribution of clades with one of three minor, relatively recent innovations that evolved repeatedly. In many clades in which the innovations evolved are small, the likelihood of recognizing or recovering those clades would be negligible for innovations with very ancient origins. Of 59 clades of marine predatory gastropods in which a labral tooth evolved, all within the past 80 million years, 42 (71%) consist of five or fewer species and 23 are represented by a single species; only two clades comprise 100 or more species. Left-handed shell coiling evolved 19 times independently among marine gastropods during the Cenozoic era (the last 65 million years). Nine clades (47%) are represented by one species, and only one clade spawned a major radiation. Of the 47 clades of marine and freshwater noncephalopod molluscs in which shell envelopment evolved, beginning 450 Ma, 13 (28%) contain five or fewer species, and seven have just one species; four clades represent major radiations of 100 or more species. Exclusively fossil clades with these three innovations are often small. Of 21 fossil clades with a labral tooth, 18 (71%) contain five or fewer species; 3 of 4 left-handed clades (75%) and 6 of 12 clades with enveloped shells (50%) are likewise small. Other repeated innovations, including eyes (47) and secondary growth of cambium in trees (59), show similar distributions of clade sizes.

Evaluation of Unique Innovations. Detailed considerations of individual cases of purportedly unique innovation invite skepticism about claims of singularity. In the presence of a diverse array of simple organic molecules on the prebiotic Earth (and likely elsewhere in the universe), "life is an expected, emergent property of complex chemical reaction networks" (ref. 3, p. 35). A unique origin of life is inconsistent with the self-organized emergence of the autocatalytic networks that define life and that characterize the chemical environment on mineral surfaces where life is thought to have originated (3, 6, 8, 86, 87). Double-layered membranes that surround and attach to the molecular machinery of a living cell arise spontaneously when fatty-acid polymers come to be oriented with their hydrophobic ends pointing toward each other and their hydrophilic ends facing the cell's interior and the external environment (8, 38). A prebiotic template for the compartments that the membranes surround can be provided by the three-dimensionally compartmentalized structure of metal-sulfide minerals in prebiotic hy-

drothermal settings (87). The conditions necessary for the formation of true cells should have been common and widespread, making a unique origin (8) highly unlikely (88).

The near-uniformity of the genetic code among organisms has been taken as evidence for a single origin of the code (8), but it is more plausibly the consequence of intense selection. The code can be thought of as a *lingua franca* among archaeal and bacterial lineages, which from the very beginnings of life have exchanged genes on a large scale compared with the limited horizontal gene exchange observed in eukaryotes (89–92). Any variant of the code that might have arisen would have been quickly eliminated, because genes encoded by variants would be unable to propagate. Deviations from the code could occur, but they appear to be confined to eukaryotes, in which lateral gene exchange is relatively rare (93, 94). The rarity of these deviations is consistent with the theoretical finding (94) that the near-universal code minimizes the effects of mutation and mistranslation. The code is therefore adapted and shaped by selection. There are also indications that the coding scheme reflects the abundance patterns of amino acids and, therefore, that self-organization favoring easily attained correspondences between nucleic-acid codons and amino acids plays a role (7, 8, 95).

The union between the purple-bacterial ancestor of the mitochondrion and a potentially anaerobic archaeal host to form the eukaryotic cell is thought to be singular (8, 19–21). Genetic integration between the two parties comprising the eukaryotic cell certainly implies that strong selection has honed this symbiosis (8, 20, 96), but it does not necessarily indicate a single origin. A diversity of biochemically similar eubacterial hosts and archaebacterial guests would have existed at the time the eukaryotic association was forged, raising the possibility that many "trial" symbioses existed before the enduring one, leading to the immense radiation of eukaryotes, emerged as the most successful instantiation.

The incorporation of a photosynthetic cyanobacterium as a plastid into the eukaryotic cell is often claimed to have occurred only once (22). It may be true that complete integration between host and guest, including transfer of large parts of the guest's genome to the host nucleus, was achieved in only one such symbiosis; however, Keeling (45) has raised the strong possibility that symbiosis between a *Synechococcus*-like cyanobacterium and a eukaryotic cercozoan amoeba (*Paulinella chromatophora*) was achieved independently. As in the case of the mitochondrion, strong selection must have led to far-reaching integration between host and guest to reduce competition among guests in the same host (8, 96, 97).

It is striking that many of the purportedly unique events in the early history of life result from the union, cooperation, and integration of previously independent components. Other ancient and more recent cases of such phenomena, multicellularity and eusociality, for example, have occurred repeatedly in separate clades (8, 17, 38, 45, 78, 98). The early unions therefore belong to a class of phenomena that have occurred throughout the history of life and that are major sources of innovation (99). Their apparent uniqueness is a reflection more of their antiquity than of true singularity. Union, cooperation, and integration are so widely advantageous by enhancing power and competitive ability that selection favoring them should be strong and common regardless of the hierarchical level at which unions take place.

Some clade-specific structures purportedly evolved only once, but all are functionally replicated in other clades. Differentiated tissues, extracellular digestion, and a nervous system each arose once at the base of Eumetazoa (24), but differentiation also appears in other divisions of multicellular life, and extracellular digestion is known in fungi. Pattern formation by Hox and other regulatory genes has a single origin at the base of Bilateria (Cnidaria plus Triplobasts) (24), but gene regulation also characterizes plants, and Hox-like genes appear in sponges (24). The nervous system is unique to Eumetazoa, but proteins involved in signaling and other functions have precedents in proteins required for food recognition, capture, and defense in unicellular organisms (100). The cyrtomatodont hinge of rhynchonellate brachiopods, in which articulation between the two valves involves resorption and remodeling of the growing hinge teeth, perhaps had a single origin (28), although the possibility that it evolved convergently in some small extinct clades cannot be ruled out.

Primary wings permitting powered flight evolved only once in arthropods (31), but functionally similar structures evolved at least three times in vertebrate clades. Feathers appear to have a single origin in the theropod dinosaur clade that includes birds (34, 35), but body covers with similar insulating and sexual functions have arisen in mammals and repeatedly in insects (101, 102). The turtle phenotype, in which the ribs lie external to the pectoral girdle (11, 33), is unique to one clade of reptiles; but differently constructed, functionally similar forms arose repeatedly in arthropods. True seeds evolved once at the base of the seed-plant clade, but close approximations appeared simultaneously in lycophytes (56). The unique angiosperm endosperm is duplicated in Gnetales (36), the amnion of amniote vertebrates has parallels in many fishes (30), and the ability to molt the outer wall in ecdysozoans (nematodes, arthropods, and their allies) is seen also in snakes.

The perception of uniqueness thus often arises from our tendency to ignore "failed experiments," closely similar or identical states that arose in minor (usually extinct) clades. Such "experimentation" is well documented at positions in the phylogenetic tree close to the origin of such major crown-group clades as gnathostomes (103), tetrapods (61, 62), mammals (104), arthropods (105, 106), molluscs (48), echinoderms (107, 108), and land plants (59). The fossil record indicates multiple origins of many innovations that are basal to some major clades and chronicles an early winnowing by selection among competing clades.

Contributing to the perception of uniqueness is the likelihood that changing conditions, mostly induced by life itself, closed the "window of opportunity" on some early innovations. Informational exchange by lateral gene transfer, for example, was prevalent among early life forms, whereas vertical (generation to generation) inheritance became the norm after the Archean era (88–90, 109). Lateral gene transfer, which allows for ready assortment and combination of chemical reactions, is highly favorable to the establishment of new pathways and complex emergent molecular architectures and the genetic code, much as horizontal cultural transmission in human societies promotes the origin and dissemination of complex ideas and technologies. With the advent of vertical transmission, such genetic exchanges became less common and more regulated, in eukaryotes becoming restricted to highly integrated symbioses and to sex.

As another example, oxygen generated by Cyanobacteria greatly restricted the anaerobic conditions favorable to the abiotic formation of combinatorial reactions of organic molecules that ultimately produced life (3, 4, 6). In more clade-specific cases, the global establishment of a well functioning structure often effectively prevents the later evolution of similar architectures, which in their early, highly imperfect states must compete against a thoroughly tested incumbent. Only when innovations arise in mutual isolation in space or time are multiple instantiations likely to last long enough to be detected.

Most innovations, however, are expected to arise multiple times in many clades, because their adaptive benefits apply under a very wide range of circumstances. Strong selection favors these functional outcomes even if the initial conditions and evolutionary pathways are different for each instantiation. As Chaisson notes, "Whenever suitable energy flow is present, selection from among

many energy-based choices rewards and nurtures those systems that engender pathways capable of drawing and using more power per unit mass up to a point beyond which too much power can destroy a system" (ref. 4, p. 161). Intense predation, beginning on seafloors during the latest Neoproterozoic era, elicited the independent acquisition by many clades of mineralized skeletons, burrowing musculature, planktotrophic larval stages, and physiologies making life on land possible (43, 44, 110).

Concluding Remarks

Reconstructing history from an incomplete and potentially biased record is fraught with difficulties and uncertainties and must inevitably be informed by backward extrapolation from the present. A literal reading of the history of life implies that many events, including evolutionary breakthroughs, occurred only once. Data and arguments from various sources, however, indicate that few, if any, innovations are truly unique. Indeed, the principles of physics and economics imply that many derived functional states are achieved many times in many clades because they impart substantial, widely applicable advantages to their bearers. This conclusion applies at all scales, from the funda-

mental molecular and genetic architecture of life to the more restricted domain of individual clades.

The perspective I advocate here tempers Kauffman's (3) and Gould's (105) assertions that the universe in general, and the domain of life in particular, is nonergodic, that is, nonrepeating. In their view, the course of history in one instantiation will not resemble that in another, because each course depends on unpredictable and improbable initial conditions and because the number of possible states is so vast that the likelihood of realizing the same adjacent state is vanishingly small (3). This low probability, however, applies only if transitions between states are random. But there is strong evidence from evolutionary convergences (30) that the transitions are not random. Some configurations stabilize and self-organize more readily than others (3, 95), and economic selection strongly favors some directions and some functional outcomes over others. These physical and economic realities therefore impart to history a certain predictability and replicability (1). By nudging dynamic systems toward some directions and outcomes, self-organization and selection set limits to the contingency of history.

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