DOWNLOAD PDF CONTINGENCY, HISTORY AND ADAPTATION IN THE EVOLUTIONARY PROCESS

Chapter 1 : Evolution and Contingency

Evolution is a strongly historical process, and evolutionary biology is a field that combines history and science. How the historical nature of evolution affects the predictability of evolutionary outcomes has long been a major question in the field.

The Structure of Evolutionary Theory. One could of course benefit considerably even from readings parts of it. Chapter 2, "The Essence of Darwinism and the Basis of Modern Orthodoxy," offers an introduction to Darwin in general and in a twentieth-century context, and is reasonably self-contained, as well. Gould, however, pleads with his readers to "read the book," the whole book SET But then perhaps no book, no matter how long, could be in a case like this. The Tolstoyan, War-and-Peace scale and ambition of the project are not out of place. That Gould himself shares this ambition is evident in the book as well. That history and, hence, at least some philosophy of history are significant is inevitable, given evolution as the subject of their scientific pursuits, inevitable, that is, once Darwin gives life evolution and thus history. In this case, however, at stake is also the introduction of a new philosophical concept of history, as part of a scientific theory, which is not inevitable, since one can also borrow such a concept from elsewhere. Revolutionary as Darwin is, along with so many others, on this score, he is not without his debts. The general appeal to history is more natural in either sense in evolutionary theory than in philosophy. As, however, a structural element of theorizing a given phenomenon which is also how history works in Darwin, and in Gould , it was largely introduced by Hegel and is arguably his greatest philosophical discovery. It would be surprising otherwise, even though Nietzsche famously preferred Lamarck to Darwin, or a certain "Lamarck" to a certain "Darwin. Had Gould dug into Nietzsche a bit deeper, he could have discovered the conceptual problematic of evolutionary theory there. In any event, Nietzsche takes our understanding of the history of morality in radically new directions, including those that Gould found converging on his concept of evolutionary history. There are many other contributions, some equally important, and reflecting equally radical and controversial views. This significance is further amplified by the shift from physics to life sciences and information sciences, and their relationships for example, in the genome project as primarily defining the relationships between science and culture during the same postmodernist period. Physics retains its scientific and cultural role, in part in conjunction with information sciences, as in quantum information theory, and new biology, specifically via chaos and complexity theory an icon, sometimes abused, of many recent discussions in the humanities as well. It is even restated, with a considerable mastery of composition, in the final and the longest footnote in the book on page and then yet again in almost closing the book. To cite this final summary: Many other aspects of it, some of them important, will have to be sacrificed. Here, however, in a more "positive spirit," such as Nietzsche invokes in On the Genealogy of Morals , I will look beyond these specific points of agreement or disagreement to consider some of the more radical questions and challenges posed by the book itself The scientific and epistemological significance of this problematic in evolutionary theory and elsewhere in modern science is unquestionable. At least from the mid-nineteenth century on, our culture may be seen as the culture of chance, or of the confrontation with chance, a confrontation which, in the absence of any counterbalancing causality, it may not yet be ready to accept SET I speak of the role of chance rather than simply chance , since the argument of the book is not primarily about chance but is more about causality and organization , The idea originates with Democritus and extends through a long chain of thinkers to Derrida in particular, and is here invoked by Gould via the complexity theorists Jacques Monod and Stuart Kauffman , While granting the significance of the Gouldian dynamics of contingency in evolution, I shall introduce a broader and in some respects more radical view of chance conceived in part on the model of quantum theory and, hence, of contingency, and suggest that this type of chance plays a role in evolutionary theory. The book does not have and did not aim to have a Part III, but it did aim to argue for such a new synthesis and to prepare for it--a Herculean labor and an immense achievement already SET ; also pp. It is clear, however, that, as announced by Gould at the outset, following his definition of contingency, and as sketched in the epilogue, that new synthesis is fundamentally defined by the role of contingency in the structure of evolutionary theory. The Spread of Excellence from Plato to Darwin []. Although this book, by contrast, treats general theory and its broad results patterns vs. The closing sections of the book pp. Would life, however we image it, be sufficient? Do we, in truth, have such a concept qua concept, life, which doubt compelled Shelley to ask in his great unfinished poem The Triumph of Life , the poem that his death interrupted, punctuated, on this very question: Would even a double question mark be enough? These, especially, as Gould stresses, the first one, remain important conceptually, historically, and culturally SET Nevertheless, Kuhn is right. The evidence pointing to evolution, including the evolution of man, had been accumulating for decades, and the idea of evolution had been suggested and widely disseminated before. Though evolution, as such, did encounter resistance, particularly from some religious groups, it was by no means the greatest of the difficulties the Darwinians faced. All the well-known pre-Darwinian evolutionary theories--those of Lamarck, Chambers, Spencer, and the German Naturephilosophen--had taken evolution to be a goal-directed process. The "idea" of man and of the contemporary flora and fauna was thought to have been present from the first creation of life, perhaps in the mind of God. That idea or plan had provided the direction and the guiding force to the entire evolutionary process. Each new stage of evolutionary development was a more perfect realization of a plan that has been present from the start. Darwin enters the stage set by this history with "his most significant and least palatable suggestion": The Origin of Species recognized no goal set either by God or nature. Instead, natural selection, operating in the given environment and with the actual organisms presently at hand, was responsible for the gradual but steady emergence of more elaborate, further articulated, and vastly more specialized organisms. Even such marvelously adapted organs as the eye and hand of man--organs whose design had previously provided powerful arguments for the existence of a supreme artificer and an advance plan--were products of a process that moved steadily from primitive beginnings but towards no goal. What could "evolution," "development," and "progress" mean in the absence of specified goal? To many people, such terms suddenly seemed self-contradictory. Kuhn Several key Darwinian concepts are indicated here, even beyond the abolition of evolutionary teleology, most especially "gradualism" or a more general principle of "gaining the knowledge of the world" or natural history from the behavior of its small or even infinitesimal parts or changes and their continuity. Leibniz, a co-inventor of differential calculus and a major influence on Riemann, was arguably the most significant precursor, as Gould notes, rightly coupling him with Linnaeus--although, as Gould explains, Charles Lyell may be an equally important influence upon Darwin in this respect , , In science, one needed quantum theory to announce a new paradigm, although there are earlier intimations, especially as concerns the idea of chance, as in thermodynamics, and philosophically one can trace this history still earlier. Decisive to this critique are the questions of chance and discontinuity, and the relationships between them, in evolution and specifically in the non-teleological view of evolution advanced by Darwin. Now, all teleology is, by definition, causal, even if, as I shall explain, this causality is hidden behind the appearance of chance, and, by virtue of its causal nature, essentially continuous. Accordingly, the questions of chance and discontinuity, or of the relationships between causality and chance and continuity and discontinuity or among all of these , may be seen as less interesting in this case. On the other hand, the role of chance and discontinuity in non-teleological views of evolution is a subtle issue, which caused a complex and sometimes ambivalent attitude on the part of Darwin himself, specifically in the relations between more local such as adaptation and more global evolutionary dynamics SET Can we dispense with chance and discontinuity, given the abolition of teleology? What are the dynamics of chance or discontinuity? How are the latter linked to causalities and continuities? What are the relationships between chance and discontinuity, or causality and continuity? These are decisive questions. For, at least in evolution, chance without causality, or discontinuity without continuity, would be almost as problematic and scientifically uninteresting as causality, natural or divine, absolutely without chance In question is an interplay of chance and causality or necessity, of which Democritus was perhaps first to speak, coupled, if one wants to trace it to the pre-Socratics, to the Heraclitean becoming, the never-the-same flow of evolution, but, on this view, the flow interrupted and reshaped by discontinuity. With Darwin and, then, with Nietzsche, this double interplay acquires an extraordinary and ultimately irreducible complexity and, as Derrida argues, becomes ultimately incalculable, preventing us from ascertaining whether, at least, some events are products of chance or causal dynamics 7. It is, again, important that all these elements and various relationships between and among them are engaged with by Gould and made parts of the structure of evolutionary theory, as he sees it. Thus, for example, the continuity and persistence of form morphological continuity or that of other constraints is just as important as punctuation, as both equally work against orthodox Darwinism. If, however, as the central thesis of this book maintains and the [postmodern? SET ; emphasis added On this view, the rise of humans, as conscious animals, is, too, a product of contingency, of a series of contingent, if sensible accidents, perhaps glorious, as Gould once called them, but accidents nonetheless. The emphasis on contingency, as the interplay of chance and causality, rather than on chance alone, is crucial, but the character of contingency is defined by the character of chance within it. This is not to say that the nature of causalities and necessities involved in evolution is not important; quite the contrary, and we need as rich and complex conceptions and theories of causal processes as we can develop. The same argument applies to continuity and discontinuity, and the relationships between them, or between them and causality and chance. Gould stresses the contingent and yet also notes the crucial significance of chance in shaping this complexity, including as concerns "the direction of evolutionary change. Textbooks of evolution still often refer to variations as "random. Darwinians have never argued for "random" mutation in the restricted and technical sense of "equally likely in all directions," as in tossing a die. But our sloppy use of "random" [As will be seen, there may be more of tossing of the dice in mutation. The problem, however, may indeed be that the complexity of the process prevents us from properly assessing how much, if at all, loaded these dice are. In any event, the mutations in question are random enough, at least as "unrelated to the direction of evolutionary change," as Gould rightly stresses. That is, they are random enough to change our view of evolution. The evolutionary survival of such mutations is of course a still different bet, more Darwinian gradualist and adaptational or more Gouldian, which supplements the Darwinian bet with other elements, such as the contingency of punctuation. Even well-adapted species, such as dinosaurs, or potentially well-adaptable species in the proper evolutionary contexts of their emergence and developments, could be "punctuated" out of existence due to external geological or cosmic events or other changes in the context. It is true that, as I have indicated, this particular book is, at least overtly, not about contingency. Gould stresses this point in the Epilog: But this book--entitled The Structure of Evolutionary Theory --does not address the realm of contingency as a central subject, and fires my very best shot in the service of my lifelong fascination for the fierce beauty and sheer intellectual satisfaction of timeless and general theory. I am a child of the streets of New York; and although I reveled in a million details of molding on the spandrel panels of Manhattan skyscrapers, and while I marveled at the inch of difference between a forgotten foul ball and an immortal home run, I guess I always thrilled more to the power of coordination than to the delight of a strange moment--or I would not have devoted 20 years and the longest project of my life to macroevolutionary theory rather than paleontological pageant. This is hardly surprising. Indeed, there is a "because" behind my "and yet. Gould "embraces this apparent paradox with delight": The paradox itself is of course only apparent, or reveals a more subtle theoretical logic. One might also say that the paradox interrupts and destabilizes the accepted logic of evolutionary theory, and leads to a new logic and, with it, new evolutionary theory, which thus "refute" the paradox, along with some of the Darwinisms and even some Darwin. As Gould adds, rightly assessing his book it is difficult to do better: The most adequate one-sentence description of my intent in writing this volume flows best as a refutation to the claim of paradox just above [It is a long sentence, but a good one, both in content and in form, structure, in its continuous flow, which I punctuate a bit here: This book attempts to expand and alter the premises of Darwinism, in order to build an enlarged and distinctive evolutionary theory that, while remaining within the tradition, and under the logic, of Darwinian argument, can also explain a wide range of macroevolutionary phenomena lying outside the explanatory power of extrapolated modes and mechanisms of microevolution, and that would therefore be assigned to contingent explanation if these microevolutionary principles necessarily build the complete corpus of general theory in principle. To restate just the two most obvious examples of the higher tiers of time exemplified in this chapter: The qualification is, again, crucial, for "following Hutton, Lyell, and many other great thinkers," Darwin "foreswore as beyond the realm of science all inquiry into the ultimate origins of things" SET In particular and most significantly, this attitude is correlative to the view that the key causalities, either more Darwinian or more Gouldian, in question in the theory are initiated by random events. These events must thus also be treated structurally as discontinuous in relation to these new causal chains as in relation to previous causal chains. In other words, the dynamics of these chains is initiated by but does not depend on and is dissociated from what triggers them.

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Chapter 2 : Evolutionary Constraints - Evolutionary Biology - Oxford Bibliographies

Ongoing debates: contingency versus convergence. The twin forces that shape Darwinian evolution are random variation and the relative fitness of those variants to the environment. As we have seen above, the process is most easily expressed in abstract terms, but until abstract models of evolution are parameterised they can lead to a wide range of predictions which may or may not correspond to the real world.

While I was traveling last week, an important paper came out on evolution in E. Some of the stories get the emphasis wrong , claiming that this is all about the rapid acquisition of complex traits, while the creationists are making a complete hash of the story. The key phrase is right there at the beginning of the title: This paper is all about how accidents in the genetics of a population can shape its future evolutionary trajectory. It is describing how a new capability that requires some complex novelties can evolve, and it is saying plainly that in this case it is not by the fortuitous simultaneous appearance of a set of mutations, but is conditional on the genetic background of the population. That is, two populations may be roughly equivalent in fitness and phenotype, but the presence of probably neutral mutations in one may enable other changes that predispose it to particular patterns of change. The role of historical contingency in evolution has been much debated, but rarely tested. Twelve initially identical populations of Escherichia coli were founded in to investigate this issue. They have since evolved in a glucose-limited medium that also contains citrate, which E. The long-delayed and unique evolution of this function might indicate the involvement of some extremely rare mutation. Alternately, it may involve an ordinary mutation, but one whose physical occurrence or phenotypic expression is contingent on prior mutations in that population. Thus, the evolution of this phenotype was contingent on the particular history of that population. More generally, we suggest that historical contingency is especially important when it facilitates the evolution of key innovations that are not easily evolved by gradual, cumulative selection. What Blount et al. Each step in evolution is dependent on prior history â€" it is contingent â€" and since many of the steps are driven by chance yet unfiltered by selection, we cannot predict the direction of evolution. Lenski has done this by setting aside 12 separate populations of E. This is a long time, and at the typical mutation rates present in these creatures, it means that every nucleotide has been mutated singly multiple times in the population â€" in other words, there has been ample time to thoroughly explore the single substitution search space. In addition, a sample of each population was taken and frozen every generations, so they can go back in time at will and examine their genome or even restart the line. These bacteria have been raised in a constant environment, one which is somewhat less than ideal: They have evolved, and even have distinctive morphological characters, and many of their properties are consistent from population to population. There is one property that would be useful for the bacteria, but that has evolved in only one of the 12 populations: How did that happen? As the abstract states, they were testing two alternatives. In one, the new ability is purely the product of an extremely rare mutation, some unlikely combination of events that gave a fortunate individual in this population the ability to take up and use citrate. If this were the case, and we rewound the tape of E. In this case, rewinding the tape of life back to before the appearance of the ability, and re-running it forward, would show an increased frequency of reappearance of the ability. Furthermore, by running the tape back further still, they can identify when the enabling change in the population first arose. By looking back at the frozen populations, they determined that the initial mutation that enabled growth on citrate actually appeared sometime between generation 31, and generation 35, These early generations were not as efficient at growing on citrate, so another mutation is thought to have occurred around generation 33, that allowed much more rapid growth. So they pushed it back further, by taking samples from earlier generations and allowing them to replicate again, replaying history. This is the lesson: There were at least 3 events in the history of this one population of E. The first was an enabling variation at around generation 20,; the second was an initial mutation that actually allowed slow citrate uptake at around generation 31,; and the third was a refinement at generation 33, that made the bacteria grow much better on citrate. The creationists are already leaping all over this result and garbling and twisting it hopelessly. Michael Behe was quick to claim vindication , saying that these results support his interpretation. I think the results fit a lot more easily into the viewpoint of The Edge of Evolution. One of the major points of the book was that if only one mutation is needed to confer some ability, then Darwinian evolution has little problem finding it. But if more than one is needed, the probability of getting all the right ones grows exponentially worse. The task quickly gets out of reach of random mutation. Wait a minute â€" has he read the paper? This is an experiment that revealed a trait that required at least three mutations. Yet there it is, produced by natural evolution, with no intelligent design required; and when the experiment is re-run with populations that had the initial enabling variant, they re-evolved the ability multiple times. It seems to me that this work demonstrates that drift, chance, historical contingency, and selection are sufficient to overcome his "big evolutionary problem", and directly refute the premise of his book. If the development of many of the features of the cell required multiple mutations during the course of evolution, then the cell is beyond Darwinian explanation. I show in The Edge of Evolution that it is very reasonable to conclude they did. This is simply baffling. Behe claims that he has shown in his book that the result observed by Lenski and colleagues could not occur without intelligent interventionâ€¦yet it did. He is trying to argue that an experiment that showed evolution in a test tube did not show evolution in a test tube. The answer does not lie in an imaginary designer, but in the reality of historical variation. And this is a lovely discovery. Even from so simple a beginning, small happenstances of history may lead populations along different evolutionary paths. A potentiated cell took the one less traveled by, and that has made all the difference.

Chapter 3 : Monthly Review | Stephen Jay Gouldâ€™s Critique of Progress

Some questions pertain to the history of biological diversity, but the greatest argument has concerned the evolution of major changes in organisms' form and function.

History of evolutionary thought Adaptation is an observable fact of life accepted by philosophers and natural historians from ancient times, independently of their views on evolution , but their explanations differed. In natural theology , adaptation was interpreted as the work of a deity and as evidence for the existence of God. Pangloss [3] is a parody of this optimistic idea, and David Hume also argued against design. The series was lampooned by Robert Knox , who held quasi-evolutionary views, as the Bilgewater Treatises. Charles Darwin broke with the tradition by emphasising the flaws and limitations which occurred in the animal and plant worlds. This illustrates the real merit of Darwin and Alfred Russel Wallace , and secondary figures such as Henry Walter Bates , for putting forward a mechanism whose significance had only been glimpsed previously. A century later, experimental field studies and breeding experiments by people such as E. The Modern Synthesis [11] What adaptation is[edit] Adaptation is primarily a process rather than a physical form or part of a body. From this we see that adaptation is not just a matter of visible traits: Many aspects of an animal or plant can be correctly called adaptations, though there are always some features whose function remains in doubt. By using the term adaptation for the evolutionary process, and adaptive trait for the bodily part or function the product , one may distinguish the two different senses of the word. The other process is speciation , in which new species arise, typically through reproductive isolation. An organism must be viable at all stages of its development and at all stages of its evolution. This places constraints on the evolution of development, behaviour, and structure of organisms. The main constraint, over which there has been much debate, is the requirement that each genetic and phenotypic change during evolution should be relatively small, because developmental systems are so complex and interlinked. However, it is not clear what "relatively small" should mean, for example polyploidy in plants is a reasonably common large genetic change. Structural adaptations are physical features of an organism, such as shape, body covering, armament, and internal organization. Behavioural adaptations are inherited systems of behaviour, whether inherited in detail as instincts , or as a neuropsychological capacity for learning. Examples include searching for food , mating , and vocalizations. Physiological adaptations permit the organism to perform special functions such as making venom , secreting slime , and phototropism , but also involve more general functions such as growth and development , temperature regulation , ionic balance and other aspects of homeostasis. Adaptation affects all aspects of the life of an organism. The following definitions are given by the evolutionary biologist Theodosius Dobzhansky: Adaptation is the evolutionary process whereby an organism becomes better able to live in its habitat or habitats. Adaptedness is the state of being adapted: An adaptive trait is an aspect of the developmental pattern of the organism which enables or enhances the probability of that organism surviving and reproducing. Adaptation differs from flexibility, acclimatization , and learning. Flexibility deals with the relative capacity of an organism to maintain itself in different habitats: Acclimatization describes automatic physiological adjustments during life; [30] learning means improvement in behavioral performance during life. Flexibility stems from phenotypic plasticity , the ability of an organism with a given genotype to change its phenotype in response to changes in its habitat , or to move to a different habitat. A highly specialized animal or plant lives only in a well-defined habitat, eats a specific type of food, and cannot survive if its needs are not met. Many herbivores are like this; extreme examples are koalas which depend on Eucalyptus , and giant pandas which require bamboo. A generalist, on the other hand, eats a range of food, and can survive in many different conditions. Examples are humans, rats , crabs and many carnivores. The tendency to behave in a specialized or exploratory manner is inheritedâ€”it is an adaptation. Rather different is developmental flexibility: The ability to acclimatize is an adaptation, but the acclimatization itself is not. Fecundity goes down, but deaths from some tropical diseases also go down. Over a longer period of time, some people are better able to reproduce at high altitudes than others. They contribute more heavily to later generations, and gradually by natural selection the whole population becomes adapted to the new conditions. This has demonstrably occurred, as the observed performance of long-term communities at higher altitude is significantly better than the performance of new arrivals, even when the new arrivals have had time to acclimatize. Fitness biology and Fitness landscape There is a relationship between adaptedness and the concept of fitness used in population genetics. Differences in fitness between genotypes predict the rate of evolution by natural selection. Natural selection changes the relative frequencies of alternative phenotypes, insofar as they are heritable. Dobzhansky mentioned the example of the Californian redwood , which is highly adapted, but a relict species in danger of extinction. The average contribution to the next generation by a genotype or a class of genotypes, relative to the contributions of other genotypes in the population. The absolute contribution to the next generation by a genotype or a class of genotypes. Also known as the Malthusian parameter when applied to the population as a whole. The extent to which a phenotype fits its local ecological niche. Researchers can sometimes test this through a reciprocal transplant. To evolve to another, higher peak, a population would first have to pass through a valley of maladaptive intermediate stages, and might be "trapped" on a peak that is not optimally adapted. A large population is needed to carry sufficient diversity. According to the misrepair-accumulation aging theory, [42] [43] The misrepair mechanism is important in maintaining a sufficient number of individuals in a species. Without misrepairs, no individual could survive to reproduction age. Thus misrepair mechanism is an essential mechanism for the survival of a species and for maintaining the number of individuals. Although individuals die from aging, genome DNAs are being recopied and transmitted by individuals generation by generation. Adaptation is the heart and soul of evolution. The Great Debate at the High Table of Evolutionary Theory [45] Changes in habitat[edit] Before Darwin, adaptation was seen as a fixed relationship between an organism and its habitat. It was not appreciated that as the climate changed, so did the habitat; and as the habitat changed, so did the biota. Also, habitats are subject to changes in their biota: The relative numbers of species in a given habitat are always changing. Change is the rule, though much depends on the speed and degree of the change. When the habitat changes, three main things may happen to a resident population: In fact, all three things may occur in sequence. Of these three effects only genetic change brings about adaptation. When a habitat changes, the resident population typically moves to more suitable places; this is the typical response of flying insects or oceanic organisms, which have wide though not unlimited opportunity for movement. It is one explanation put forward for the periods of apparent stasis in the fossil record the punctuated equilibrium theory. By this means, the population adapts genetically to its circumstances. Habitats and biota do frequently change. Therefore, it follows that the process of adaptation is never finally complete. On the other hand, it may happen that changes in the environment occur relatively rapidly, and then the species becomes less and less well adapted. Seen like this, adaptation is a genetic tracking process, which goes on all the time to some extent, but especially when the population cannot or does not move to another, less hostile area. Given enough genetic change, as well as specific demographic conditions, an adaptation may be enough to bring a population back from the brink of extinction in a process called evolutionary rescue. It should be noted that adaptation does affect, to some extent, every species in a particular ecosystem. This became known as the Red Queen hypothesis , as seen in host- parasite interaction. Co-adaptation Pollinating insects are co-adapted with flowering plants. These co-adaptational relationships are intrinsically dynamic, and may continue on a trajectory for millions of years, as has occurred in the relationship between flowering plants and pollinating insects. Mimicry A and B show real wasps ; the rest are Batesian mimics: A common example seen in temperate gardens is the hoverfly , many of whichâ€”though bearing no stingâ€”mimic the warning coloration of hymenoptera wasps and bees. Such mimicry does not need to be perfect to improve the survival of the palatable species. Adaptations serving different functions may be mutually destructive. Compromise and makeshift occur widely, not perfection. Selection pressures pull in different directions, and the adaptation that results is some kind of compromise. Diversity, Evolution, and Inheritance [62] Consider the antlers of the Irish elk , often supposed to be far too large; in deer antler size has an allometric relationship to body size. Obviously, antlers serve positively for defence against predators , and to score victories in the annual rut. But they are costly in terms of resource. Their size during the last glacial period presumably depended on the relative gain and loss of reproductive capacity in the population of elks during that time. Here the risk to life is counterbalanced by the necessity for reproduction. Elongated body protects their larvae from being washed out by current. However, elongated body increases risk of desiccation and decreases dispersal ability of the salamanders; it also negatively affects their fecundity. As a result, fire salamander , less perfectly adapted to the mountain brook habitats, is in general more successful, have a higher fecundity and broader geographic range. It must reduce his maneuverability and flight, and is hugely conspicuous; also, its growth costs food resources. The most vital things in human life locomotion, speech just have to wait while the brain grows and matures. That is the result of the birth compromise. Much of the problem comes from our upright bipedal stance, without which our pelvis could be shaped more suitably for birth. Neanderthals had a similar problem. However, as previously stated, there is always a trade-off. This long neck is heavy and it adds to the body mass of a giraffe, so the giraffe needs an abundance of nutrition to provide for this costly adaptation. For example, the polyploid cordgrass Spartina townsendii is better adapted than either of its parent species to their own habitat of saline marsh and mud-flats. Exaptation Features that now appear as adaptations sometimes arose by co-option of existing traits, evolved for some other purpose.

Chapter 4 : A conceptual taxonomy of adaptation in evolutionary biology | Emanuele Serrelli - calendrierde

to examine the effects of contingency that are inherent to the core evolutionary processes of mutation, selection, and drift. Previous analyses of this experiment have shown numerous calendrierdelascience.comlve populations underwent rapid improvement in fitness that decel-erated over time (2, 3, 22, 23).

The term usually describes factors that limit or channel the action of natural selection. It is not equivalent to evolutionary stasis absence of change or even to factors that cause stasis. Evolutionary stasis may be caused by stabilizing selection, but stabilizing selection caused by the external environment is not usually considered a constraint. In a general sense all evolution is constrained. There are no Darwinian demons, immortal organisms that can reproduce infinitely fast, and the concept of constraint is most useful in relation to specific traits, selective agents or ecological contexts. Constraints occur when a trait is precluded from reaching, shifted away from, or slowed down in its approach to a defined selective optimum. Interest in the interplay between selection and constraints goes back to Darwin, and specifically to his concept of correlation of growth, which he used to explain how traits may change as side effects of selection on other traits. The fundamental idea is that selection acts on variation so that the structure and availability of variation may constrain what selection can do. Constraint thinking also has links to orthogenesis, the notion that evolution is driven in particular directions by some internal lineage-specific force rather than by external selection caused by interactions with the environment. Orthogenesis was rejected during the modern synthesis due to a lack of plausible mechanism, accumulating evidence for local adaptations, and an emerging understanding of macroevolution as a messy historical process rather than a rectilinear march toward perfection. The modern synthesis saw increasing emphasis on functional explanations based on external natural selection while structural explanations based on development became marginalized. This was influenced first by the realization that selection can act efficiently on minute differences, and later by the empirical findings of large amounts of genetic variation both on molecular and organismal levels. Hence, mainstream evolutionary biology increasingly took it as given that the necessary variation for selection to act was available. After a nadir in the 60s, a structuralist perspective with an emphasis on developmental constraints started to reemerge. This was manifest first in the revival of concepts such as heterochrony and allometry, which may be seen as specific constraints on evolution, and later in the emerging field of evolutionary developmental biology, or evodevo, where the study of developmental constraints is central. An important element in the modern treatment of constraints is that constraints are not just seen as limitations and explanations of last resort, but are also assigned positive explanatory roles based on channeling variation in directions that may facilitate and explain adaptation. Overview Few concepts in biology are as manifold and lacking in consensus as that of constraints. The Chaos of Constraint Terminology. On the top level are genetic constraints, which are reasonably well operationalized in terms of standing genetic variation. Levels of genetic variation may limit evolution if they are absent or too low, or if variation in different traits are bound up with each other by genetic correlations. The underlying cause of genetic constraints is developmental constraints, which control the input of new genetic variation through mutation, and thus determine genetic constraints in interaction with selection. Selective and functional constraints refer to effects of selection on other traits or for other functions than the focal adaptation, and thus explain how genetic correlations constrain evolution. They also help explain patterns of genetic variation that stem from fundamental trade-offs and physical limitations that no biological system can circumvent. Phylogenetic and historical constraints are orthogonal to this scheme. Here the emphasis is on the role of ancestry in determining the subsequent course of evolution. This is both because the species may inherit particular traits or developmental systems that constrain the possible variation that forms the basis for new adaptations, and because the ancestral position in a complex adaptive landscape can influence which local adaptive peak is eventually reached. Schwenk and Richardson and Chipman provide other classifications of constraint terminology. Futuyma is a recent review of explanations for stasis in evolution showing that maladaptation is common and that there is room for constraints as an explanatory factor alongside adaptation. Gould and Amundson provide historical overviews of structuralist positions in evolutionary biology in which developmental and historical constraint concepts are central. The changing role of the embryo in evolutionary thought. Cambridge Studies in Philosophy and Biology. Cambridge, UK, and New York: The chaos of constraint terminology. A review of constraint terminology with an immortal title. Constraints on phenotypic evolution. An influential review of types of constraint and their relationships. Evolutionary constraint and ecological consequences. A recent review of mechanisms for evolutionary stasis with discussions of the role of constraint. The structure of evolutionary theory. Developmental constraints in a comparative framework: A test case using variation in phalanx number during amniote evolution. Journal of Experimental Biology Part B: Molecular and Developmental Evolution B: A classification of constraint terminology emphasizing the fundamental distinction between generative and selective constraints. Discuss how to test constraint in a comparative setting through the example of phalanx numbers in amniotes. A utilitarian approach to evolutionary constraint.

Chapter 5 : Evolution Topic: Ongoing debates: contingency versus convergence

The process of natural selection: NS-ADAPTATION In evolutionary biology, species are sometimes considered able to "adapt" or "adapt themselves"9 to their environments (adaptation is actively undertaken by species).

What Determines the Outcome? Earthly organisms must be made from materials that are present on Earth. Natural selection favors the individuals in a population that survive and reproduce the best relative to others present, in the current environment. The italics in the previous sentences highlight the three main contingencies of evolution: Changes in the environment lead to changes in the type of characteristics that are favored. The outcome of the evolutionary process is determined by these three contingencies. Thus, it is worth examining them in more detail to determine whether we can reasonably expect the evolutionary outcome that has occurred so far on our Earth to be similar to the outcome of an evolutionary process in another world. The elements that were common on Earth at the time that life was thought to have originated were carbon C , hydrogen H , oxygen O , nitrogen N , phosphorous P and sulfur S. All biological molecules are combinations of these fundamental elements. Eventually, the molecules we know as nucleotides were formed, and then they combined into self-replicating RNA -based forms called ribozymes. If we take the ability to self-replicate as the defining feature of life, then these ribozymes were probably the first life on Earth. DNA is a giant polymer with a sugar-phosphate backbone of nucleotides and nitrogenous "rungs" made of different combinations of C, N, H and O. DNA forms the universal genetic code of information used by all life. Once the trial and error process of early biochemistry produced self-replicating RNA, then it appears likely that the evolution of DNA as the genetic code may have occurred quite rapidly. At that point, other types of self-replicating molecules that could possibly have occurred were at a disadvantage, because a self-replicating system that worked was already beginning to dominate the use of resources. So, the first main contingency of life on Earth may be the genetic code itself on which all life is based. Though it is probably not the only way that information could be coded in a molecule, it is the way that became established on the early Earth, and nothing has come along to supplant it. Another influence of the early materials present on Earth was the fact that water is the universal solvent. Water has very special chemical properties that we largely take for granted, and these properties have dramatically shaped the chemistry of biological life. It is important to recognize, however, that water is not the only possible solvent. Life based on a different set of initial elements, and a different solvent, might be entirely different than the life we know on Earth. Most characteristics of organisms that matter to survival and reproduction can be described in a given population by an average value and a range of genetic variation around the current average. Evolution proceeds when natural selection favors certain variants that survive or reproduce better than others within their environment, and thus contribute more than their share of progeny to the next generation. This process of differential survival and reproduction of individuals with different characteristics leads to a change in the average value of characters so that the population comes to look more like the favored variants change over time and descent with modification. The key here is that this variation involves slight differences from the current average. Thus, descent with modification means that as evolution proceeds, the average characteristics are modified into new forms. The modifications of the bones in the vertebrate limb for very different functions figure 3 are an example of this type of evolutionary change. Even a huge evolutionary step like the colonization of land probably proceeded in this way, when a few lobe-finned fishes began to spend time scooting along muddy shores on their weak fins. Later lineages show modifications of this crude beginning of terrestriality, leading to the amphibians only partially terrestrial , and later to the fully terrestrial reptiles. Change over time and descent with modification can be seen clearly in the evolution of terrestrial vertebrates. Rarely, a variant form that is radically different appears in a population - one that does not fit within in the usual distribution of variation. Such radically different forms may have been very important in the evolution of major innovations during the history of life. It is probable, however, that the first occurrence of a major new characteristic was only a crude version of its final evolutionary form that permitted organisms to take on a new function and that was then further modified by natural selection acting on small variations. The key point here is that if a variant is not produced for some reason, that characteristic cannot and will not evolve in real populations, no matter how advantageous it might be. For example, it would be handy for large mammals to construct their skeletons from titanium instead of bone. This would allow a much lighter weight skeleton, and would probably permit the evolution of much larger body sizes, since the size of terrestrial vertebrates is largely limited by the strength of bone. However, titanium is not a material that is used by organisms with the exception of a few prokaryotes , which appear to use almost every element on Earth, see the next chapter. Thus, a variant within a mammal population that has a titanium skeleton is highly unlikely to ever appear. Instead, the best-working form of a skeleton that can be made with biological materials will be favored by natural selection. Natural selection is the differential survival or reproduction of individuals within a particular population in a particular set of environmental circumstances. No single set of characteristics is universally favored in all organisms, because the characters that lead to high survival in one situation will not necessarily lead to good survival in a different environment. As the evolution of life on Earth has proceeded, there have been changes in the environment due to periodic physical changes on Earth. Radical climate changes have been caused by movement of the continents. These enormous physical events have led, in some cases, to major extinctions, and they have certainly affected the characters that have been favored in organisms at particular times. Even more importantly, life has changed its own environment. Consider the first life on land, colonizing bare rock. Soil was formed as the first bacterial colonists died and decomposed. This allowed plants to take root, whose decomposing bodies further added to the soilbuilding process. The evolution of flowering plants on land has provided not only food but also habitat for many different kinds of terrestrial organisms. The diversity of insects, for example, would not be at current levels, were it not for the diversity of flowering plants that have evolved. In turn, plant diversity has increased due to the effects of the insects themselves on speciation. In life on Earth, many species evolve together "coevolve".

Chapter 6 : Repeated evolution and the impact of evolutionary history on adaptation

If that be so, evolution has a definite 'direction' and is not prey to the vagaries of chance, at least certainly not to the same extent implied by contingency. There is an optimum plan towards which evolution would move and many features are bound to come up. Evidently contingent and convergent evolution have somewhat dichotomous features.

Twitter I tested these hypotheses exactly as Gould suggested: To understand what I did, imagine in The Man in the High Castle that a time-traveling historian took her time machine back to different points in history to see whether the Allied victory in World War II depended on Roosevelt surviving the assassination attempt. If she were correct, then she would expect to see the Allies win far more often when she watched from points after Roosevelt survived. Indeed, what I did was similar, only without a time machine or insanely high stakes. After all, if an outcome depends on a given event, such as a collection of mutations, then the outcome becomes more likely after that event. These experiments kept me occupied for the better part of three years, during which I tested more than 40 trillion cells. They showed that Ara-3 was not simply lucky enough to hit a jackpot any of its siblings could have gotten. We knew that the history involved three phases: To figure out which mutations contributed to each phase, we had to go into the historical record of frozen samples, isolate clones from different time points, sequence them, and identify interesting mutations. In many ways, it was similar to the way a historian scours the historical record for evidence with which to identify events that might have led to an outcome of interest. There is still more to plumb, but the following, much of which comes from the innovative work of a team led by Erik Quandt, who is now a postdoc at the University of Texas at Austin, is substantially complete. Early in the history of Ara-3, a clone evolved that was able to compete better for scarce glucose by eating faster, but at the price of sloppiness. As it ate, it leaked a metabolic by-product into the broth called acetate, which is the acid found in vinegar. Think of a messy toddler spilling half of his dinner on the floor. After running out of the glucose, the cells would then turn to eating the acetate. The acetate presented an opportunity, however, and just before 20, generations, a mutant evolved that would switch to eating the acetate early. This mutant founded a new lineage of cells in the population, which was now made up of two coexisting cell types: A few thousand generations later, another mutation occurred in one of the glucose-acetate users. This mutation altered the tricarboxylic acid TCA cycle, the metabolic pathway by which cells process acetate, resulting in a mutant that was more specialized for growing on acetate. Now a baby crawls over and eats the dropped food. This mutant founded a third lineage in the population, which coexisted with the other two. Later, a third mutation occurred in an acetate-specialist that tweaked the TCA cycle again and made it even better at using the acetate. The family dog realizes there is food on the floor and is even better at snatching it up. In January , more than 33, generations into the LTEE, one population called Ara-3 was much cloudier than the 11 others top graph. A trait had evolved in this population that allowed it to use citrate in the broth as a food source. Illustration by Tom Dunne. What does this have to do with citrate? As it happens, citrate is also metabolized via the TCA cycle, so the history of adaptation to growth on acetate coincidentally evolved cells that were ready to grow on citrate even before they could do so. The stage was set for an extraordinarily rare mutation that occurred in an acetate super-specialist cell at around 31, generations. This mutation was a duplication that placed two identical stretches of DNA side by side. In that duplicated DNA was a gene called citT, which encoded a protein that could transport citrate into the cell. The evolution of a type of E. Was the emergence of an acetate ecology what led Ara-3 to take such a different evolutionary path? Quandt found that some of the other populations had one or both of the first two sorts of acetate-adaptive mutations. It was the third mutation that set apart Ara None of the other populations had it in addition to the other two mutations. To continue the metaphor, none of the other populations seem to have gotten a dog. Has contingency played this role in nature? Work done by Joseph Thornton and his colleagues at the University of Oregon and then the University of Chicago suggests that it very well might have. It governs metabolism, stress and immune responses, and aspects of development. This evolutionary innovation sets apart the glucocorticoid receptor from its close relative, mineralocorticoid receptor, a regulator of salt concentration in the body that responds to cortisol and a few other hormones. The adaptive landscape shows the contingency of the evolution of citrate-eating in the LTEE. Each step on the landscape is a mutation. To climb Mount Citrate, citrate-eating had to evolve, which required multiple mutations. The Ara-3 population started out climbing Mount Glucose like the other 11 populations. There were many paths up Mount Glucose, but Ara-3 happened to take one that led it to collect the mutations that allowed it to evolve citrate-eating and start climbing Mount Citrate. They used computer programs to infer from the modern receptor and its relatives the sequences of three of its ancient ancestors. They then expressed these resurrected ancestral proteins in a modern organism and studied how their sequences, structures, and functions had changed during evolution. The next earliest protein, AncGR1, was resurrected from million years ago and had similar sensitivity. When the researchers engineered a version of AncGR1 that had the five mutations, the result was a protein that was unresponsive to any hormone. What was going on? The answer came when the team discovered that two other mutations that had occurred during this period were also important. When they were added to the version of AncGR1 engineered to have the other five mutations, however, the result was a protein specifically sensitive to cortisol. With regard to the evolution of cortisol specificity, it was purely fortuitous that they stuck around for the millions of years needed for the five sensitivity-shifting mutations to accumulate. Had evolution taken another path, the glucocorticoid receptor would not have evolved because no potential for it to do so would have existed. In bony vertebrates, the receptor sensitive to the hormone cortisol, called the glucocorticoid receptor, evolved over millions of years. Over 10 million years, a series of mutations shifted sensitivity, leading to AncGR2, which is sensitive only to cortisol. These mutations alone, however, would have killed receptor function gray dotted line. They were able to accumulate only because of other mutations that permitted the sensitivity-shifting mutation to work but were otherwise silent. These permissive mutations reveal the contingency in this important innovation in vertebrate evolution. Replay evolution again from million years ago, and the glucocorticoid receptor might not evolve again. It is possible that creatures much like modern bony vertebrates would have evolved without the receptor, but the details of their physiology would have been different, with unknown ramifications. Perhaps more saliently, subtle changes in the developmental programs that the glucocorticoid receptor partly regulates have driven much of bony-vertebrate evolution. Strange as it may seem, the evolution of bony vertebrates, including the origin of humans, has been shaped by happenstance during the evolutionary changes in this single protein lineage. This realization is all the more staggering when one considers that this story is almost certainly not isolated. Future research will no doubt uncover other such stories. Nevertheless, studies thus far have shed enough light to reveal some details of the landscape of evolutionary contingency. Indeed, those studies impart significant lessons that will inform future work and that I think point to a key role for evolutionary potential in determining the scope and effect of the contingency intrinsic to the evolutionary process. Across the Greater Antilles, anole species with similar trait modifications that match comparable habitats evolved in a predictable fashion. Other biologists have identified similar instances of repeated ecomorph evolution among Hawaiian spiders, African cichlids, and Canadian sticklebacks. Natural selection drives similar outcomes under similar conditions, showing that evolution can and does repeat itself. The 12 initially identical populations have evolved in strikingly parallel ways over the course of the experiment. But this convergence has not been unalloyed, because the populations have diverged as well. They display unique genetic, physiological, and ecological quirks beneath their similarities that show that each has happened onto a unique evolutionary path due to chance differences in their histories. This lesson serves as a warning that convergence should not be overinterpreted because it can hide significant differences. Those contingent details can be quite important. The glucocorticoid-receptor evolution research shows that the importance of a particular history is not restricted to the lab, but also has mattered in the natural world. It is unclear how common this story is in protein evolution. Few proteins have had their molecular evolution worked out in similar detail so far. They also show how it matters by illuminating a key insight so glaringly obvious that we tend to forget it and its consequences: Evolution generally does not work from a blank slate, but from what exists. The deterministic part of evolution, natural selection, works by sorting through variation that arises. After all, natural selection will favor a mutation if it provides an immediate benefit, but generally not if it simply increases the potential for beneficial variants to evolve down the road. Natural selection is not a chess player that can see several moves ahead. The epitome of opportunism, it sees only what is helpful or hurtful in the present moment. As a consequence, natural selection can speedily and deterministically assemble collections of immediately beneficial mutations, but how those collections affect later evolutionary potential will be largely coincidental. Hence, where evolution can go next is a contingent by-product of the details of this process and how it changes evolutionary potential by making unrealized traits or outcomes more or less likely. Evolutionary potential holds promise as a means of approaching questions of evolutionary contingency and repeatability. For instance, evolutionary potential helps to explain how evolution can repeat itself while still being contingent. Evolutionary repetition will be more likely when prior history has either increased the potential for evolution to follow the adaptive path or paths leading to a given outcome or else has reduced the potential to go down other paths with different outcomes. In the case of the anoles, for instance, the ancestral lizards that colonized the Caribbean had a prior evolutionary history that left them with physical traits that natural selection could easily tweak to repeatedly produce the same diversity of ecomorphs on each of the islands. Adaptation is more likely to recur if it requires only quantitative changes in existing traitsâ€”such as toe pad and body size, or leg and tail lengthâ€”and the anoles had the right existing traits. The evolutionary potential for similar ecomorphs to arise, and hence for repetition and convergence, would no doubt have been less likely and common had the evolution of qualitatively new traits or body parts been necessary. The anoles thus seem to have come onto the scene well-equipped to radiate, and their repeated radiations may have been virtually guaranteed. Other instances of repeated adaptive radiations may have involved ancestral organisms with similarly high intrinsic radiative potentials. If this idea is correct, repeated radiations could well be contingent events in that they depend on the existence of organisms with histories that have made them ready to radiate. Similar framing could also be applied to other occurrences of parallel evolution as well as to cases of convergent evolution. Indeed, this framing makes clear that evolutionary contingency does not mean that repetition never happens, although it may help explain why and under what conditions it does or does not happen. Many aspects of the contingency intrinsic to the evolutionary process still need to be elucidated, including the conditions under which it may have the most or least significant effects and the levels at which it is important.

Chapter 7 : Adaptation - Wikipedia

Background. Whether natural selection can erase the imprint of past evolutionary history from phenotypes has been a topic of much debate. A key source of evidence that present-day selection can override historically contingent effects comes from the repeated evolution of similar adaptations in different taxa.

Received Apr 26; Accepted Jun This article has been cited by other articles in PMC. Abstract Background Whether natural selection can erase the imprint of past evolutionary history from phenotypes has been a topic of much debate. A key source of evidence that present-day selection can override historically contingent effects comes from the repeated evolution of similar adaptations in different taxa. Yet classic examples of repeated evolution are often among closely related taxa, suggesting the likelihood that similar adaptations evolve is contingent on the length of time separating taxa. To resolve this, we performed a meta-analysis of published reports of repeated evolution. Results Overall, repeated evolution was far more likely to be documented among closely related than distantly related taxa. However, not all forms of adaptation seemed to exhibit the same pattern. The evolution of similar behavior and physiology seemed frequent in distantly related and closely related taxa, while the repeated evolution of morphology was heavily skewed towards closely related taxa. Functionally redundant characteristicsâ€”alternative phenotypes that achieve the same functional outcomeâ€"also appeared less contingent. Conclusions If the literature provides a reasonable reflection of the incidence of repeated evolution in nature, our findings suggest that natural selection can overcome contingent effects to an extent, but it depends heavily on the aspect of the phenotype targeted by selection. Electronic supplementary material The online version of this article doi: Parallel evolution, Convergent evolution, Phylogenetic distance, Taxonomic distance, Homoplasy, Many-to-one mapping Background The independent evolution of the same phenotype in different taxa implies to many observers that some underlying selection pressure has been shared among taxa to produce the convergent phenotype. While similarities in phenotype can arise independently in taxa by chance [1], there are many cases in which natural selection is responsible for repeated evolution [2 â€" 5]. Spectacular examples include the replicated morphologies that reflect similarities in habitat use among Caribbean Anolis lizards [6 , 7] or three-spined stickleback fish [8]. Such examples are striking because they appear to override the idiosyncrasies inherent in the process of evolutionary differentiation [9]. For example, Gould [10] argued that evolutionary outcomes are contingent on a complex sequence of unique historical events that invariably leave an imprint on the phenotypes of descendent taxa. The vagaries of evolution will therefore lead phylogenetically divergent taxa to respond in different ways to similar selection pressures. There is extensive empirical and theoretic work to support this view [9 , 11 â€" 15]. Yet cases of repeated evolution seem to refute it by presenting clear evidence that natural selection can override the contingent nature of evolution. This in turn suggests that the phenotypes of taxa are shaped by present-day ecology more so than past evolutionary events. The seemingly conflicting views of historical contingency and ecological determinism have been the subject of much debate reviewed by [4] and [16]. Members of the same genus or species tend to occupy similar environments [17] and tend to share key aspects of their genome or developmental pathways that can predispose them to follow similar evolutionary trajectories e. It is not surprising, then, that closely related taxa are often exposed to similar selection pressures or that they subsequently respond to those selection pressures in a similar manner. The key point of contention then is time. This predicts the likelihood of similar adaptations evolving independently in different taxa will decrease with the phylogenetic separation of those taxa. Consider the textbook examples of flight in birds and bats through the repeated evolution of the wing [21], or vision in vertebrates and cephalopods through the repeated evolution of a lensed eye [22]. In both instances, there are probably a limited number of adaptive options: There may also be developmental constraints that limit the pool of potential outcomes that can be expressed and bias organisms to converge on similar phenotypes [3 , 5]. Whether adaptation is or is not contingent therefore has important implications for our understanding of the adaptive process and the predictability of evolution more generally. There have been at least two investigations of the likelihood of repeated adaptive evolution as a function of evolutionary time. He found an apparent increase in the incidence of unique adaptations coupled with a reduction in repeated evolution with increasing geological time. However, he argued that this almost certainly reflected the increasing difficulty in distinguishing unique from repeated evolution over vast stretches of geological time e. He concluded that adaptive evolution was not contingent on past evolutionary events and that convergent evolution has probably been frequent throughout the history of life [20]. Although the perspectives taken by these two studies were different, the discrepancy in their conclusions might also reflect the type of repeated evolution examined: Parallel evolution is arguably less likely among distantly related taxa because the probability of two taxa sharing the same genetic mechanism presumably decreases with the length of time separating those taxa [23]; but see [2]. When adaptations arise through different genetic pathways, however, the probability of convergent adaptations evolving is likely less contingent on the length of time separating taxa [5].

DOWNLOAD PDF CONTINGENCY, HISTORY AND ADAPTATION IN THE EVOLUTIONARY PROCESS

Chapter 8 : PCNL Library -Cosmic Purpose and the Contingency of Human Evolution

There could be no Darwin without contingency anymore than without history, as Darwin's concept of history is itself crucially shaped by the concept of contingency as the interplay of chance and causality (without ultimate causes) in evolution.

Cosmic Purpose and the Contingency of Human Evolution Ernan McMullin Department of Philosophy Notre Dame University I am grateful to the other members of our consultation at the Center of Theological Inquiry in Princeton who, over the several years of our dialogue, helped so much to sharpen for me the issues that are discussed in this paper. A version of the paper from an earlier stage in the dialogue appeared as "Evolutionary contingency and cosmic purpose" in a Festschrift for Michael Buckley, S. Himes and Stephen J. Smith claims that Big Bang cosmology effectively disproves the existence of a Creator. One of his arguments runs like this. According to Big Bang theory, the universe began from a singularity. Such singularities are inherently chaotic and unpredictable. No physical laws connect them to later states; in fact, the form taken by later physical laws, the relative magnitude of the four fundamental forces, for instance, is not determined by the initial singularity and is, in principle therefore, a random outcome. Thus, "God has no basis on which to compute what will emerge from the singularity. This, therefore, according to Smith, constitutes an argument against the sort of Creator that religious people normally believe in, namely one whose purposes in creating the universe included the bringing to be of the human race. But if the physical processes involved are such that the agent cannot tell in advance how to act in order to achieve the desired end, then purposive action is effectively blocked. Extending this plausible premise from human agency to the agency of a Creator may not, however, be as simple a matter as Smith is assuming. Does God anticipate the future by extrapolating from a knowledge of the present, as we do? Does God have to rely on the predictability of a particular physical process in order to make use of that process to achieve a Divine end? The role played by chance in that theory seemed from the beginning to call in question the teleological character of the overall evolutionary process. Yet if this be so, how is one to reconcile it with the traditional Biblical understanding of human origins? One possible response is to point to the overall directionality of the evolutionary process, its apparent tendency to lead to greater and greater degrees of complexity, however that elusive term be defined. Even if the multitude of individual mutations and crossings of causal lines that compose evolutionary process were to be inescapably random in nature, the long-term direction of the process itself could then be relied on to lead to the sort of superior adaptability associated with intelligence. Christians sympathetic to Darwin were inclined to orthogenetic interpretations of evolutionary process of this sort in which chance was in the end overcome by something like necessity. First, I want to sketch two opposing trends in the understanding of evolutionary process, one which represents it as more or less predictable, and the other which stresses its contingency. In recent years, thanks in particular to the writings of Stephen J. Gould, the latter trend has attained considerable prominence. In the second part, I will first analyze, and then make use of, the notion of teleological explanation in order to see how far one can go in attributing purpose to evolutionary process on scientific grounds. In the third part, finally, I will explore the implications of the traditional religious view of the cosmos as the work of a Creator for whom the existence of human beings could be construed as in some appropriate sense fulfilling Divine purpose. One way in which the contingency of the evolutionary account of natural selection might be countered from the scientific point of view would be to suppose that God acted in some sort of "special" way to bring about the appearance of humanity. And this has, indeed, been a fairly standard response on the part of Christian writers. But there is another alternative. If the Creator escapes from the limits imposed on the creature by temporality, as indeed the traditional Augustinian account supposes, might not the effect of contingency be blunted since the Creator would no longer be dependent on a knowledge of the present for an anticipation of the future? Predicting evolution A common view of biological evolution is that, given the right environment, it will necessarily occur and in the course of time necessarily give rise to intelligence. Textbook presentations of Darwinian theory often make a progressive process of this sort seem like a simple consequence of natural selection in operation. Heritable variations that favor differential survival of descendants will necessarily tend to spread in the population. There may be additional complications involving geographical isolation, environmental change and the like, but the impression is of a gradual but steady drift towards greater complexity. Organic structures become more complex as new organs develop and old ones find new uses. Intelligence itself, with the enormous advantage it confers in terms of survival and propagation, may then seem an almost inevitable development, if the time-scale be generous enough. This "upward and onward" view of the action of evolution finds some support in the text of The Origin of Species itself: Natural selection acts, as we have seen, exclusively by the presentation and accumulation of variations which are beneficial under the organic and inorganic conditions of life to which each creature is at each successive period exposed. The ultimate result will be that each creature will tend to become more and more improved in relation to its conditions of life. This improvement will, I think, inevitably lead to the gradual advancement of the organization of the greater number of living beings throughout the world. One recent strong supporter of the inevitability thesis is Nobel-prize biochemist, Christian de Duve. In his book, Vital Dust , he argues that as we have come to understand the complex processes of the living cell, we have been able to give a more and more satisfactory account of the developments that could have led up to the appearance of the first cell. In this organic cloud, which pervades the universe, life is almost bound to arise, in a molecular form not very different from its form on Earth, wherever physical conditions are similar to those that prevailed on our planet some four billion years ago. This conclusion seems to me inescapable. Those who claim that life is a highly improbable event, possibly unique, have not looked closely enough at the chemical realities underlying the origin of life. Life is either a reproducible, almost commonplace manifestation of matter, given certain conditions, or a miracle. Too many steps are involved to allow for something in between. Herbert Spencer formulated a "law" of evolution that would, he believed, hold not only for living things but for the physical world generally. Organic structure, he claimed, tends to become more and more differentiated over time, with new forms of integration constantly appearing. Following Lamarck, he maintained that the use or disuse of an organ could lead to hereditable changes of function. This conjunction finds its most striking expression, perhaps, in the work of Pierre Teilhard de Chardin. He sought an explanation for the steady "complexification" he found in the fossil record of life, in a "psychic" or "radial" energy that operated directively, unlike the "tangential" energies treated in physics and chemistry. Though he allows for a degree of "groping" along the way, evolution is for him "a grand orthogenesis of everything living toward a higher degree of immanent spontaneity," "a spiral which springs upwards as it turns. From one zoological layer to another, something is carried over: Few other evolutionary philosophers were quite so confidently orthogenetic in their understanding of the evolutionary process. But philosophers have been on the whole more likely than biologists to see the operation of evolution in terms of law, of a force analogous to Newtonian gravity that relentlessly alters the composition of the gene-pool to create more and more complex organisms. In recent years, the "progressivist" view of evolution is even more likely to be found among physical scientists, especially those who speculate about the existence of intelligent life elsewhere in the cosmos. If one is to devote expensive resources to SETI, as the search for extraterrestrial intelligence has been dubbed, it is important to have at least some sort of estimate of the likelihood of success. Frank Drake, a highly-regarded radio-astronomer eager to direct his Arecibo radio-telescope to the search, in formulated an "extraterrestrial civilization equation" involving seven factors that should yield such an estimate if the magnitude of each factor could be roughly estimated. The number of extraterrestrial civilizations in our galaxy with both the capacity for, and an interest in, interstellar communication would be given by the product of these factors, two of them intended to specify the likely number of planetary systems in the galaxy, the others dependent on the likelihoods of various outcomes: Darwinian natural selection is taken to operate in a steady way, favoring the spread of hereditable variations that promote differential survival of descendants. Though the potential role of environmental factors and physiological constraints in inhibiting this process is not denied, the tendency is to minimize these other aspects of neo-Darwinian theory, and to regard the central role of natural selection as warranting a confidently progressive outcome, "given sufficient time. The contingency of evolution Those who shaped the "new synthesis" in evolutionary biology over the past half century were never comfortable with the predictive uses of evolutionary theory by exobiologists and others, and were flatly opposed to orthogenesis in any shape or form. Ernst Mayr and Theodosius Dobzhansky were among those who expressed their skepticism about this way of understanding evolutionary modes of explanation. The most outspoken critic was, perhaps, George Gaylord Simpson who in This View of Life developed an extended polemic against the assumptions underlying the predictivist account. He emphasized, in particular, the fundamental differences between such non-historical natural sciences as physics and chemistry and the historical sciences: The latter deal with unique events for which the notions of law applicable in physics, on which people like Drake and Sagan draw, simply do not work. The complexity of the interactions between environment and gene-change is so great that any attempt to abstract "trends" or "tendencies" is bound to fail. Since mutations in DNA: Pure chance, absolutely free but blind, at the very root of the stupendous edifice of evolution: It is today the sole conceivable hypothesis. First, they represent the convergence of previously unrelated causal chains: The course of evolution is thus itself unpredictable in detail. Stephen Jay Gould takes a much stronger line regarding the contingency of evolutionary change. He will have no truck with "upward courses" or "trends," or with predictability of even the most modest kind. And his emphasis is not on the randomness either of the mutations that afford the material for natural selection nor of the genetic drift in founder populations. Rather, it is on the lack, in general, of connection between the multiple lines of causality that affect singular historical events, such as changes in the gene-composition of a population. In his popular essays, he returns over and again to the flexibility of the evolutionary process that makes it something other than simple selectionist accounts would lead one to expect. In the title essay of Eight Little Piggies, he argues that the pentadactyl limb we share with so many other mammalian species "just happens to be. Rather, the number may derive from: We are trained to think that the "hard science" models of quantification, experimentation, and replication are inherently superior and exclusively canonical, so that any other set of techniques can pale by comparison. But historical science proceeds by reconstructing a set of contingent events, explaining in retrospect what could not have been predicted beforehand Contingency is rich and fascinating; it embodies an exquisite tension between the power of individuals to modify history and the intelligible limits set by laws of nature. He has long been a critic of the gradualism of the traditional Darwinian account of the operation of natural selection, urging instead a "punctuated equilibrium" in which long periods of stasis, when species remain more or less unchanged, are interspersed with moments of relatively sudden speciation. What excites Gould most about the "Cambrian explosion," as it has been called, is not just the fact that the phyla appeared over such a relatively brief time nor that no new phyla have appeared since, but that the vast majority of the arthropod "ground-plans" found in the Burgess shale have no modern representatives. It is this decimation of phylum-candidates, this "lottery" as he terms it, that Gould sees as testimony to the effects of historical contingency. The conventional response, of course, would be that the four surviving phyla were in some way better adapted for changing environmental conditions. Gould regards this as implausible. But even if this were to have been the case, under a different environmental scenario the list of survivors he claims would have been quite different. And everything that came later would then have taken a quite different direction. His claim is that in such episodes natural selection of the usual sort would cease to operate; it would in large measure be a matter of luck which among all the existing species would survive to propagate themselves in a depopulated world. Furthermore, the causes of such massive extinctions are a matter of chance, relative to the prior history of the affected populations. And so he concludes: Since dinosaurs were not moving toward markedly larger brains, and since such a prospect may lie outside the capabilities of reptilian design, we must assume that consciousness would not have evolved on our planet if a cosmic catastrophe had not claimed the dinosaurs as victims. One specific source of contingency to which he often returns is the constraint set on possible adaptive lines of development in a particular population by the availability in some corner of that population, for quite other reasons, of the appropriate anatomical framework for that development. Had those species not been present, as they might well not have been, Gould remarks, amphibians could not have invaded the land, which in that event might still be inhabited by insects only. But "contingency" is ambiguous in this context: Accepting the first by no means commits one to the second. Or that consciousness would not have developed if an asteroid had not hit or if climate change had covered Africa in forest three or four million years ago? The massive evidence for parallel evolution of such organs as the eye or of physiologically very similar species ought to give one pause in making such claims of unlikelihood. It seems as though contingency has in many instances been overridden by strong selective advantage.

Chapter 9 : Contingency & evolution - Gene Expression

Mandibles and teeth of ungulates have been extensively studied to discern the functional significance of their design. Grazing ungulates have deeper mandibles, longer coronoid processes, flatter incisor arcades, and more hypsodont molars in comparison to browsers.

But stand back, and you will see a picture full of meaning. Something like this happens over and over again as we study the past. Big history helps us stand back from the details and see the patterns. By doing so, it can transform our ideas of what history is about. Contingency and Pattern in Human History Most historians study highly contingent processes. This was an extremely unpredictable event. His gun might have misfired; he might have missed his target; he might have had cold feet; he could have not been born, or been born with a slightly different genetic make-up or Many things could have changed the course of events. Such contingencies are not confined to human history. The American geologist, Walter Alvarez, proved that the disappearance of most species of dinosaurs about 67 million years ago was due to the landing of an asteroid off the coast of Yucatan, which created the equivalent of a nuclear winter and destroyed most large species on earth. That event cleared the way for the evolution of mammal species, which, until then, had consisted mostly of small, timid shrew-like creatures. Collingwood, for example, argued that the natural sciences study regular, law-obeying processes such as the workings of gravity, while historians study the unpredictable actions of conscious, self-aware and freely acting women and men. The misunderstanding may arise, in part, from a reaction against extreme forms of determinism, which argued that all of reality was patterned. The French mathematician, Pierre-Simon Laplace once wrote that: An intellect which at a certain moment would know all forces that set nature in motion, and all positions of all items of which nature is composed, if this intellect were also vast enough to submit these data to analysis, it would embrace in a single formula the movements of the greatest bodies of the universe and those of the tiniest atom; for such an intellect nothing would be uncertain and the future just like the past would be present before its eyes. Not all events were time-reversible. Then quantum physics found contingency in the heart of the material world. The behavior of individual sub-atomic particles can never be predicted with perfect accuracy. You cannot tell, for example, when a particular atom of Uranium will undergo radioactive decay. This is not just a matter of experimental practicalities but an intrinsic quality of matter and energy. Reality is fuzzy at small scales. You can never bring it into perfect focus. But contingency is not just present at small scales. Here tiny differences in the initial conditions seem to get magnified over time. This is the famous "butterfly effect". An even more spectacular example of contingency at very large scales is the apparently serious speculation that the entire Universe may be the result of a "quantum fluctuation" at the moment of the big bang. So modern physicists, like historians, are familiar with contingency. Yet they also know that there are powerful patterns that allow us to establish what we routinely describe as "scientific laws". In practice, we often find that contingency and pattern seem to flow into each other because most events in both history and the natural world are governed by varying degrees of probability. As a result, contingency seems to give way to pattern and vice versa in subtle and often beautiful ways. Indeed, the same mechanisms that generate apparently random processes at one scale may generate predictable processes at different scales. Two centuries ago, Immanuel Kant already understood that this complex relationship shapes human history as well as the physical world. Whatever concept one may hold â€¦ concerning the freedom of the will, certainly its appearances, which are human actions, like every other natural event are determined by universal laws. However obscure their causes, history, which is concerned with narrating these appearances, permits us to hope that if we attend to the play of freedom of the human will in the large, we may be able to discern a regular movement in it, and that what seems complex and chaotic in the single individual may be seen from the standpoint of the human race as a whole to be a steady and progressive though slow evolution of its original endowment. Yet many historians still feel uncomfortable with the idea that patterns shape human history as much as agency and contingency.

Colin Renfrew has noted a similar resistance among prehistorians. For most prehistorians, he writes: It is a rich palimpsest, testifying to human creativity, and perhaps little more is to be expected than the collection and collation of regional narratives. Similarities include pyramid-like monumental architecture, the construction of calendars, the evolution of writing, states, cities and trade and the appearance of a division of labor by gender, class and ethnicity. As Renfrew points out, these odd parallels "must imply some commonality both in practicality and in potential, as both are products of the human condition. There are, to put it frankly, aspects of human history that cannot be adequately handled using the familiar mantras of agency and contingency. Few historians feel comfortable at these large scales, and that may be why historians rarely discuss the large patterns. In the next section, I want to discuss some patterns that can be seen once we shift to the scale of human history as a whole. That is a scale of approximately , years. The S-Curve One of the most fundamental and revealing of the large patterns in human history is the "S-curve" describing population growth. The S-curve is a fine example of how the unpredictable behavior of many individuals can yield clear patterns because, with minor modifications, this pattern seems to describe the population histories of all species, from bacteria to chimpanzees. The "S-curve" or logistic curve, describes a pattern of growth familiar in many fields, from population dynamics to the study of innovation. The idea is ancient. Adam Smith wrote in The Wealth of Nations: The S-curve describes this relationship. When a species is young and exploring the niche to which it is adapted by natural selection, its numbers will grow rapidly because plenty of resources are available. Eventually, though, the species will find it is using all the resources it can extract given its genetic endowment. Then it will settle into a wobbly demographic equilibrium. It will overshoot the available resources, collapse below them, then overshoot them again, creating the indefinitely extended, if shaky, horizontal upper arm of the S-curve. For the rest of its time on earth, members of the species will make minor demographic and ecological adjustments for climatic changes or diseases or other unexpected events. Thousands or even millions of years later, the species will die out or evolve into a new species when climatic change, competition from other species, or some other factor reduce the available resources. But while the species survives we will see little long-term change. If you want to find history in the biological realm you have to move to higher taxonomic levels, to the level of the genus, or family or order, or even to the history of life as a whole, and you have to move to scales of millions of years. Then you can see evolution and change, driven, for the most part, by natural selection. But at the level of the species you do not find history. Except, that is, in the case of our own species, Homo sapiens. Remarkably, the simple form of the S-curve that I have just described does not characterize the history of our own species. This stunning fact is fundamental to understanding the large patterns of human history. For most species, the upper bar of the S-curve prevents sustained growth. Our earliest ancestors were also subject to the brutal Malthusian logic of the S-curve. These innovations forced the heavy upper arm of the S-curve upwards in small steps, each of which allowed a small increase in populations. The difference was merely that in human history the upper bar of the S-curve was slowly rising. Though small, that difference was transformative. It explains our dynamism and creativity as a species. It explains why human cultures display such variety in technologies, organization, clothing, housing, artistic styles, and modes of thought. Yet it also explains why, when seen at large scales, human communities seem to have evolved on parallel trajectories, for in all societies rising populations and increasing control of resources created similar opportunities and challenges that yielded similar outcomes. The distinctive human form of the S-curve explains why we are the only biological species on earth with a history and it explains why that history is patterned. We can distinguish three main patterns. The first, or "Paleolithic," regime characterizes the era before agriculture appeared, about 10, years ago. At first sight, graphs of human population growth or energy use may suggest that little changed during the Paleolithic era. That impression is misleading. Our ancestors broke the logic of the S-curve from the moment they first appeared. We know of no other large species capable of migrating into such a diversity of environments. Trans-ecological migrations on this scale required a sustained ability to adapt that is unique to our species. Earlier hominine species, as well as earlier species of elephants, apes and tigers, had migrated between Africa and Asia because, across this vast range, they found familiar environments. But migrating to Australia was a different matter. That required advanced sea-going skills, and the ability to adapt fast to an unfamiliar suite of animals and plants. Our species was the first large land species to make the crossing. Entering ice-age Ukraine, Russia and Siberia was an equally tough challenge. You had to be able to control of fire, to sew well-fitting clothes and hunt mammoth and, in regions of peri-glacial steppe, to construct buildings such as the mammoth-bone houses that Olga Soffer excavated at sites such as Mezhirich. Each of these migrations was made possible by "innovations", by new ways of extracting resources from the environment, or new ways of "adapting". The second, or "Agrarian", regime typifies human communities during the last 10, years. Most noticeable is a more forceful raising of the upper bar of the S-curve. While this may seem just a matter of pacing, the consequences were transformative. Agriculture, and the technologies associated with it, enabled human communities to settle the world more intensively as well as more extensively, because even the simplest forms of agriculture could support perhaps 50 times as many people as most forms of foraging. Agriculture raised productivity by rearranging landscapes, plants and animals so as to increase the production of those species most useful for humans. Agriculture could support larger, denser, more variegated and more interconnected human communities. A division of labor emerged as humans used their ecological creativity to find new niches within human society, as potters, priests and peddlers. However, even this regime could not escape the iron upper bar of the S-curve, which periodically hammered population growth. There were inherent limits to energy flows because agriculture tapped only recently generated energy. Rates of innovation were also limited by the shortcomings of agrarian era technologies of communications and information storage, and by the generally anti-commercial attitudes and methods of tribute-taking elites. Slow rates of innovation discouraged investment in innovation because the returns were uncertain and remote, which explains why agrarian era elites generally regarded conquest as a more reliable strategy of growth. At the same time populations rose much faster than in the Paleolithic era. Peasants, unlike foragers, have many reasons for maximizing fertility.