

Molecular Theory of Evolution

A. MOLECULAR CLOCK HYPOTHESIS

If evolution were only divergent (i.e., if there were no homoplasy), and if all lineages evolved at the same, constant rate, then the number of differences between two species would be a straightforward index of the time since they diverged from their common ancestor. In that case, we could determine the phylogeny i.e., the relative order of branching—simply by the degree of difference between pairs of taxa. In the year 1965, Emile Zuckerkandl and Linus Pauling first coined the term “molecular clock theory” which suggested that —

“the rate of evolution of a given protein or DNA molecule is approximately constant over time and among evolutionary lineages”. More specifically, it proposed that there exist a statistical proportionality between the time elapsed since the last common ancestor of two contemporary homologous protein chains and the number of amino acid differences between their sequences.

Thus, in simple words — due to mutation, a sequence of protein or DNA changes from one molecular morph to another at a constant rate in the evolutionary history of all such organisms that diverged from a common ancestral stock. Since this alteration in the morph of a molecule happens at a fixed interval of time (as though the ticking of a clock), the rate of mutation within them reflects the evolutionary relatedness between two molecules – hence the term “molecular clock” has been ascribed.

Logic behind molecular clock hypothesis:

Logic behind molecular clock hypothesis may be provided from the works of Emile Zuckerkandl and Linus Pauling (1965) and other molecular biologists:

1. Protein sequencing studies have revealed that the haemoglobin of different mammals which diverged from a common ancestral stock approximately 80 million years ago, differ from human haemoglobin in an almost similar number of amino acids (Zuckerkandl and Pauling, 1965; Kimura and Ohta, 1972).

Haemoglobin of	Difference in amino acids
Man and horse	43
Man and pig	42
Man and rabbit	39
Man and mouse	41

Thus, the similarity in the number of amino acid substitution in different animals probably suggests a similar rate of amino acid substitution.

2. Dickerson (1972) described the cytochrome-c of rabbit, cow and kangaroo differ from human cytochrome-c by 9, 10 and 10 amino acids respectively which probably indicates a similar rate of amino acid substitution in the cytochrome-c molecules in the three animals.
3. Kohen et al. (1972) described that rate of nucleotide substitution in the DNA in different primates was identical.

DNA of	Divergence from ancestor (10 ⁶ years)	Difference in nucleotides	Nucleotide substitution/ DNA strand/10 ⁶ years
Man and Chimpanzee	15	2.4	0.08
Man and Gibbon	30	5.3	0.09
Man and Green monkey	45	9.5	0.10
Man and Capuchin monkey	65	15.8	0.12

Information from the fossil record on the absolute time of divergence of certain taxa may be used to calibrate a molecular clock-to determine its rate-and to estimate the divergence times of other taxa that have not left a good fossil record. For example, suppose the proportion of base pairs that differ between the $\Psi\eta$ -globin pseudogene sequences of two primate species is 0.0256. Assuming a molecular clock,

$$D=2rt,$$

where, D is the proportion of base pairs that difference between the two sequences, r is the rate of divergence per base pair per Million years, t is the time (in Million years) since the species common ancestor, and the factor 2 represents the two diverging lineages.

If D = 0.0256 and r = 0.001534, as estimated from the data in the Figure below, then $t = D/2r$, or, $t \cdot = 8.3$, and 8.3 Million years is our best estimate of when the two species diverged from their common ancestor.

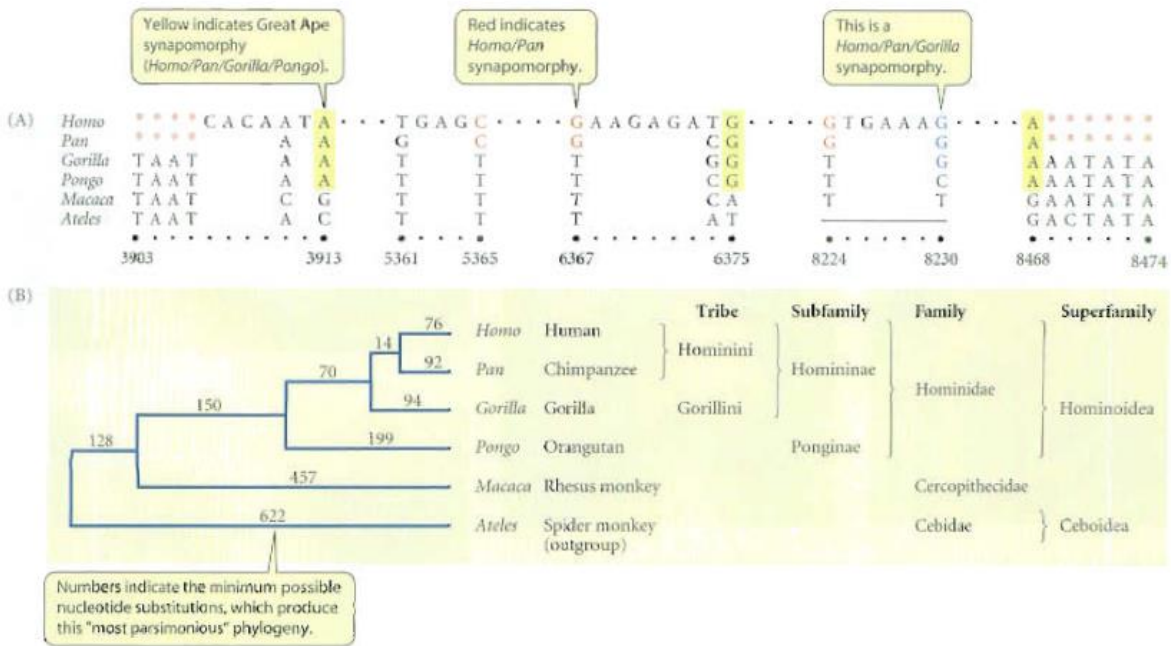


Figure: Evidence for phylogenetic relationships among primates, based on the $\Psi\eta$ -globin pseudogene.

(A) Portions of the sequence in six primates. *Macaca*, an Old World monkey, and *Ateles*, a New World monkey, are successively more distantly related outgroups with reference to the Hominoidea. Sequences are identical except as indicated. Using *Ateles* and *Macaca* as outgroups, positions 3913, 6375, and 8468 exemplify synapomorphies of the other four genera, and position 8230 provides a synapomorphy of *Gorilla*, *Pan*, and *Homo*. Synapomorphies of *Pan* and *Homo* include base pair substitutions at positions 5365, 6367, and 8224, and deletions at 3903-3906 and 8469-8474 (red asterisks). Autapomorphies (unshared derived states) include 3911 and 3913 (*Macaca*), 8230 (*Pongo*), 6374 (*Gorilla*), 5361 (*Pan*), and 6374 (*Homo*).

(B) The most parsimonious phylogeny based on the $\Psi\eta$ -globin sequence, using *Ateles* as an outgroup. The minimal number of changes is indicated along each branch. A tree that split up the *Homo*·*Pan*·*Gorilla* group would be 65 steps longer, and one that split *Homo* and *Pan* would be 8 steps longer. The figure includes one of several proposed classifications for humans and apes (Delson et al. 2000). (A. after Goodman et al. 1989; B. after Shoshani et al. 1996.)

Charles Langley and Walter Fitch (1974) were among the first to use data from fossils to test the molecular clock hypothesis. From the amino acid sequences of seven proteins, they estimated the number of nucleotide differences between pairs of species of mammals. Langley and Fitch found a strong but inexact correlation between the number of molecular differences and time since divergence. Their clock could be used for coarse, but not fine, estimates of phylogeny.

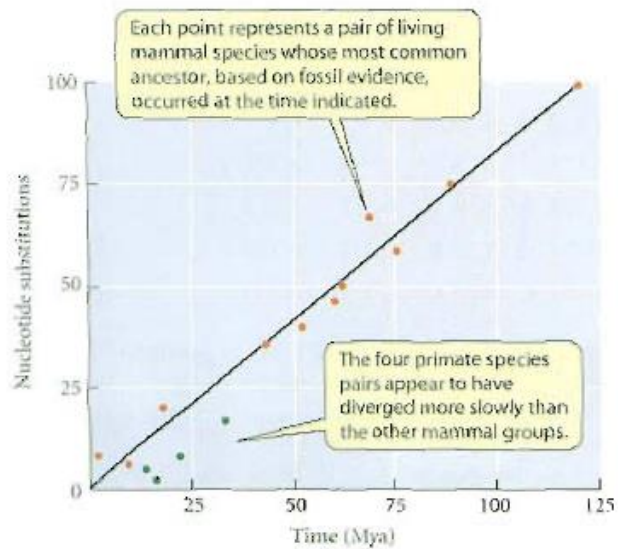


Figure: Base pair substitutions versus time since divergence, illustrating the approximate constancy of the rate of molecular evolution. Each point represents a pair of living mammal species whose most recent common ancestor, based on fossil evidence, occurred at the time indicated on the x-axis. The y-axis shows the number of base pair substitutions inferred from the difference between the two species in the amino acid sequences of seven proteins. The four green circles represent pairs of primate species. (After Langley and Fitch, 1974.)

Difficulties encountered by Molecular Clock Hypothesis:

Considerable amount of data was submitted by Goodman (1976, 1981) to challenge the molecular clock hypothesis:

1. From protein sequencing studies, Goodman et al. (1976, 1981) suggested that the rate of evolution through amino acid substitution has become slower in hominids than in old-world monkeys after their separation from the common ancestral stock.
2. DNA sequencing studies have revealed that the rate of evolution through nucleotide substitution has been much slower in hominids than in old-world monkeys
3. Ou and Li (1992) sequenced 54 proteins in rodent and found 15 proteins have faster rate of amino acid substitution, 12 proteins have slower rate of amino acid substitution and 7 proteins have similar rate of amino acid substitution.
4. DNA sequencing revealed that the nucleotide substitution rate is considerably higher in rodents than in human lineage.

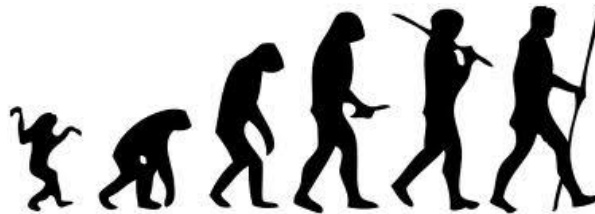
Current status of Molecular Clock Hypothesis:

Taking cue from the present day knowledge it can be inferred that the Molecular Clock Hypothesis may be acceptable with following modifications:

1. The rate of neutral and silent mutations of molecules remains approximately constant in all lineages from a common ancestral stock (Li, 1997). Several amino acid substitutions has occurred at a constant

rate in haemoglobin and cytochrome-c of different mammals although the normal functioning of these proteins remained unaffected suggesting that these substitution involved neutral mutation only (Kimura, 1971, 1981).

2. The rate of mutations which were not silent or neutral may vary in different lineages of a common ancestral stock (Eastal and Collect, 1994; Li, 1997). Certain proteins exhibited a similar rate of amino acid substitution in rodent and man – might be a case of silent mutation; certain proteins exhibited higher or lower rate of mutation in rodent and man – might be the case of non-synchronous mutations.
3. The variable rate of non-synchronous mutations in different lineages of a common ancestral stock may be due to:
 - Two lineages, after their separation from common ancestral stock, may differ in their DNA repair ability
 - A lineage with shorter generation time may show a higher rate of evolution than a lineage with longer generation time
 - A lineage with higher metabolic rate may show a faster rate of evolution than a lineage with lower metabolic rate
 - A drastic reduction in the population size of a particular lineage may increase the rate of evolution of certain proteins in that lineage.



B. PUNCTUATED EQUILIBRIA

Punctuated equilibria are patterns of evolution in which long-term equilibria of species are punctuated by relatively rapid speciation events. It is an alternative to *gradualism*, a pattern in which gradual directional change within species eventually leads to speciation. Punctuated equilibria were first proposed in 1972 by two American paleontologists, which they intended as a description of the pattern that they observed in the fossil record. Gradualism had been the pattern that evolutionary scientists expected to reconstruct from the fossil record, ever since the writings of Darwin. Both gradualism and punctuated equilibria are descriptions of the patterns rather than explanations of the processes that may cause them.

Pattern

- Prior to the proposal of punctuated equilibrium, evolutionary scientists assumed that the characteristics of all species evolved gradually, tracking the gradual changes of the environments in which they lived.
- This would produce an evolutionary tree in which the branches gradually curved. For example over the course of hundreds of millions of years, from widely spaced points on evolutionary trees that were provided by the fossil record.
- They further assumed that this pattern of gradualism also held on a fine scale, for example over the course of millions or tens of millions of years.

Remark:

They could not confirm gradualism on a fine scale from the fossil record, because, they claimed, so much of it was missing. This was the same argument, “the extreme imperfection of the fossil record,” that Darwin had used.

- Gould and Eldredge pointed out that the fossil record indicated most evolutionary lineages remained virtually unchanged for long periods of time, and that when evolutionary transformation did occur, it occurred rather quickly.
- This produced an evolutionary tree with branches that were straight or bent at nearly right angles, rather than branches that gradually curved.
- They believed that paleontologists had finally found enough fossils to conclude that the pattern of evolutionary change was not gradual.
- Paleontologists should, they said, believe what they see in the fossil record, rather than appealing to missing fossils of organisms that may not ever have existed.

For most groups of organisms, the fossils are insufficient to distinguish a gradualistic from a punctuated pattern of the origin of any given species. There are a few fossil assemblages, however, that are sufficiently complete that it may be possible to discern the pattern of change over time. Example:

- Trilobites were marine, abundant, had hard shells, evolved into many species, and persisted for most of the Paleozoic era.
- For all these reasons, their fossil record may be more complete than that of any other group of organisms.
- When the pattern of trilobite evolution was reconstructed, the result was one that both gradualists and punctationalists could cite as evidence.
- A small amount of gradual change appeared to occur in all of the species; a significant amount occurred in some, as a gradualist would point out.
- But the rate of change seemed very slow, relative to the differences among the species, and in some cases the changes fluctuated back and forth, resulting in no net transformation of characteristics, as punctationalists would point out.
- In the end, the gradualists have been unable to establish any unbroken series of gradual changes leading to the diversity of species that we see today in the world.
- The pattern appears, to many evolutionary scientists, to be of species that appear somewhat suddenly and persist relatively unchanged for millions of years before becoming extinct.

The punctuations in the fossil record have often been cited by critics of evolutionary science as evidence that the evolutionary transitions did not occur; they often refer to them as “gaps” in the fossil record. Most of them claim that such gaps could be bridged only by a Creator inventing new and complex designs. However, the punctuations those appear to have produced new species are in reality quite small. Between older and more recent species, transitional forms have been found. These “missing links” appear to have had a punctuated evolutionary origin.

Studies of Darwin’s finches on the Galápagos Islands show that characteristics such as body and beak size in birds change gradually, tracking environmental changes such as wet vs. dry years, and that these changes are of a magnitude as great as the differences between species. However, these changes exhibit no

consistent directional change—the beaks evolve to be larger, then evolve back to being smaller— and the formation of new finch species has not been verified. On the other hand, studies of *Mimulus* flowers in western North America show that a small number of genetic changes can immediately result in the flower having a different pollinator, resulting in immediate reproductive isolation. Although the *Mimulus* species can still cross-pollinate, they are usually classified as different species. These observations seem very long-term to human observers, but over evolutionary time they must be considered very brief. Both of these examples can be interpreted as either gradualism or punctuated equilibrium.

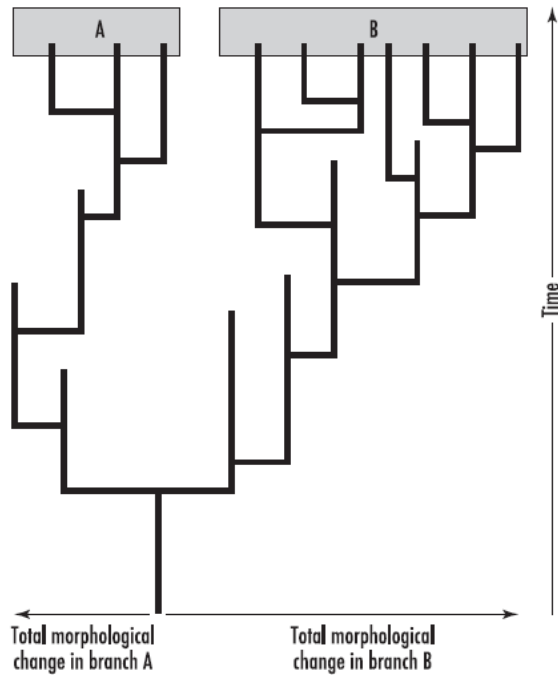


Figure: This figure represents a hypothetical example of punctuated equilibria in two branches from a common ancestor. Each vertical line represents the persistence of a species in time. Horizontal lines represent the evolutionary origin of a species, which is not instantaneous but occurs rapidly enough that, on this timescale, the slope is not visible.

Lineage B, perhaps because of a different breeding system, speciates more often than lineage A. Two results of this could be that (1) lineage B has more species at the present time than lineage A (shaded boxes); and (2) lineage B has undergone more morphological change (horizontal axis) than lineage A, even though no morphological change at all occurred within any species during its time of existence. Species sorting can produce patterns of evolutionary change and speciation even if evolutionary change does not occur within any species.

The Process

Although punctuated equilibrium theory denotes a pattern, not a process, the credibility of the pattern hinges largely on the discovery of a process that could produce it. The punctuation proposed by Gould, Eldredge, and other evolutionary scientists may appear sudden on the scale of geological time but is not instantaneous. In the fossil record, a speciation event that occurred over the course of 10,000 years would be difficult or impossible to detect; it would be indistinguishable from an instantaneous origin. Some critics of punctuated equilibrium have equated it with the “hopeful monster” theory of geneticist Richard Goldschmidt, or the saltation model proposed by Hugo DeVries in which a major evolutionary transition occurs within a single generation. This is an incorrect comparison. The punctuation event, if observed on a human timescale, would certainly appear slow and gradual and require at least several thousand generations—but probably not several million.

The processes necessary for punctuated equilibrium would not, in fact, be any different from those already understood to occur in populations. Instead of slow directional selection over millions of years, the pattern would be: (1) rapid directional selection followed by (2) a long period of stabilizing selection. Defenders of punctuated equilibrium insist that there are good reasons for believing that directional selection can be rapid, and that stabilizing selection should be the norm.

Why would directional selection appear rapid? Two reasons have been proposed.

1. *Speciation often occurs during events of relatively rapid and major environmental change.*

- One major example would be the rapid origin of many diverse types of invertebrate animals near the beginning of the Cambrian period, and the rapid origin of many diverse types of mammals, some of them very large, from relatively few, small mammalian ancestors, during the Paleocene epoch.
- The rapid evolution of invertebrates in the Cambrian period may have been spurred by the origin of grazing animals and the end of Snowball Earth.
- With the extinction of the dinosaurs, newly evolved mammalian forms encountered very little competition.
- Directional selection would occur rapidly when severe environmental changes selected the most extreme individuals in the evolving populations.
- Alternatively, speciation may occur not as a result of a whole species experiencing rapid environmental change but as a result of part of the species dispersing to, and being isolated in, a new environment: This “peripherally isolated population,” though not the entire species, then experiences a rapid environmental change.
- Not all major periods of evolutionary innovation occur in conjunction with catastrophic environmental change. Flowering plants, and modern bony fishes, both evolved at times of relatively stable climate.
- An example closer to home is the evolution of human brain size. The brains of australopithecines and similar hominin species were only about 25 cubic inches (400 cc) in volume, similar to the brains of modern chimpanzees, and they did not make and use stone tools. The brains of early *Homo* species, such as some attributed to *Homo habilis*, were larger, about 50 cubic inches (800 cc), and they made crude stone tools. The brains of *Homo ergaster* and other *Homo* species were yet larger, more than 60 cubic inches (1,000 cc), and they made more advanced stone tools. The brains of Neandertals and *Homo sapiens* were and are the largest, more than 90 cubic inches (1,500 cc), and these species made the most advanced tools. This sounds like gradualism, until one considers that australopithecine brain size changed relatively little during the one million to two million years that each species persisted. The same was true of the early *Homo* species, the middle *Homo* species, and the most recent *Homo* species. Most strikingly, the earliest *Homo sapiens* had brains of fully modern size (and perhaps capability) 100,000 years ago. While some cases of brain size increase have occurred (e.g., the brain size of *Homo erectus* such as Peking man was greatest just before its extinction, and later Neandertals had larger brains than early Neandertals), these changes were much smaller than the differences in brain size between the species. Apparently, australopithecines had an equilibrium brain size, then early *Homo*, after its punctuated origin, had a larger equilibrium brain size, then later *Homo* species, after punctuated origins, had the largest equilibrium brain sizes. Another possibility is that the appearance of a new species in the fossil record represents the migration of that species from a different location, rather than the origin of that species. Most environmental changes cause species to migrate rather than evolve. This is what happened after the most recent of the ice ages.

2. *Speciation often occurs in small populations.*

- Evolutionary change can occur more rapidly in small populations, if sufficient genetic variability is available. This is partly due to the reduced competition: In a large population, individuals with new characteristics would have to compete with many others, while in a small population, these novel individuals may survive and breed well, so long as they can handle the new environment.

- Another reason is that processes other than natural selection (such as genetic drift) can occur in small populations but not in large ones.
- A small population, on the other hand, would not be likely to leave much or any fossil record. Just by chance, the first fossil formed (and if a paleontologist is lucky enough to find it) would already have been noticeably different from the ancestral population – different enough to be called a new species.

Why would stasis and stabilizing selection be the norm, once a species originates?

Genes seldom function in isolation. Almost every gene works together with other genes to produce an organism. Natural selection, therefore, favors genes that work in teams. Most mutations produce genes that do not work even in isolation, and of the ones that do work, they are ineffective members of teams. Therefore, evolutionary scientists expect that over time, most small, isolated populations will become extinct. Once a good team of genes has evolved, it is stable (and experiences stabilizing selection) because most departures from it are inferior in function.

This explains why even the gradual, directional changes seen in the fossil lineages of trilobites involve mostly changes in size or number of existing parts, rather than major changes in the parts themselves. Another reason that stasis would be the norm for a species is that gradual evolutionary change may be occurring in individual populations, with many of the populations evolving in different directions from the others. As members of these populations crossbreed, their different evolutionary directionalities partially cancel one another, resulting in stasis for the species as a whole. Yet another reason that stasis would be the norm is that species usually respond to relatively minor environmental changes not by evolving but by migrating to a new location. A large, widespread environmental change is necessary to induce evolutionary change, which may then occur rapidly, according to the punctuated equilibrium model.

Species sorting

Punctuated equilibria, on a fine scale, could produce what appears to be gradualism on a coarse scale through a process known as species sorting. It has been called species selection, but since natural selection operates on individuals and not on groups, this term is not preferred. As Niles Eldredge explains it, think of a species as a real evolutionary entity: It is born (speciation), it lives, it dies (extinction); and before it dies, it may produce progeny (speciation). One species can be more fit than another if it produces more new species.

1. *Species sorting can produce the appearance of directional change*

Consider the example presented above regarding the evolution of human brain size. The directional increase in human brain size occurred because early *Homo* survived longer than the australopithecines, and later species of *Homo* survived longer than the early species. The overall increase in brain size resulted from rapid directional selection when each species originated but also from differential persistence of the species.

2. *Species sorting can affect the pattern of evolution.*

Consider two lineages that are more or less equally well adapted to environmental conditions, and whose populations consist of individuals with more or less equal fitness. The only difference between the two lineages is that one of them is more “speciose” than the other – that is, one lineage tends to fragment into more new species than the other. This could occur because its offspring tend to disperse further, into new and isolated habitats, or because it is very good at evolving isolating mechanisms. In the more speciose lineage,

genes do not mix as well as in the less speciose lineage. This relatively simple difference in dispersal or gene mixture is enough to cause one lineage to produce more species than the other. If each species is equally likely to survive, perhaps by chance, into the next geological era, the lineage that produces more species is less likely to die out. This is how species sorting, quite apart from the quality of adaptation, can cause one lineage to persist longer than another.

A possible real example is the ginkgo tree. During the Mesozoic era, there were numerous ginkgo species, only one of which (*Ginkgo biloba*) survives today. Had the ginkgo lineage been represented by only a few species during the Mesozoic, the entire lineage might be extinct today. Gradualism was very clearly the idea that Charles Darwin had in mind. Darwin took a chance when he declared that if evolution did not occur in gradual steps, one could “rightly reject my whole theory.” Huxley told him, “You load yourself with unnecessary difficulty ...” by insisting on gradualism. According to the defenders of punctuated equilibria, Huxley was right.

The difference between gradualism and punctuated equilibrium is that the former posits gradual directional selection, and the latter posits periods of stabilizing selection punctuated by periods of rapid directional selection. Both models appeal to the same Darwinian processes of natural selection, plus some genetic drift. Though the proponents of each approach defend their views passionately, the impression that outside observers often get – that punctuationists are undermining Darwinian evolution, and that the theory is in crisis – is quite incorrect.

Reference:

1. Evolution by Douglas Futuyma
2. The Selfish Gene by Richard Dawkins
3. Strickberger's Evolution