Punctuated Equilibrium vs. Phyletic Gradualism

Monalie C. Saylo[1], Cheryl C. Escoton[1] and Micah M. Saylo[2]

[1] University of Antique, Sibalom, Antique, Philippines
[2] DepEd Sibalom North District, Sibalom, Antique, Philippines
net_saylo@yahoo.com

Abstract

Both phyletic gradualism and punctuated equilibrium are speciation theory and are valid models for understanding macroevolution. Both theories describe the rates of speciation. For Gradualism, changes in species is slow and gradual, occurring in small periodic changes in the gene pool, whereas for Punctuated Equilibrium, evolution occurs in spurts of relatively rapid change with long periods of non-change.

The gradualism model depicts evolution as a slow steady process in which organisms change and develop slowly over time. In contrast, the punctuated equilibrium model depicts evolution as long periods of no evolutionary change followed by rapid periods of change. Both are models for describing successive evolutionary changes due to the mechanisms of evolution in a time frame.

Keywords: *macroevolution, phyletic gradualism, punctuated equilibrium, speciation, evolutionary change*

1. Introduction

Has the evolution of life proceeded as a gradual stepwise process, or through relatively long periods of stasis punctuated by short periods of rapid evolution? To date, what is clear is that both evolutionary patterns – phyletic gradualism and punctuated equilibrium have played at least some role in the evolution of life.

Gradualism and punctuated equilibrium are two ways in which the evolution of a species can occur. A species can evolve by only one of these, or by both. Scientists think that species with a shorter evolution evolved mostly by punctuated equilibrium, and those with a longer evolution evolved mostly by gradualism.

But how do these evolutionary patterns differ from one another? What are their similarities in terms of how evolution occurs? In the following discussion, the differences and similarities between punctuated equilibrium and phyletic gradualism will be presented.

2. Nature of Evolution

Both phyletic gradualism and punctuated equilibrium are speciation theory and are valid models for understanding macroevolution because some lineages are best explained by phyletic gradualism, some by punctuated equilibrium, and some by both.

Punctuated equilibrium and phyletic gradualism are contrasting patterns of evolution among a spectrum of patterns found in the fossil record. In punctuated equilibrium, species tend to show morphological stasis between abrupt speciation events, whereas in phyletic gradualism species undergo more continuous change [4].

Both gradualism and punctuated equilibrium describe the rates of speciation. For Gradualism, changes in species is slow and gradual, occurring in small periodic changes in the gene pool, whereas for Punctuated Equilibrium, evolution occurs in spurts of relatively rapid change with long periods of non-change [1].

The gradualism model depicts evolution as a slow steady process in which organisms change and develop slowly over time. In contrast, the punctuated equilibrium model depicts evolution as long periods of no evolutionary change followed by rapid periods of change. Both are models for describing successive evolutionary changes due to the mechanisms of evolution in a time frame. How these changes occur incrementally differs between the two models [1].

Phyletic gradualism was proposed by Charles Darwin. It holds that:

- Natural selection gradually changes the average features of a species by preferentially removing less fit individuals from the breeding stock.
- If this process continues long enough, a single species may change imperceptibly into a new species. The original species therefore undergoes phyletic extinction.
- Evolutionary change occurs all the time and is not concentrated in lineage-splitting speciation event.
- The absence of missing links is a result of the many breaks in the rock record. If stratigraphic sequences were more complete, we should find more missing links.

Gradualism is selection and variation that happens more gradually over a short period of time that it is hard to notice. Small variations that fit an organism slightly better to its environment are selected for a few more individuals with more of the helpful trait survive, and a few more with less of the helpful trait die. Very gradually, over a long time, the population changes and the change is slow, constant, and consistent [1, 6].

Punctuated equilibrium is an evolutionary pattern that models species as undergoing very little evolution for long periods of time before suddenly evolving fairly rapidly. It was proposed as an alternative hypothesis by Eldridge and Gould to explain the gaps in the fossil record - the fact that the fossil record does not show smooth evolutionary transitions. The apparent gaps in the fossil record result because speciation events happen too quickly for the fossil record to appear continuously. Based on punctuated equilibrium hypothesis, speciation events occur rapidly in geological time that is over hundreds of thousands to millions of years and that little change occurs in the time between speciation events. In other words, change only happens under certain conditions, and it happens rapidly [10].

The essential features that make up Punctuated Equilibrium are as follows:

- Paleontology should be informed by neontology;
- Most speciation is cladogenesis rather than anagenesis;
- Most speciation occurs through peripatric speciation;
- Large, widespread species don’t change or change slowly;
- Daughter species develop in a geographically limited region;
- Daughter species develop in a stratigraphically limited extent;
- Sampling of the fossil record will reveal a pattern of most species in stasis, with abrupt appearance of new species;

- Adaptive change in lineages occurs mostly during periods of speciation;
- Trends in adaptation occur through the mechanism of species selection.

The theory of punctuated equilibrium provides palaeontologists with an explanation for the patterns which they find in the fossil record. This pattern includes the characteristically abrupt appearance of new species, the relative stability of morphology in widespread species, the distribution of transitional fossils when those are found, the apparent differences in morphology between ancestral and daughter species, and the pattern of extinction of species [7].

The central proposition of punctuated equilibrium embodies three concepts: stasis, punctuation and dominant relative frequency. Stasis refers to a long period of relatively unchanged form; punctuation is radical change over a short duration; and dominant relative frequency is the rate these events occur in a particular situation [1, 6].

Furthermore, Punctuated Equilibrium holds that:

- Evolutionary change is connected in speciation events.
- Most species remain pretty much the same once they have come into being. This lack of substantial change over millions of years is called stasis.
- Speciation events are normally confined to small populations-peripheral isolates-that have become separated from the bulk of the species. As these isolated populations are small and transient, we should not expect to find them in the fossil record.

So the absence of the missing links is neatly explained by this theory.

3. Processes/Mechanisms

Evolutionary anthropologists, biologists, and palaeontologists interested in macro-evolutionary questions, examine and attempt to explain changes in the lineages of past and present organisms. These studies are ultimately interested in understanding how and why species change over time, how new life forms can appear in the fossil record, and how miniscule changes in trait frequencies build up to result in significant morphological changes.

Phyletic gradualism and punctuated equilibrium are contrasting patterns of evolution among a spectrum of patterns found in the fossil record. In punctuated equilibrium, species tend to show morphological stasis between abrupt speciation events that is dramatic and jarring in effect from a sudden cataclysmic event which causes species to either become extinct or to evolve rapidly in order to survive. In phyletic gradualism, species undergo more continuous change, a slow process with less noticeable evolutionary changes which causes species to adapt gradually to new environmental and biological selection pressures over the course of their history in order to survive [1].

In phyletic gradualism, species continue to adapt to new environmental and biological selection pressures over the course of their history, gradually becoming new species. It holds that a species population changes gradually, that is, there is no clear line of demarcation between an ancestral species and a descendant species unless a splitting - cladogenesis event occurs or the gradually changing lineage is divided arbitrarily. During this process, anagenetic evolution occurs at a smooth, steady and incremental but not necessarily constant or slow rate on a geological timescale. New species different from their ancestors arise by the gradual transformation and ultimate gradual splitting of ancestral species into descendant species lineages. Once species are well adapted to an environment, selective pressures tend to keep them that way. A change in the environment that alters the selective pressure would then end the stasis or lead to extinction [1, 3].

Punctuated equilibrium as suggested by Gould is due to macromutations wherein change comes in spurts. There is a period of very little change, and then one or a few huge changes occur, often through mutations in the genes of a few individuals. Mutations are random changes in the DNA that are not inherited from the previous generation, but are passed on to generations that follow. Though mutations are often harmful, the mutations that result in punctuated equilibrium are very helpful to the individuals in their environments. Because these mutations are so different and so helpful to the survival of those that have them, the proportion of individuals in the population who have the mutation/trait and those who don't changes a lot over a very short period of time. The species changes very rapidly over a few generations then settles down again to a period of little change [1].

Hence, punctuated equilibrium is the result of one or a few mutations that cause large change. However, any sudden rapid change in a species can also be the result of other causes such as huge and sudden changes in the environment that result in more rapid changes in the organisms through harsher selection.

It also proposes that most sexually reproducing species will experience little net evolutionary change for most of their geological history, and that when phenotypic evolution does occur, it is localized in rare, rapid events of branching speciation called cladogenesis remaining in an extended state called stasis. Cladogenesis is the process by which species split into two distinct species rather than one species gradually transforming into another. Thus, it is considered a model for discontinuous tempos of change at one biological level only; the process of speciation and the deployment of species in geological time [1, 2].

The punctuational model states that species do not arise as an entire population evolves, but rather when a segment of a population becomes isolated and undergoes a speciation event. One primary difference between the punctuational and gradualistic models of evolution is that under the gradualistic model, the entire parent population slowly morphs into the descendant species. However, under the punctuational model, only a small segment of the parent population buds off into the descendant population, permitting the original parent population to continue to persist [1, 3].

So, how does punctuated equilibrium works? Punctuated equilibrium predicts that a lot of evolutionary change takes place in short periods of time tied to speciation events. Here’s an example of how the model works:

1. *Stasis*: A population of organism would be experiencing stasis, living, dying, and getting fossilized every few hundred thousand years. Little observable evolution seems to be occurring judging from these fossils.

2. I*solation*: A drop in sea level forms a lake and isolates a small number of the population of organism from the rest of the population.

3. *Strong selection and rapid change*: The small, isolated population experiences strong selection and rapid change because of the novel environment and small population size. The environment in the newly formed lake exerts new selection pressures on the isolated organism. Also, their small population size means that genetic drift influences their evolution. The isolated population undergoes rapid evolutionary change. This is based on the model of peripatric speciation.

4. *No preservation*: No fossils representing transitional forms are preserved because of their relatively small population size, the rapid pace of change, and their isolated location.

5. *Reintroduction*: Sea levels rise, reuniting the isolated organism with their sister lineage.
6. *Expansion and stasis*: The isolated population expands into its past range. Larger population size and a stable environment make evolutionary change less likely. The formerly isolated branch of the organism lineage may out-compete their ancestral population, causing it to go extinct.
7. *Preservation*: Larger population size and a larger range move us back to step 1: stasis with occasional fossil preservation.

This process would produce the following pattern in the fossil record: stasis, rapid change, and then stasis. Evolution appears to happen in sharp jumps associated with speciation events [4].

Furthermore, Eldredge and Gould's insights into paleontological processes lead them to the understanding of how punctuated equilibrium works through the concept of paleospecies [2, 4].

First, modern species appear to have derived from cladogenesis, the splitting of a daughter species from an ancestral species rather than transformation of the ancestral species in toto. This is a multiplication of species, and without it, the diversity of the living systems that we see would be impossible.

Second, the mode of speciation most often seen is also identified from modern populations. That mode is allopatric speciation of peripheral isolates, or peripatric speciation. Peripatric speciation states that a population of an ancestral species in a geographically peripheral part of the ancestral range is modified over time until even when the ancestral and daughter populations come into contact, there is reproductive isolation. Sympatric speciation is the production of a daughter species within the geographic range of the parent species are rare events.

Third, the frequency with which peripatric speciation occurs in modern lineages can be seen as rare. This rarity means that a species may produce zero, one, or perhaps a few daughter species during its entire time span of existence.

Fourth, the period of transition between parent species and daughter species is short compared to the period of time a species exists as a distinct form. When a small sub-population is isolated from the rest of the population of a species, the particular set of variations in the sub-population is much smaller than that in the remainder of the population. These variations, when in conjunction with suitable features of geographic locale, climate, and resources, can lead to rapid development of reproductive isolation from the ancestral population. The reduction in variation due to small sub-population size is known as the founder effect.

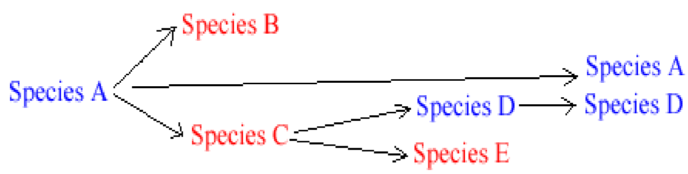
Fifth, significant adaptations developed or accentuated in the daughter species can lead to the rapid dispersal and establishment of a daughter species throughout the range of the ancestral species, or into new ranges. The ecological processes of dispersal and succession can occur very quickly compared to evolutionary processes of change.

Sixth, the principles of gene flow, genetic homeostasis, and large population size inhibit widespread ancestral populations from much directional adaptive change. Any adaptive change found in the ancestral population is likely to be small and unrelated to evolutionary trends.

Both phyletic gradualism and punctuated equilibrium are speciation theory, where speciation means the origin of a new species in nature. Two patterns of evolutionary change can be used to sum up how both theories works.

a. Anagenesis is applicable to phyletic evolution is the transformation of unbranched speciation.

b. Cladogenesis is the transformation of branched speciation. Cladogenesis promotes biological diversity, that means there will be more species. It also offers the opportunity for a species to remain in existence.



According to phyletic gradualism, it was assumed that evolving lineages were changing at variable rates, but changing pretty well continuously (anagenesis). Speciation was often seen as a by-product of this process of change: sometimes lineages had become so different from their starting points that they had evolved into a new species (the chronospecies concept). Speciation by splitting (cladogenesis) could also happen, but the process was no slower or faster than normal rates of lineage evolution [2, 3].

On the other hand, evolution by punctuated equlibria, was quite different, both in pattern and process. Anagenesis was unimportant, and rapid morphological change at cladogenesis was all. The normal state of a lineage was stasis, essentially an absence of change for long periods. From time to time, speciation happens, but such speciation events are rapid and revolutionary. The pattern of punctuated equilibria is rectangular, and virtually all of evolution happens at speciation [2].

4. Applications

Both phyletic gradualism and punctuated equilibrium are evolutionary patterns which help us understand how evolution occurs. In this particular point of discussion, the concepts of how these evolutionary patterns are applied can be tackled by citing instances wherein organisms undergo either of the evolutionary patterns or both at the same time.

The concept of gradualism and punctuated equilibrium as evolutionary patterns can both explain how organisms changed through time. Organisms of the same species for example can evolve either by gradualism or by punctuated equilibrium or both.

The concepts of punctuated equilibrium can be applied from the biology of extant organisms to that of fossil organisms. This proceeds on the simple inference that past life went about its business in much the same way as present life does [1, 5].

- Punctuated Equilibria postulates that speciation events comprise most of the evolutionary change seen in adaptation. This is a consequence of the inhibitory effects of gene flow, genetic homeostasis, and large population sizes. The adaptations of newly speciated daughter populations are forever excluded from the ancestral population because of reproductive isolation.

- PE explains the abrupt appearance of new species in the fossil record. The splitting of lineages in the mode of allopatric speciation followed by ecological dispersal and succession would result in geologically abrupt appearance of the daughter species everywhere except the limited geographic area where the speciation took place. Most speciation takes place as peripatric speciation, which is confined to a limited geographic region, and after which ecological principles argue for relatively rapid reintroduction and spread into new habitats for the daughter species. Since the critical change occurs in such a small region and in such a limited population, the probability of finding specimens which document the transition from ancestral to daughter species is very low. A population which can exploit resources untapped by current populations will grow and spread at somewhere near its theoretical intrinsic rate of increase. The cases of introduced species in modern times, the starling in North America, for example demonstrate the extreme rapidity in which a species may spread across large geographic extents.

- PE explains the relative stasis of most species. A species may produce a few daughter species during its duration. Large interbreeding populations are unlikely to change much due to genetic homeostasis and gene flow from far-flung parts of the range.

- PE asserts species selection as the way in which major adaptive trends proceed. Closely related species are often likely to overlap in niche space. Ecological processes may cause the displacement and possible extinction of certain species due to competition with other species. If adaptive change in large populations is largely inhibited, then each species represents a hypothesis that is tested in competition. This is one of the more controversial points in PE.

- PE also makes a statement concerning the pattern of fossils found. This pattern has both geographic and stratigraphic components. If peripatric speciation is the mode of speciation, then the place where transitional fossils between a parent and daughter species will be found will be limited in geographic region. Because the time needed for transition from parent to daughter species is short compared to the total residence time of either, the stratigraphic extent of transitional fossil sequences will be very brief.

Within the context of organizational behavior, the punctuated equilibrium model consists of deep structures, equilibrium periods and revolutionary periods. Deep structure is the set of fundamental choices a system has made of (1) the basic parts into which its units will be organized and (2) the basic activity patterns that will maintain its existence. Equilibrium periods are characterized by the maintenance of organizational structures and activity patterns, where small incremental adjustments are made to adjust for environmental changes without affecting the deep structure. Revolutionary periods occur due to significant changes in the environment that lead to wholesale upheaval where a system's deep structure comes apart, leaving it in disarray until the period ends and choices are made around which a new structure forms [2, 5].

One of the key punctuations noted in the research is major environmental change caused by technological innovation where a technological discontinuity triggers a period of instability, which is closed by the emergence of a dominant design or business paradigm. The introduction of a disruptive or competence destroying IT innovation can be considered a punctuation that interrupts the existing stasis, destroying the existing deep structure. It should be noted that revolutionary outcomes, based on interactions of system's historical resources with current events, are not predictable and they may or may not leave a system better off [2].

In linguistics, punctuated equilibrium was proposed as a model for language histories using computational phylogenetic methods show that punctuational bursts play an important factor when languages split from one another [2].

Punctuated Equilibrium has also played a role in social and political theory particularly in policy studies as one of many cross-overs of evolutionary theory into social theory. Punctuated equilibrium in social theory is a method of understanding change in complex social systems, particularly how policy change and the development of conflicts seem to progress in extended periods of stasis, punctuated by sudden shifts in radical change [1, 2, 6].

The model states that policy generally changes only incrementally due to several restraints, namely lack of institutional change and bounded rationality of individual decision-making. Policy change will thus be punctuated by changes in these conditions, especially change in party control of government or changes in public opinion. Thus, policy is characterized by long periods of stability, punctuated by large, but rare, changes due to large shifts in society or government. This has been shown to be particularly evident in current trends of environmental policy and energy policy [2, 4].

In general, the original formulation of the theory has been used to explain patterns of change in groups and organizations where periods of stasis are punctuated by brief and intense periods of radical change. Two widely known applications of the theory of punctuated equilibrium in the social sciences are in organizational theory and in the study of small work groups. As some researchers have noted, these applications of the original theory have shifted its focus of attention from a theory about change in populations to a theory about change within entities.

5. Examples

Evidence gathered to elucidate the relative importance of punctuated equilibrium and phyletic gradualism is drawn from many areas of evolutionary biology, from empirical observation of the fossil record to theoretical studies of evolutionary mechanisms. The theory of phyletic gradualism would most benefit from studies demonstrating that the fossil record revealed gradual transitions from one form to another in a wide range of taxa; this has only been shown in a limited number of taxa. Conversely, if the fossil record indicates that the evolution of life has involved long periods of stasis, punctuated by relatively short periods of rapid morphological change, then the theory of punctuated equilibrium would be supported.

Nevertheless, observed patterns in the fossil record alone are not sufficient to confirm the theory of phyletic gradualism; the mechanisms behind the pattern must also be described and demonstrated. Many studies, in fact, demonstrate that evolutionary processes can and do maintain morphological features and invoke rapid evolution. Therefore, while some fossil evidence supports Darwin's more traditional concept of phyletic gradualism, overwhelming evidence from the fossil record and theoretical studies is now suggesting that punctuated equilibrium is the foremost pattern in macroevolution [4].

Scientists have scrutinized the fossil records of many organisms looking for evidence of punctuated evolution. One group of coral-like sea organisms in particular, called bryozoan shows this kind of pattern. The well-preserved fossil record of bryozoans shows that one species first appeared about 140 million years ago and remained unchanged for its first 40 million years. Then there was an explosion of diversification, followed by another period of stability for vast amounts of time [2, 4].

However, it is also important to note that we observe examples of gradual, non-punctuated, evolution in the fossil record too. By viewing the fossil record, it is clear that in many cases punctuated equilibrium occurred. These examples are as plentiful as they are diverse. In fact, it has been proven that from small shell fish to large dinosaurs, punctuated equilibrium was the process of evolution. The following examples of Punctuated Equilibrium proven by the fossil record were discovered in a lake in Montana by Horner, J.R., D.J. Varrichio, and M.B. Goodwin. The search for fossils began in 1992 and these examples were discovered:

- 50 specimens of lambeosaurids, transitional between *Lambeosaurus* and *Hypacrosaurus*.
- Transitional pachycephalosaurid between *Stegoceras* and *Pachycephalosaurus*.
- Transitional tyrannosaurid between *Tyrannosaurus* and *Daspletosaurus*

The fossils showed 5 million years of evolutionary stasis, followed by rapid evolutionary change. The rapidly changing environment lead to such change. In the case of the T-rex for example, when the sea level rose, drowning the Judith River Formation for 500,000 years, the dinosaurs were forced to move to smaller areas. A small population of T-rexes were separated due to rising water levels hence, being separated from a large gene pools lead to rapid evolution [2, 4].

Adaptive radiations are clearly evident in the fossil record. The best known example, perhaps, is the Cambrian explosion, which lasted from 565 to 605 million years ago. This surprisingly short amount of time witnessed the evolution of the majority of the body plans that we recognize today. The Cambrian explosion thus demonstrates that profound morphological evolution can occur in a short period of time. Other adaptive radiations, such as the mammalian radiation and the evolution of flight in birds, are consistent with the theory of punctuated equilibrium as well. However, the question of which mechanism promotes adaptive radiation still remains unanswered. To answer this, we look to the fossil record. When we do, we recognize that adaptive radiations tend to follow mass extinction events. For example, the end-Cretaceous extinction brought the end of dinosaurs, which then allowed the adaptive radiation of mammals. One explanation for the timing of the mammalian radiation and the dinosaur extinction is that the extinction freed ecological niches, allowing the diversification of mammals. A second explanation for adaptive radiation has been used to explain the evolution of flight in birds. Although the feather probably did not initially evolve in response to selection for flight, the evolution of the feather did allow birds to explore previously unavailable niches, allowing for the adaptive radiation of Aves [1, 2, 6].

The so called living fossils provide good evidence that evolutionary mechanisms can maintain morphological characters for long periods of time. A good example of a living fossil is *Gingko biloba*, which appear to have remained morphologically unchanged for 40 million years. Strong evidence for morphological stasis also comes from horseshoe crabs, which show little morphological stasis despite typical genetic divergence among the clade. The fact that a typical amount of genetic divergence occurred in the horseshoe crab clade demonstrates that morphology was not maintained by a lack of additive genetic variation, but by some other mechanism such as stabilizing selection. Whether stabilizing selection or some other mechanism is maintaining morphological stasis is still under much debate. Nonetheless, in the case of the gingko and horseshoe crab, it is clear that morphological evolution can be constrained by some evolutionary force [1, 2, 6].

Studies of the fossil record, adaptive radiation, and living fossils suggest that periods of morphological stasis are maintained by some evolutionary force, and that periods of adaptive radiation are not only possible, but readily identifiable in the fossil record. The proliferation of empirical and theoretical studies aimed at elucidating the truth about macroevolution has deepened our understanding of the evolutionary processes that determine the pattern of life on earth. Furthermore, these studies not only demonstrate that punctuated equilibrium is the predominating pattern in the history of life, but provide evidence that evolutionary processes can and do incite this pattern. Phyletic gradualism is evident; although it does not predominate, gradualism seems to be important in at least some taxa. The evolution of life, thus, has been affected by both punctuated equilibrium and phyletic gradualism, but current data suggests that the former likely plays a more significant role [2, 4].

The best known example of gradualism may be the evolution of humans. Instead of fast advancements and spontaneous spurts of rapid evolution humans followed a linear pattern of evolution - a pattern of gradual evolution. This is shown by the existing fossil record that shows slow and steady evolution over a long period of time. Although the fossil record is still incomplete, the slow gradual changes that make *Homo sapiens* unique have been documented. Another group of fossils that provides support for the theory of phyletic gradualism was the foraminifera fossils [8, 9].

6. Analysis

Evolution in the first three billion years of life on earth was a shining example of Gradualism. Life on earth was made up only of unicellular organisms that evolved extremely slowly in a linear fashion. It is the idea that for long periods of time there is equilibrium and followed by short periods of very fast evolution. This is described as a possible explanation for the Cambrian explosion.

However around 640 million years ago something changed the rate of evolution. Over a 40 million year span, a mass diversification of life occurred. This time period is known as the Cambrian Explosion. Interestingly, enough animals representing present day major phyla and those that are now extinct appeared during this period. There are fossil records showing appearances of early arthropods, primitive chordates and the precursors to vertebrates [2].

It is important to note that by the standards of recorded human history, which covers only about 7,000 years, speciation is still a very gradual process under punctuated equilibrium theory. Punctuated equilibrium argues for much faster speciation than traditional evolutionary theory, but does not involve the proposition that new species appear in a generation or two. It is an evolutionary theory according to which hundreds or thousands of generations are needed for speciation, and natural selection must favor or at least permit all changes at every step. The novelty of punctuated equilibrium lies in its two proposals about rates of evolutionary change: (1) change happens rapidly, by geological standards, during speciation, and (2) change happens slowly or not at all after speciation [1, 6].

Before punctuated equilibrium, most scientists assumed that evolutionary change occurs slowly and continuously in almost all species, and that new species originate either by slow divergence from parental stock of sub-populations or by slow evolutionary transformation of the parental stock itself. Punctuated equilibrium proposes that most species originate relatively suddenly and then do not evolve significantly for the rest of their time on earth. Most species thus have a sudden or punctuated origin and then remain in stasis or equilibrium until extinction [1, 5].

The punctuated equilibrium hypothesis states that speciation events occur rapidly in geological time - over hundreds of thousands to millions of years and that little change occurs in the time between speciation events. In other words, change only happens under certain conditions, and it happens rapidly. Instead of a slow, continuous movement, evolution tends to be characterized by long periods of virtual standstill or equilibrium punctuated by episodes of very fast development of new forms [1, 3, 7].

Punctuated Equilibrium is a theory about how the evolutionary process works based on patterns of first appearances and subsequent histories of species in the fossil record. The theory holds that species originate too rapidly to enable their origins to be traced by palaeontologists – there is punctuation, and then persist unchanged through geological time in stasis - equilibrium. All is due to a mysterious shared homeostasis that is postulated to regulate the collective morphology of individuals. When species-level homeostasis is working, species persist unchanged; when species-level homeostasis breaks down, speciation results [7].

Eldredge and Gould proposed punctuated equilibrium to explain one of the most notable features of the fossil record: most species seem to appear suddenly, already clearly differentiated from the earlier, similar species from which they presumably evolved, and then remain unchanged until becoming extinct. Traditional evolutionary theory proposed that gradual evolutionary changes are rarely observed in the fossil record because that record is radically incomplete. Fossils form only under certain special conditions, fossil-bearing rocks are eroded as well as deposited, and our knowledge even of those fossils that have been formed is fragmentary [1, 3].

Eldredge and Gould agree that the fossil record is incomplete but contend that it could not be incomplete enough to account for the near-complete absence of gradualistic change from the fossil record. Rather, they propose that species normally originate too quickly for normal geological processes to record the event; a single bedding plane often compresses tens of thousands of years into a thin slice. Furthermore, according to punctuated equilibrium, speciation usually occurs when small populations cut off from interbreeding with related groups, for example by loss of a watercourse connecting two lakes, or by colonization of an island —evolve rapidly in isolation. Because there are fewer individuals in such an isolated population, favorable mutations can spread more readily. A small, isolated, rapidly-evolving population may become extinct without leaving any trace at all in the fossil record. Eldredge and Gould argued that if it does eventually break out of its isolation and spread over a wider area, it is likely to be observed in the fossil record as making a sudden or punctuational appearance, fully formed. They also proposed that the appearance of stasis or unchanging form manifested by most species in the fossil record is not an artifact produced by gross imperfections in the fossil record, but a raw fact. Evolutionary change in living forms occurs mostly during speciation events and hardly otherwise [3, 4].

The gradualistic model holds that evolution proceeds at a slow, continuous pace. Darwin attributed the abrupt, transitionless appearance of novel forms in the fossil record to the imperfection of the record. Gradualism is selection and variation that happens more gradually over a short period of time that it is hard to notice. Small variations that fit an organism slightly better to its environment are selected for: a few more individuals with more of the helpful trait survive, and a few more with less of the helpful trait die. Very gradually, over a long time, the population changes and the change is slow, constant, and consistent [1].

The theory of Gradualism holds that large evolutionary changes in species are the result of many small and ongoing changes and processes. If evolution proceeds via the accumulation of small steps, we should see a smooth continuum of creatures across the fossil record. But instead, we see long periods where species do not change, and there are gaps between the changes [7].

It should be noted that even Darwin did not expect the rate of evolutionary change to be constant. The imperfection of the fossil record due to erosion and periods unfavorable to fossil preservation also causes gaps, although it probably cannot account for all of them. Some transitional sequences exist, which despite an uneven rate of change, still show a gradual continuum of forms. The fossil record still shows a great deal of change over time. The creationists who make note of the many gaps almost never admit the logical conclusion:

If they are due to creation, then there have been hundreds, perhaps even millions, of separate creation events scattered through time [2].

Charles Darwin understood that evolution was a slow and gradual process. By gradual, Darwin did not mean perfectly smooth but rather stepwise with a species evolving and accumulating small variations over long periods of time until a new species was born. He did not assume that the pace of change was constant, however, he recognized that many species retained the same form for long periods.

The gradualism model or phyletic gradualism posits that evolutionary change occurs very slowly, and at a constant rate. If true, then one would expect to see change in lineages spread uniformly over time. But that isn't what is observed. In the fossil record, one often sees species remaining in stasis, or unchanged, for long periods of time, then bursts of new species quickly at irregular intervals.

Punctuated equilibria explains that species remain in stasis because speciation required certain special conditions for isolation and change to occur, and that these conditions are usually met at the periphery of a species's range, and not all of the time. In addition, speciation can occur very rapidly once it gets going--in some cases as quickly as 50,000 years-- far faster than the fossilization process could accurately track in a gradual way. Therefore, one should expect to see long periods of stasis or equilibria, broken up or punctuated by bursts of speciation [1].

If evolution is gradual, then, there should be a fossilized record of small, incremental changes on the way to a new species. But in many cases, scientists have been unable to find most of these intermediate forms. Darwin himself was shaken by their absence. His conclusion was that the fossil record lacked these transitional stages because it was so incomplete.

The incompleteness of the fossil record has many contributing factors. Geological processes may cause to confusion or error, as sedimentary deposition rates may vary, erosion may erase some strata, compression may turn possible fossils into unrecognizable junk, and various other means by which the local fossil record can be turned into the equivalent of a partially burned book, which is then unbound, pages perhaps shuffled, and from which a few pages are retrieved. Beyond geology, there remains taphonomy -- the study of how organisms come to be preserved as fossils. Hard parts of organisms fossilize preferentially. The conditions under which even those parts may become fossilized are fairly specialized. All this results in a heavily skewed distribution of even what parts of organisms become fossilized, and that affects which features of morphology are available for use in classification. The issue of geography enters into all this, as a consequence of the fact that living lineages occupy ecological niches and those niches are bound to certain features of geography [2, 3, 5].

That is certainly true in many cases because the chances of each of those critical changing forms having been preserved as fossils are small. But in 1972, Eldredge and Gould proposed punctuated equilibrium explaining that species are generally stable, changing little for millions of years. This leisurely pace is punctuated by a rapid burst of change that results in a new species and that leaves few fossils behind [6].

According to this idea, the changes leading to a new species don't usually occur in the mainstream population of an organism where changes wouldn't endure because of so much interbreeding among like creatures. Rather, speciation is more likely at the edge of a population, where a small group can easily become separated geographically from the main body and undergo changes that can create a survival advantage and thus produce a new, non-interbreeding species [2, 7].

This hypothesis predicts that the fossil record at any one site is unlikely to record the process of speciation. If a site records that the ancestral species lived there, the new species would probably be evolving somewhere else. The small size of the isolated population which is evolving into a new species reduces the odds that any of its members will be fossilized. The new species will only leave fossils at the same site as the old one if it becomes successful enough to move back into its ancestral range or different enough to exist alongside its relatives [7].

Allopatric speciation suggests that species with large central populations are stabilized by their large volume and gene flow. New and even beneficial mutations are diluted by the population's size and are unable to reach fixation due to factors such as constantly changing environments. If this is the case, then the transformation of whole lineages should be rare, as the fossil record indicates. Smaller populations on the other hand, which are isolated from the parental stock, are decoupled from the homogenizing effects of gene flow. In addition, pressure from natural selection is especially intense, as peripheral isolated populations exist at the outer edges of ecological tolerance. If most evolution happens in these rare instances of allopatric speciation then evidence of gradual evolution should be rare [4].

The essential features of phyletic gradualism are described by Eldredge and Gould. In this Darwinian perspective, paleontology formulated its picture for the origin of new taxa. The following are its tenets:

1. New species arise by the transformation of an ancestral population into its modified descendants.
2. The transformation is even and slow.
3. The transformation involves large numbers, usually the entire ancestral population.
4. The transformation occurs over all or a large part of the ancestral species' geographic range.

These statements imply several consequences, two of which seem especially important to paleontologists:

1. Ideally, the fossil record for the origin of a new species should consist of a long sequence of continuous, insensibly graded intermediate forms linking ancestor and descendant.
2. Morphological breaks in a postulated phyletic sequence are due to imperfections in the geological record.

Darwin did think that a daughter species arose from a population of the parent species. So do punctuated equilibrists. Darwin did think that the transformation would be slow, but he did not think that it would be even. Darwin did not think that the transformation would involve large numbers, and certainly not the entire parent population. Darwin did not think that the transformation would occur across the entire ancestral range.

A growing body of evidence indicates that both gradualistic and punctuational speciation have often occurred in the history of life, and that morphological stasis or long-term stability of form - the equilibrium of punctuated equilibrium is, as Eldredge and Gould claimed, often real, rather than an artifact of dropout in the fossil record. Several unusually perfect series of fossils have been discovered that have allowed paleontologists to trace the detailed history of entire groups of related organisms. In most such cases, paleontologists have observed gradualistic speciation, punctuational speciation, and morphological stasis, all in a single series of rocks, with punctuational speciation occurring about 10 times more frequently than gradualistic speciation. Observing gradualistic speciation and punctuational speciation in a single series of fossils proves both gradualism by direct observation, and punctuated equilibrium by disproof of the alternative possibility that gaps are responsible for the relatively sudden appearance of species in this case [1, 2, 3].

The punctuated equilibrium theory of Niles Eldredge and Stephen Jay Gould was proposed as a criticism of the traditional Darwinian theory of evolution. Eldredge and Gould observed that evolution tends to happen in fits and starts, sometimes moving very fast, sometimes moving very slowly or not at all. On the other hand, typical variations tend to be small. Therefore, Darwin saw evolution as a slow, continuous process, without sudden jumps. However, if you study the fossils of organisms found in subsequent geological layers, you will see long intervals in which nothing changed – in equilibrium, punctuated by short, revolutionary transitions, in which species became extinct and replaced by wholly new forms [1, 6].

In the fossil record, the phyletic gradualism hypothesis should manifest itself with long sequences of transitional forms also called missing links in every lineage. This is true for some lineages at some scales, but there are gaps in the fossil record. Based on the punctuated equilibrium hypothesis, the apparent gaps in the fossil record result because speciation events happen too quickly for the fossil record to appear continuously [2, 4].

Punctuated equilibrium attempts to answer a major problem with the fossil record. For almost a century, naturalistic science assumed that the gaps in the fossil record would eventually be filled, and there would be a semi-complete record of so-called transitional forms between the various species. In fact, the opposite happened, and the gaps became even more pronounced. The actual fossil record indicates species seemingly appearing from nowhere, and without the long, slow, gradual changes expected by classical evolutionary theory. Punctuated equilibrium seeks to answer this problem by supposing that evolution doesn't occur steadily, but sporadically [1, 2, 6].

Despite a better agreement with available evidence, there are many scientific problems with punctuated equilibrium itself. The mechanism for punctuated equilibrium is assumed to be small groups of a particular organism separated in some way from the main population. This would accelerate the transmission of mutated genes through the population, and much more quickly produce a new species. However, multiple studies have found that inbreeding such as this produces extremely negative effects, which run counter to the idea of rapid advancement. The fossil record also calls into question the plausibility of this notion. The so-called Cambrian Explosion for instance, is the sudden emergence of almost every biological type known to man. In a geological blink of an eye, this seems to contradict the idea of broad genetic stability intermixed with localized change [2, 3].

Both theories claim that they can explain the gaps in the fossil record. The Gradualism theory states that the fossil record is incomplete and that it is unlikely that all stages of evolution would be preserved let alone found. However there have been a few species that show Gradualism through the fossil record. Punctuated Equilibrium claims that the gaps in the fossil record are not just missing links but the actual process of evolution. They claim that the evolution happens too rapidly to be found in a fossil record [2, 7].

In the present it is still difficult to decide which statement is true concerning the gaps in the fossil record since a limited number of fossils have been collected and recorded. Research is ongoing today and it is possible that in the next few hundred years we may have an answer.

7. Conclusions

Both phyletic gradualism and punctuated equilibrium are evolutionary patterns which help us understand how evolution occurs.

Evidences indicate that both gradualistic and punctuational speciation have often occurred in the history of life, and that morphological stasis or long-term stability of form - the equilibrium of punctuated equilibrium is often real rather than an artifact of dropout in the fossil record. Paleontologists have observed gradualistic speciation, punctuational speciation, and morphological stasis, all in a single series of rocks with punctuational speciation occurring about 10 times more frequently than gradualistic speciation.

At present, research is still ongoing on the evolutionary patterns of life; which of these evolutionary patterns has a great influence on the existence of very diverse groups of organisms on earth. And it is possible that in the next few hundred years we may have an answer. But remember that these are just both theories and one or both could be proven right or wrong.

References

[1] Eldridge, N. and Gould, S. 1972. Punctuated equilbria: An alternative to phyletic gradualism in models of paleobiology. In T. J. M. Schopf (ed.), *Models in Paleobiology*, 82-115. Freeman, Cooper, San Francisco.
[2] Eldredge, Niles. *The Pattern of Evolution* New York: W. H. Freeman, 1998.
[3] Eldridge, Niles "Species, Speciation, and the Environment." Actionbioscience. October 2002 [cited January 10, 2003]. <http://www.actionbioscience.org/evolution/eldredge.html>.
[4] Eldredge, N. 1971. "The allopatric model and phylogeny in Paleozoic invertebrates." *Evolution* 25:156-167.
[5] Gould, Stephen J., and Niles Eldredge. "Punctuated Equilibria: The Tempo and Mode of Evolution Reconsidered." *Paleobiology* 3 (1977): 115–51.
[6] Gould, Stephen Jay. PUNCTUATED EQUILIBRIUM. Reviewed by Philip D. Gingerich. Harvard University Press 2007. ISBN 0-674-02444-3
[7] Gould, Stephen Jay. *The Structure of Evolutionary Theory.* Cambridge, MA: Harvard University Press, 2002.
[8] Haviland, W. A. and Crawford, G. W. 2009. *Human Evolution and Prehistory*. Nelson Education Ltd.
[9] Lehman, S.M. 2010. *Introduction to Evolutionary Anthropology*. Pearson Education Canada: Toronto.
[10] Ridley, Mark. Evolution. 3rd ed. Blackwell Publishing.
[11] http://mechanismsevo.blogspot.com/2007/09/phyletic-gradualism.html
[12] http://www.talkorigins.org/faqs/punc-eq.html
[13] http://www.biology-online.org/dictionary/Phyletic_gradualism
[14] http://www.examiner.com/green-culture-in-fort-lauderdale/punctuated-equilibrium-vs-phyletic-gradualism-sustainable-evolution-of-the-auto-industry
[15] http://www.google.com.ph/search?q=punctuated+equilibrium+vs+phyletic+gradualism&btnG=Hanapin&hl=tl&client=firefox-a&hs=SB5&rls=org.mozilla%3Aen-US%3Aofficial&channel=s&sa=2
[16] http://www.blackwellpublishing.com/ridley/a-z/Phyletic_gradualism.asp
[17] http://www.jstor.org/pss/2400345
[18] http://www.springerlink.com/content/2850k7r0n3nq3201/
[19] www.pbs.org/wgbh/evolution/library/.../l_035_01.html
[20] http://palaeo.gly.bris.ac.uk/benton/reprints/2003eolss.html
[21] http://biopinionated.com/2008/02/06/how-can-chaperones-act-in-evolution-chapter-iii-blogging-in-just-science-08/punctuated-equilibrium/
[22] http://www.biologie.uni-hamburg.de/b-online/library/cat-removed/u4aos2p4.html
[23] http://www.deusdiapente.net/science/evolution.php?query=punk

Authors

Monalie C. Saylo. She is working as a teacher at the University of Antique, Sibalom, Antique, Philippines teaching general, biological and physical sciences. She took her Bachelor's degree in Biology at Central Philippine University and her Master's degree in Biology at West Visayas State University. Currently she is enrolled in Ph. D. Science Education major in Biology at West Visayas State University, Iloilo City, Philippines.

Cheryl C. Escoton. She is working as a teacher at the University of Antique, Sibalom, Antique, Philippines teaching financial accounting and management. She took her Bachelor's degree of Accountancy and Master of Management at the University of the Philippines in the Visayas. Currently she is enrolled in Doctor of Management program at Central Philippine University, Iloilo City, Philippines.

Micah M. Saylo. He works as an elementary teacher at DepEd Sibalom North District, Sibalom, Antique, Philippines. He is a graduate of Bachelor of Elementary Education at Polytechnic State College of Antique.