Evolution

Basic Patterns of Evolution

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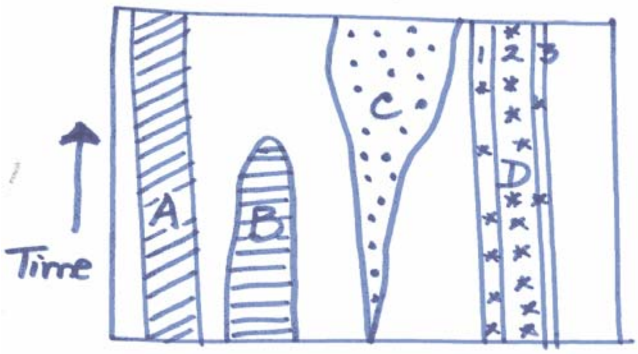
George Gaylord Simpson, who worked at New York's American Museum of Natural History and Harvard University for many years, was the principal palaentological contributor to the synthetic Theory of Evolution. He developed a neat conceptual framework or an adaptive grid describing major evolutionary patterns. It was divided into a series of broad or narrow adaptive fields or zones on the basis of interaction of organisms and their environment. All the members of the same major group (say reptiles) occupy one major adaptive zone as they all possess *common general adaptations*. Now, within the broad zone, each species of reptiles (say, Krait or lizard) forms a narrow, distinct field of its own because of a unique combination of special and general adaptations. Simpson suggested that the adaptive zones can be represented diagrammatically as bands or pathways on an adaptive grid (i.e. A, B, C, and D) and the gap or discontinuities between these major zones are unstable ecological zone. They can be different widths and are environments of strong negative selection. The zones in turn are further partitioned into subzone (1,2,3 etc.).

The basic patterns of evolution can now be described in terms of adaptive grid as:

1. movement of evolutionary line within subdivisions of subzones as *microevolution*
2. Movement from one major zone or subzone to the others as *Macroevolution* and
3. from one major set of zones into others *Megaevolution*.

Figure 10.1 : The Adaptive Grid



Evolutionary phenomena can also be dealt with at three levels, in another way as proposed by Goldschmidt:

1. Evolutionary changes occurring within the population – *Microevolution* 2)Evolution of races and species (Speciation)
2. Evolution of all the major groups beyond species as *MacroEvolution* .Some authors, however like Simpson divided evolution of major groups further into two subtypes:
    a. M*acro Evolution* –Evolution of genera, families and order.
    b. *Mega Evolution* – Evolution of classes and phyla.

Still another biologist *Rensch* termed this as *Trans-Specific Evolution* to cover all evolutionary changes beyond establishment of a good species.

Now a days, the term Mega evolution has become redundant and macroevolution is used to describe all evolutionary changes beyond species level.

As we all know that evolution is described as the process of gradual modification in the living organisms and this process can be brought about by two fundamental patterns:

Sequential evolution and (2) divergent evolution.

Sequential evolution – Evolution at its simplest involves relatively minor changes in the gene pool of a population from one generation to the next with corresponding modification in genotypic frequencies and range of phenotypic variation. Though, no new populations result from the change, but at the same time the descendent population is also not genetically same as its predecessor. Thus, evolution of modified gene pools from pre-existing ones is called sequential evolution by Paleontologists ,working with short-time series, geneticists studying laboratory populations and field biologists investigating isolated natural populations are all examples of sequential evolution. A combined genetic and field study of scarlet tiger moth (*Panaxia dominula*) conducted for 23 years (1939 to 1961) by a group of British geneticists is an ideal example which shows all the characteristic features of this type of evolution:

1. It produces rather *random changes* or fluctuations over long periods of time, with relatively *little difference* between the genotypic combinations and frequencies at the beginning and end of the studied period.
2. This type of evolution, by itself, never produces new populations from old, but only produces *temporal temporary changes* in a population continuum.
3. The changes are *non-directional*.

Thus, sequential evolution reflects the conservative nature of biological inheritance.

Divergent Evolution – is the second major pattern, which results in origin of new populations from the old ones. Its unique features are:

1) It usually results from the forces that operate over a *long period of time*.
2) The changes are *cumulative*, and
3) Occur in a *particular direction*/are *directional*.

This type of evolution is more familiar to us and the entire biological diversity is a classical manifestation of this evolution ranging from a bacterium to a mango tree to a cockroach to a lion etc.

In fact, the two types of evolutionary patterns are intimately related. Not even a single population exists which exclusively shows sequential evolution, because all populations ultimately fragment and undergo divergent evolution, if studied over a long period of time. However, the elemental evolutionary forces for both the types are same to a great degree but additional factors viz. isolation must cooperate to produce the latter.

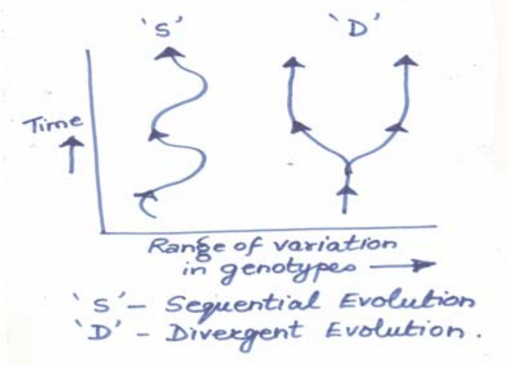


Figure 10.2

Time

Range of variation in genotypes

Now that we know about the forces responsible for bringing about evolutionary change, we can move to study different levels of evolutionary patterns.

1) ***Microevolution*:**

Evolution resulting from the interaction of variation, mutations, natural selection and genetic drift to produce relatively small population changes is frequently called as *microevolution*. Sequential evolution is always the product of microevolutionary process and divergent evolution at its simplest is also nothing but microevolution.

"*Micromutations*" or "little mutations" as described by Goldschmidt, is considered to be the ultimate source of new alleles or gene combinations, in addition to *recombination* which also changes the gene frequency in the gene pool of the population. These two forces produce variation in the hereditary material, which can be molded by impact of the other two forces (Natural Selection and Genetic Drift). A third elemental force responsible for fixing in populations of non-adaptive or neutral characteristics is *genetic drift*, which plays an important role in evolution, particularly in small populations. However, the impact of the total environment on the reproduction and selection of gene combinations is through the force of *natural selection*. It doesn't directly produce new genes or gene combinations, but helps to mould or differentially select genetic variations present in a population.

Thus, the whole process of microevolution can be conjectured as follows. The elemental forces of evolution i.e. Mutation, recombination and migration produce variations in the genetic material. They start or the initiate microevolutionary process by providing new grist whereas natural selection and genetic drift once sort out these variations like a grindstone to help establish the process.

Dia from savage

2) ***Speciation:*** The origin of new populations can occur in two basic ways:

(i) in a successional manner (*species transformation*). It results in successional replacement of pre-existing population by the new ones e.g. palaoentological series, and

(ii) in a divergent manner (*species divergence*) or *diversification*. It results in the splitting of parental population into two or more new populations with the appearance of genetic divergence. Isolation is the additional factor, which establishes genetic divergence. (This topic has been dealt with in detail in the chapter "role of isolation").

3) ***MacroEvolution:*** It is an evolutionary pattern, which results in the production of new adaptive types through a process of population fragmentation and genetic divergence. As we have already seen, it operates *above the species level* and the changes occur within a *short period of time*.

This type of evolution involves:

- (i) an early formative phase; and
- (ii) a subsequent period of expansion and proliferation and is characterized by
  - (a) subdivision of group into several new subgroups
  - (b) invasion of several new environmental situations, and
  - (c) Diversification of structure and biology.

The concept of macroevolution or adaptive radiation as such was given by Osborn in 1910 in relation to mammalian evolution. He wrote in "Age of Mammals" that adaptive radiation might be defined as that phenomenon where representatives of large systemic groups adapt themselves to a number of mutually exclusive ways of life.

In mammals, he recognized five main lines of evolution in the limbs and feet, which make them suitable, or fit for living in diverse habitats and follow a different mode of locomotion. These five groups are:

- (i) Swift running in terrestrial habitats e.g. lions, tigers etc.
- (ii) digging habitats for underground life viz. moles and shrews.
- (iii) Swimming in amphibious and aquatic mammals e.g. whales and porpoises.
- (iv) Climbing in arboreal habitat e.g. squirrels, and
- (v) Parachuting and flying in aerial habitats e.g. bats.

Other lines of specialization were also observed in teeth and diet.

The *steps* involved in this process of adaptive radiation as exemplified by mammalian evolution can be conjectured as follows:

(1) *Invasion of an unoccupied territory*:

In a new adaptive zone, the number of individuals i.e. original colonizers are less, it's almost free from the enemies and moreover there are abundant resources and more opportunities to avail new habitats. Therefore, there is no competition of food and virtually *no intra-specific* competition leaving the adaptive zone vacant. This makes it available for the new "colonizer" populations for occupation armed with general adaptations. The original colonizer species may either move to a new territory or may become extinct.

(2) *Adaptive Radiation*: Due to availability of abundant resources and diverse habitats, there is a population increase, which leads to high selection pressure. Therefore, the newly entered populations enter all the available habitats of the new adaptive zone. Some forms radiate which involves requirements of new adaptive characteristics, operating at all taxonomic levels.

The acquisition of new adaptive characters may open up new ways of life e.g. in evolution of vertebrates, the development of lungs and legs opened up the land for colonization. Similarly the development of wings opened up air for birds. The colonizer populations which already have such characteristics, which could be of use in future (i.e. the *pre-adapted species*), are better adapted for colonization.

Because, evolution of adaptation always involves jumping of non-adaptive zones (the zones of strong negative selection). Longer the gap, greater the number of pre-adaptations required.

Usually, a “generalized” organism is able to jump or cross over better. The “jump” is then followed by “specialization”.

Now, when the pre-adapted colonizer population enters a new habitat, it undergoes *specialization*. It enters all the available habitats and starts adapting itself according to the conditions and need. It therefore gets split up into several sub-populations, each of which evolve independently but simultaneously in different directions. This is known as “*adaptive radiation*”.

Evolution of reptiles and horse represent the best-documented examples of macroevolution in the fossil records.

Evolution of Horse family Equine from *Hyrecotherium* to *Equus* exhibited gradual changes in the structure of teeth, limbs, hoof, size etc., from a small fox-like browsing creature with padded feet to modern horse with large size, grazing habits and hoofed feet. Similarly, the reptilian evolution showed following *essential features* of macroevolution, which are principal characteristics of macroevolution in all groups, from tree ferns to seed plants, from trilobites to insects. These common elements provide the key to understanding the process of evolution above the species level.

(1) All macroevolution follows the acquisition of new *general adaptation* or entrance into a new adaptive zone. Darwin’s finches radiated after an apparently generalized finch ancestor arrived to occupy the previously unoccupied Galapagos Islands. Reptiles radiated after completely terrestrial developments was established as a general adaptation.

(2) Macroevolution always involves *evolutionary divergence*. It’s not linear but radiating. Usually radiation follows general adaptation and the invasion of a new adaptive zone through special adaptation in different divergent descendent lines. The radiation of archosaurian reptiles from the generalized thecodants is a typical example.

(3) Adaptive radiation tends to produce evolutionary lines that converge to special adaptation with other distantly related groups differing in their matrix of general adaptation. The ichthyosaurs show a marked evolutionary *convergence* with a number of fish groups in their body form, manner of locomotion, food habits (fishes) and free-swimming pelagic life. They are convergent in special adaptations but still share a group of general adaptations with all other reptiles.

(4) Macroevolution produces groups of *parallel special adaptations* among divergent but related stocks sharing a common background of general adaptation. Among the reptiles, group after group has invaded adaptive zones in aquatic habitats. Representatives of every order except the cotylosaurs, the synapsid orders, the eosuchians, rhynchocephalians and flying reptiles have invaded the water and become completely aquatic. Repeated trials of the same general habitat or group of adaptive zones by divergent lines are always typical of adaptive radiation. A corollary of this principle is the feature of ecologic replacement in macroevolution where there are repeated evolutionary experiments with the same broad group of zones, some groups arise, flower and become extinct to be replaced by parallel groups that invade the same zone and undergo differentiation in their turn.

(5) The phytosaurs (Triassic), of the order Thecodontia, and the crocodiles provide an example of both parallelism and ecologic replacement. The phytosaurs were very successfully adapted to aquatic life, but as they became extinct, the crocodiles derived from a different group of thecodonts, replaced them. The adaptations included location of eyes and mostrils dorsally, a large muscular tail used in locomotion, similar dentition

for capture of aquatic prey, and devices for ensuring respiration while nearly completely immersed in water. The specialized phytosaurs have been replaced by the specialized crocodiles and their allies, who in their turn are becoming extinct.

(6) As a rule, macroevolution ultimately leads to extinction. As general adaptation is replaced by special adaptation, groups became rigidly specialized to narrow adaptive subzones and are unable to move into new major zones. Since all adaptive zones must finally change and disappear, all groups locked into a narrow zone are doomed. Evolutionary progress however consists of moving out of old zones into new zones through the acquisition of new complexes of general adaptations e.g. Rhyncocephalia was extremely successful up through the cretaceous but is unknown as fossils in the last 75 million years. A single species, the tuatara, is a relict of the order and survives today in Newzealand.

(7) Large-scale evolutionary replacements of one higher taxon by another may be either due to *competitive ecological displacement* (new group outcompeted the original one); or to the extinction of the earlier group for an unrelated reason followed by the radiation of the second group (*Independent replacement*). The latter theory seems more plausible.

(8) A common denominator runs through the entire picture of macroevolution, whether seen in Darwin's finches or in the ruling reptiles. At every step in evolution, natural selection creates a vast array of adaptive experiments that occasionally break out of their present adaptive zones into new groups of zones. *Every new breakthrough is dependent upon the breakthroughs previously achieved* e.g. an alga didn't become a seed plant in a single step, nor did fish develop directly into men. The adaptive shifts directly responsible for human beings or sunflowers were not possible without all the progressive evolutionary shifts that preceded them. *An individual shift depend upon opportunity, ecologic access and the taking on of new general adaptation* e.g. the reptiles could not have evolved if amphibians had not previously invaded the land. The adaptive experiments created by selection within an adaptive zone are of two types. Many are *special adaptations* taking their possessors into narrower and narrower sub-zones. Others, which are at the base of any breakthrough to a new zone, are in the direction of outermost limits of the present zone. *Repeated attempts and combinations are apparently developed by selection until one line makes the breakthrough* e.g. constant, divergent probing of the limits of an unoccupied zone by many different branches of the same line is provided by frogs and their many adaptations to reproduction out of the water. One of the experiments took advantage of the opportunity and led to the reptiles. The multiple attempts at crossing the barrier can even lead to extinction or failure, but at the foundation of every successful breakthrough a series of divergent testings of the unstable environment have taken place.

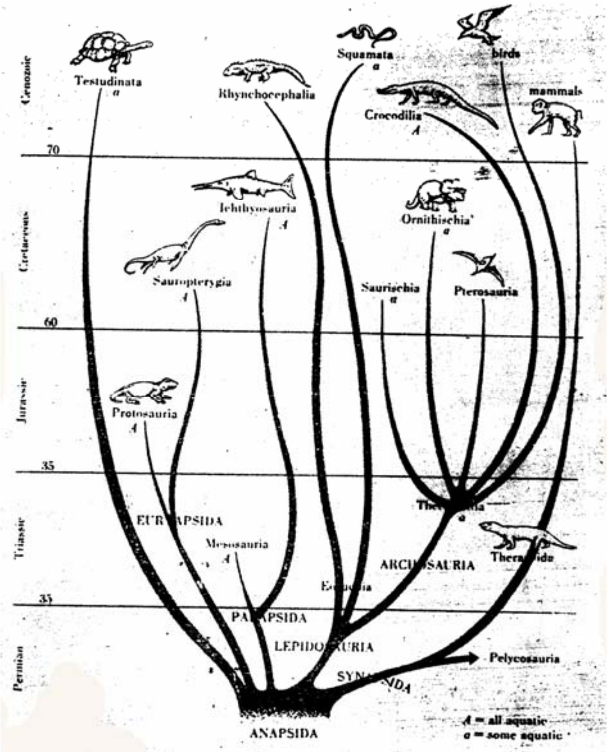


Figure 10.5 : *The general pattern of reptile evolution.*

Saltation VS. Gradualism

Now, we examine the causes for what one of the architects of Evolutionary Synthesis, Bernhard Rensch called “evolution above the species level” or another paleontologist, George Gaylord Simpson addressed the “tempo and mode” of evolution in the long term. Have higher taxa evolved, as Darwin proposed, by successive slight changes, or by the sudden origin of drastically new features?

If, between even the most extremely different organisms, there existed a full panoply of all possible intermediate forms, each differing from similar forms ever so slightly, we would have little doubt that evolution is a history of small changes. Such is often the case when we examine differences among individuals in a population, among populations of a species, and among closely related species, such as those in the same genus. Moreover, quite different species are often connected by intermediate forms, so that it becomes arbitrary whether the complex is classified as two genera or as one. Nonetheless, there exist many conspicuous gaps among phenotypically similar clusters of species. No living species e.g. bridges the gap between whales (Cetacean) and other mammals, nor between vascular plants and bryophytes. Such gaps are subject of probably the most enduring controversy in evolutionary biology.

Biologists can entertain *three hypotheses* to explain phenotypic gaps:

(1) Distinct groups of organisms don’t originate from a common ancestor, but instead represent independent origins of life. We can immediately dismiss this hypothesis, based on extensive evidence from molecular biology and cell structure for the common origin of all living beings.

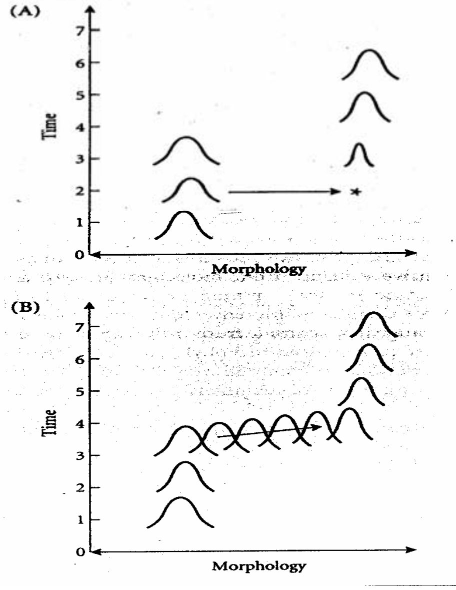
(2) The gaps exist because of origin and fixation of single large mutations, or other drastic genetic changes, that radically alters the phenotype. This hypothesis is of “*macromutation*” or “*saltation*”.

(3) Most differences among higher taxa have arisen by successive fixation of slight phenotypic changes from the state of their common ancestors. If we had a complete fossil record of all the ancestral populations, it would present a gradual history of phenotypic change. We, however lack such a record in most instances because the fossil record is extremely sparse.

The more rapid a gradual change is, the less likely it is to be preserved in the very incomplete fossil record. The hypothesis of "*Punctuated Equilibrium*" holds that most evolutionary changes in morphology, although perhaps continuous in the sense of passing through many intermediate stages, have been so rapid that the fossil record presents the appearance of a discontinuous change. This proposition is very different from the saltation hypothesis, which holds that intermediates never existed e.g. the most recent common ancestor of whales and bats, didn't have a mixture of cetacean and chiropteran features, nor were its forelegs intermediate between fins and wings. Instead, it probably had the shrewlike characteristics of the early-generalized placental mammals.

(If each of two diverging lineage's (viz. those leading to whales and bats) generated reproductively isolated species at each stage of divergence, and if each such species persisted to the present with little further change, the most divergent species would today be connected by an array of intermediates, including the phenotype of their common ancestor. Many such "morphoclines" exist in clades that've recently experienced adaptive radiation. However, the fossil record is the only possible source of evidence for gradual evolution: (1) If intervening species with intermediate morphology become extinct; (2) If speciation seldom occurs or (3) if the intervening species themselves continue to evolve.

Figure 10.4a : Two hypotheses accounting for phenotypic gaps in a fossil lineage. (A) Saltation, or macromutation. A single mutational change (asterisk), in a single individual, changes morphology discontinuously. Its descendants vary around the new morphology and replace the ancestral form. (B) The mean of a quantitative character changes gradually, but so rapidly that the intermediate stages may not be recovered from a coarse fossil record.



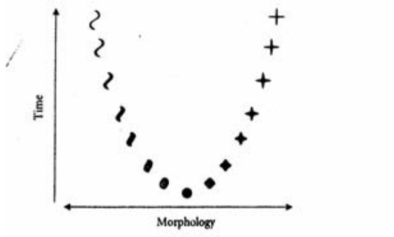


Figure 10.4 b : Two very different taxa may have evolved gradually from a common ancestor, but without any form ever having existed that was precisely intermediate between them.

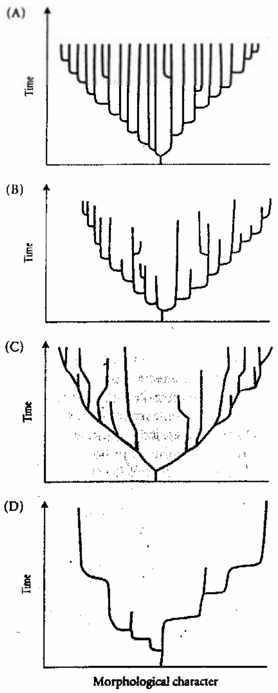


Figure 10.4C: Conditions under which contemporaneous species do or do not provide evidence on whether a character diverged gradually. (A) Punctuational evolution, in which newly arisen species "freeze" intermediate phenotypes and survive to the present. (B) The same pattern, but most intermediate species become extinct. (C) A pattern similar to B, but in which some evolutionary change occurs within species. (D) Episodic, but almost entirely anagenetic, evolution of diverging lineages that seldom speciate. Evidence of gradual evolution is provided by living species in case A, but must be sought in the fossil record in the other cases.

In adjudicating between gradualism and salutation it's important to distinguish between the evolution of *taxa* and of their *characters*. Higher taxa often differ in many characters e.g. not only feathers, but a great many other features distinguish modern birds from dinosaurs. Gradualists hold that higher taxa didn't arise discontinuously, but rather that many of their characters evolved independently and sequentially (*mosaic evolution*). Almost all-contemporary biologists agree on this.

Arguments for Gradualism

Darwin was well aware of "sports" – what we now call mutations with large, discontinuous effects on one or more features, but held that most evolution is based on the slight individual differences that we observe within populations (now known as *polygenic variation*). This gradualist position was reaffirmed by neo-Darwinian viz. Ronald Fisher and has been the majority opinion ever since (Maynard Smith, 1983). The chief arguments of *contemporary gradualists* are based on:

1) intermediates among both living and extinct species.
2) functional considerations
3) fitness effects of mutations (pleiotropy) and
4) the genetics of species differences.

The fossil record for the origin of mammals from a group called morganucodontids viz. *Kuchneotherium* is an important test case for general theory about how major evolutionary transitions take place. We notice two important conclusions – 1) the changes from reptilian to mammalian characters evolved in gradual stages; 2) and the large scale differences between them concern adaptations (viz. high energy, high metabolic rate, upright than sprawling gait, mammalian teeth and jaw articulation). Since these changes are surely adaptive and would have been brought about by cumulative action of natural selection over a long period (40 million years), the accumulation of many small-scale changes resulted in the large-scale change from reptile to mammal.

This idea is recognized as an *Extrapolative Theory*. Macroevolution takes place by the same process – natural selection and adaptive improvement – as has been observed within species and at speciation, but the process operates over a much longer period. While this model is not the only model for the evolution of major groups, it's most important and the only one that can be illustrated with detailed fossil evidence. It can also be thought of as "neo-Darwinian" theory of macroevolution. According to this theory, most characters show variation, and the character evolves as its frequency distribution is altered by selection, without recourse to extraordinary kinds of variation. Natural selection, on ordinary variation and mutation, is adequate. It's not a single line of evolution, with each new step being added on to the one before. Each phase of evolution contains radiation into many evolutionary lines.

Arguments for Saltation: An extreme saltation would be a radical transformation of many characteristics in a single mutational event e.g., the paleontologist Otto Schindewolf believed that the differences among higher taxa have arisen discontinuously, declared that "the first bird (*Archaeopteryx*) hatched from a reptilian egg". A similar position was held by Richard GoldSchmidt, which had made a major contribution to genetics by stressing that genes act by controlling the rates of biochemical and developmental reactions. Despite his excellent work on the genetics of variation in moths, he argued in "*The Material Basis of Evolution*" that species and higher taxa arise not from genetic variation that resides within species, but instead in *single evolutionary step* as completely new genetic systems. He denied gene mutations a role in evolution, believing instead that higher taxa arise by complete "repatterning" of the chromosomal material. These "*systematic mutations*" would give rise to bizarre creatures, most of which would have no chance of survival, but some few would be "hopeful monsters" adapted to new ways of life".

Prominent figures in Evolutionary Synthesis (viz. Mayr, 1942; Simpson, 1944) and later Neo-Darwinians (e.g. Charlesworth, 1982; Templeton, 1982) criticized Goldschmidt sharply.

Mutations showing effects in early stages of development or regulatory genes can have large phenotypic consequences. Such *homeotic mutations of Drosophila* (e.g. *antenna paedia and bithorax*) are classical examples that such mutations can happen. These mutations are examples of macromultations or "monsters". They argued that the vast majority of "monsters" would be hopeless, e.g. an *Archaeopteryx* with a suddenly shortened tail could not fly without corresponding changes in the muscular and nervous systems. They noted that major mutations usually have deleterious pleiotropic effects. Neo-Darwinians have always accepted that some such genetic changes, such as those caused by *allelic dominance and threshold effects*, play a role in evolution. Perhaps the most dramatic single gene differences are those with strong *heterochronic effects* e.g. few allelic differences between metamorphosing and neotenic *Ambystoma* salamanders The homeotic genes that control A-P patterning, in *Drosophila* are called as HOX GENES,and they have been subsequently found in all animal phyla [Futuyama,1992] . Such genes are regulatory in function.

The standard neo-Darwinian argument (e.g. Fisher) is that developmental macromutations are evolutionary inconsequential, which may arise from time to time, but will always be selectively disadvantageous because they introduce a gross change into a fairly well-adjusted machine: they soon disappear from the population. No one can deny, however, that macromutations, occur, but a macromutation producing a new complex set of adaptations would require a miracle!

In summary, substantial differences in certain characters of some species have surely evolved by selection on single alleles with large effects. Some of the novel features (*synapomorphies*) of higher taxa may well have arisen this way, although we are not yet sure about this. This idea has some modern supporters and as a rare theoretical possibility cannot be ruled out. But, there is no evidence that single “macromutations” have been responsible for multiple characters and substantial differences in morphological organization, that distinguish most higher taxa. Therefore, the theory of hopeful monsters should be regarded as no more than a hypothesis as it’s implausible in theory and unsupported in fact. On the other hand, the abundant evidence of mosaic evolution, as seen in origin of mammals from reptiles, transition of reptiles to birds etc. is adaptive and therefore must have proceeded in many stages and has been overwhelmingly gradual.

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