Review Article

What good is a long neck for a giraffe? Evolutionary insights revisited

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Abstract

The evolution of the giraffe's neck is a complex process involving several anatomical, physiological, and behavioural modifications. However, the reasons behind the evolution of the neck in giraffes and the associated evolutionary events remain unresolved. Various theories explaining evolution in general and giraffes' neck evolution in particular are discussed in the context of present-day evolutionary genetics. This review also critically evaluates the scientific validation and logic of these theories.

Keywords: Bottleneck phenomenon, Darwinism, founder effect, genetic drift, *Giraffa camelopardalis*, Lamarckism, mutation theory, neural theory, population genetics, variations.

Introduction

The giraffe, with its long neck, legs, and coat pattern of irregular patches, is a fascinating animal. Giraffes are the tallest land animals, with males (bulls) typically growing taller and heavier than females (cows). Males can reach heights of over 5.5 m and weigh up to 1,930 kg, while females are approximately 4.5 m tall and weigh up to 1,180 kg.[1] It also has the largest eyes among land animals, and these are placed posteriorly to ensure more field vision.[2] Unlike most other mammals, it is capable of colour vision. The tail is about 1 m in length. Giraffes possess a pair of horns. The coat patches provide excellent camouflage, offering some protection from predators. Giraffes do not sweat or pant; instead, thermoregulation is facilitated by the coat patches, which may function as 'thermal windows' due to the presence of vascular plexuses beneath them. [2,3]

Giraffes reach their full size by the age of four. They are capable of running at speeds of up to 50 km/h. They live in non-territorial groups of up to 20 individuals. Their gregarious nature enables them to remain vigilant against predators. With excellent eyesight, they can spot an enemy from one kilometre away, and they have a lifespan of up to 26 years. The gestation period lasts 15 months. The newborns are about two metres tall, weighing approximately 100 kg.[1] Giraffes are primarily found in the grasslands and open woodlands of East Africa. They are also protected in certain reserves in southern Africa. The West African subspecies has confronted a significant population decline and is now confined to a small range in Niger.[1] Traditionally, giraffes have been classified as a single species, *Giraffa camelopardalis*, which is further divided into nine subspecies (Figure 1). However, mitochondrial DNA studies have revealed genetic uniqueness in four or even six groups, making each group distinct from the others, likely due to reproductive isolation. [4,5]

According to a survey, giraffe populations declined by 36 - 40% between 1985 and 2015 due to habitat loss and illegal hunting.[4] Recently, the International Union for Conservation of Nature (IUCN) classified the species as "vulnerable. [5]

Figure 1. *Giraffa camelopardalis*: This giraffe subspecies inhabits the grasslands of South Africa. In the image on the right, the giraffe's neck is held upright, while in the image on the left, the neck is positioned at shoulder level.

The long neck of the giraffe: A case study in evolution

The long neck of the giraffe is often cited as an example supporting both Lamarckian and Darwinian concepts of evolution.[6]

Lamarckian theory and explanations

According to Lamarck, giraffes inhabited environments where surface vegetation was insufficient to sustain large populations. Over generations, they stretched their necks to feed on foliage from taller trees. This repeated stretching became a habit, and over time, the elongated neck developed as an acquired trait, which was then inherited by subsequent generations. Lamarck's theory suggests that acquired characteristics become heritable. This is known as the theory of the inheritance of acquired characteristics. A supplementary proposition to this is the theory of use and disuse, which states that the evolutionary development of an organ depends on its use.

With constant use, an organ becomes more developed, whereas disuse leads to its degeneration or even disappearance; often cited examples being the vestigial organs. In the case of the giraffe, the argument was that neck elongation occurred because of its constant use.[6]

Darwinian theory of natural selection with explanations

According to Darwin, nature poses several challenges to organisms in the form of harsh climatic conditions, food scarcity, and natural disasters such as floods and droughts. In such situations, traits that enable organisms to survive these challenges better than others in the same environment are said to be selected by nature. Thus, nature favours traits that are better suited to overcome environmental challenges, and this process is referred to as natural selection.[6]

Darwinian theory explained that giraffes evolved from horse-like ancestors with shorter necks. In habitats dominated by tall trees and sparse ground vegetation, giraffes with longer necks had a competitive advantage, as they could access food unavailable to shorter-necked individuals. Over time, long-necked giraffes thrived, while shorter-necked ones were outcompeted and eventually eliminated. Thus, long-necked giraffes were naturally selected.[6]

Alternative explanations

The explanations offered by Lamarck and Darwin are considered speculative and lack direct scientific evidence. Several such speculative theories can be proposed for explaining the evolution of giraffe's long neck. For example, let us consider another possibility. In a population of deer-like animals, a dominant mutation caused neck elongation in some individuals, allowing them to feed on tall foliage. These mutated individuals became reproductively isolated, eventually forming a new species.[7-9]

Advantages and disadvantages of a long neck

The elongated neck of a giraffe provides distinct advantages, such as access to food that is unreachable for other animals. However, it also presents challenges and causes several disadvantages some of which are discussed below:

Anatomical adaptations

Giraffes' neck consists of seven cervical vertebrae as in other mammals, each measuring about 30 cm, compared to 5 cm in similar-sized even-toed ungulates like buffalo. Elongation of the seven cervical vertebrae alone is not the single event that happened during the evolution of giraffe. It necessitates several anatomical and physiological modifications during evolution. To support its massive 2.5 meter-long, 250-kg neck and head, the muscles and ligaments must be strong.[7] Giraffes have large ligaments known as nuchal ligaments (*ligamentum nuchae*) that run from the back of the neck to the base of the tail. These ligaments function like a giant elastic band, pulling the neck back over the front legs to maintain an upright position. [1,2] The sturdy forelegs further aid in supporting the neck. Limb bones are strengthened through increased mineralization, thereby achieving higher bone density, rather than an increase in diameter of the bones. In fact, 80% of skeletal calcium is deposited in the leg bones.[2] The tongue, which is about 50 cm long, along with the prehensile upper lip, allows the giraffe to browse leaves from tall trees.

Postural challenges during drinking

Giraffes must lower their heads to drink, which presents several challenges. While their long necks are advantageous for reaching high foliage, they are not long enough to reach ground-level water sources. To drink, giraffes splay their front legs sideways and bend down, lowering their bodies to access the water. This awkward posture makes them vulnerable to predators such as lions and crocodiles. As a result, they tend to drink quickly, taking large gulps, up to approximately 54 litres in one go. Despite their size, giraffes can survive for up to three weeks without drinking. Lowering their heads also causes a rapid change in blood pressure, which is managed through specialized physiological and anatomical adaptations.[10]

Blood flow

The blood pressure must be maintained high for supplying blood to the head i.e., up to a height of 2.5 to three metres (8-12 feet) and this is achieved by increasing the heart rate. The heart is very large, weighing roughly 10-11 kg and could fill four litres of blood. The heart beats at 150 bpm to pump blood up to the head.[10] Furthermore, the blood vessels in the neck are made extra thick to withstand the high blood pressure and to prevent rupturing of blood vessels. The blood vessels expand when the giraffe lowers its head and contract when head is raised again. These changes allow a controlled flow of blood during upward and downward movements of the head and prevents fainting. A maze of blood vessels known as *rete mirabile* present at the base of the brain acts like a sponge and soaks up blood for controlling blood volume and regulates blood flow to the brain when the animal lowers its head.

Similarly, special 'control valves' are present in the jugular veins.[8] These valves prevent blood from draining too quickly when the head is raised.[11]

Another challenge is managing the high blood pressure in the legs, which could force blood out of the capillaries. This is addressed by filling the intercellular spaces with fluid under high pressure, a mechanism further supported by the giraffe's highly impermeable and tough skin. The fibrous connective tissue, known as the *inner fascia* which is associated with the skin also helps prevent blood pooling. Additional adaptation to prevent profuse bleeding is the positioning of all arteries and veins deep within the giraffe's legs, with only extremely small capillaries distributed superficially. Furthermore, the red blood cells are small, only about one-third the size of human RBCs, which help them manage the high blood pressure and facilitate easier passage through the narrow capillaries, particularly in the brain and extremities. The smaller red blood cells also provide a greater surface area, allowing for a higher and faster rate of oxygen absorption into the blood, ensuring an adequate oxygen supply to all parts of the body, including the head. These adaptations appear to be interactive and interdependent with the giraffe's long neck.[12]

Regurgitation

As ruminants, giraffes regurgitate cud for further digestion which requires strong muscular contractions to move food back to the mouth through the lengthy oesophagus. The oesophagus is, therefore, very much muscular.[10,12]

Respiration

The long trachea increases the volume of *dead air*, i.e., the air that does not participate in gas exchange. To compensate for this, giraffes have larger lungs and slower breathing rates. When a giraffe takes a new breath, the oxygen-depleted air from the previous breath is not fully expelled. The larger lungs help mitigate this issue by ensuring enough lung volume so that the dead air is accommodated as a small percentage of the total air inhaled. [10,12]

Mother giraffes also face challenges during childbirth, as the calf's neck is proportionally as long as that of an adult.

Food-based explanation for long necks

The question why giraffes developed long necks still remains unresolved. The explanation that it evolved to help giraffes reach tall trees has been refuted by many biologists, even during Darwin's lifetime. Notably, Darwin himself did not use the giraffe as an example in the first edition of *On the Origin of Species*. He later included it in the sixth edition, responding to the criticisms raised by Mivart who accepted evolution, nevertheless expressed disagreement with the concept of natural selection.[11,12] Darwin was well aware of the problems associated with the extraordinary evolution of the neck of the giraffe that required modifications of several parts simultaneously and acknowledged the difficulties in explaining this through natural selection. He himself conceded at one point that 'on the principle of natural selection this is scarcely possible'.[13]

Both Lamarckian and Darwinian theories suggest that the giraffe's long neck evolved as an adaptation for feeding on twigs and leaves from tall trees, though they differ in the mechanisms proposed for this evolutionary process. Critics of the food-based explanation pointed out that female giraffes, being shorter by about two feet, would face disadvantages during droughts.[11,14] Despite this, they survive quite well. Similarly, as per this view, young giraffes up to four years of age would also struggle to gather food due to their shorter necks.[15]

It is known that, although adult giraffes prefer *Acacia* leaves during the wet season, they also browse on many other plants, including bushes, shrubs, and low-growing grasses, during the dry season. Generally, giraffes prefer to feed at shoulder height, which is about 60% of their maximum height. Young and Isbell have observed that the preferred feeding heights vary depending on the male-female composition of the group.[16] Females in female-only groups feed at a height of 1.5 m, while those in male groups feed at 2.5 m. Meanwhile, males in male groups feed at 3.0 m. This indicates that a height of 3 m is sufficient for giraffes to outcompete all other ungulate browsers. If so, there seems to be no reason for giraffes to evolve to a height of 5 m. [2,5] Likewise, the observation that both male and female giraffes frequently bend their necks to browse on plants at lower levels suggest that longer necks are not specifically evolved for feeding on leaves from tall trees.[17] Gould asks, "if such a habit is so beneficial, why many other animals such as antelopes also evolved the same ability?"[18] A counterargument is that the various species of giraffids (e.g., sivatheres) evolved when they coexisted with large herbivore competitors such as mastodonts, deinotheres and baluchitheres, that later became extinct. [5,19]

The "Neck-for-Sex" hypothesis

Male giraffes engage in neck-based dominance contests, a behaviour known as "necking". It involves fights between adult males that may potentially influence reproductive success. This theory suggests that longer necks provide an advantage during necking.[20] If the long neck evolved in response to intersexual competition, it can be reasonably assumed that necking behaviour evolved first, and neck elongation followed it as a result of selection. Conversely, necking would be ineffective until giraffes had sufficiently long necks. This implies that there is no direct relationship between the evolution of necking behaviour and neck length. Mitchell *et al*., observed that the differences in neck morphology between male and female giraffes are minimal. The longer necks in males can be attributed to their greater body mass. According to their findings, sexual selection is unlikely to be the driving force behind the evolution of long necks in male giraffes.[21]

Other explanations

Increased height increases the reach of vision and vigilance. According to some evolutionists, the giraffe's long neck, coupled with its excellent vision, may enable it to spot predators far away. [1] While this is true, it must be noted that giraffes have virtually no enemies except lions. However, lions typically attack giraffes only when they are desperate, and the giraffe is in a vulnerable position, such as when drinking water with its legs spread sideways. Giraffes defend themselves primarily by kicking.[9] A kick from their heavy, hooved, long legs can be deadly to predators. According to Hitching, a lion is no match for a 900-kilogram giraffe, as a single blow from the giraffe's hoof can kill a lion.[8] He states, "This explains why they supposedly evolved long legs… but not why they evolved long necks."

Other reasons cited for the giraffe's long neck include thermoregulation and facilitating forward travel at high speeds.[9] Gould concludes that "the giraffe's neck cannot provide evidence for any specific adaptive scenario, Darwinian or otherwise. Truth be told, the giraffe's neck serves better as an example of the many challenges in explaining evolution through Darwinism".[9,22]

How did neck elongation happen in giraffes?

The giraffe (*Giraffa camelopardalis*) is the only living member of the genus *Giraffa*, and there is no evidence that any animal similar to it ever existed. Nine subspecies of *Giraffa camelopardalis* are recognized. Neck elongation in giraffes is believed to have begun around 14 million years ago, with the ancestors of modern giraffe emerging approximately five million years ago. [23,24] The fossils of *Giraffa camelopardalis* recovered from East Africa revealed that they were one million years old.[2]

Regarding the evolution of giraffes, although a significant number of giraffe bone fossils have been recovered, the individual bones are more or less of the same shape and size. Studies involving the dating of existing fossils suggest that the giraffe has remained largely unchanged for about at least one million years. In giraffes, the cervical vertebrae and leg bones are greatly elongated. However, no fossils have yet been recovered to provide insights into the step-by-step evolution of the giraffe's neck and leg bones.[9] Additionally, the origins of all three major lineages of pecorans which include giraffes, deer, and cattle remain unclear due to significant gaps in the fossil record. It is believed that at the beginning of the Pleistocene, giraffes inhabited large parts of Eurasia and Africa. Some evolutionists speculate that the ancestor of the giraffe was an elk-sized animal called *Palaeotragus*, whose fossils were recovered near Athens. *Palaeotragus* is thought to be an early giraffid that gave rise to two groups of descendants during the Pleistocene. One of these groups included the heavy-bodied sivatheres, which were about the size of elephants and once roamed Africa and India.[25] Sivatheres had short necks and elaborate horns (ossicones) resembling palmate or flat antler-like structures. Their bones were generally only half as long as those of modern giraffes. A second branch of the sivathere group is hypothesized to be the ancestor of the family Giraffidae, with the giraffe evolving as a separate lineage during the Miocene epoch. Another animal proposed as the primitive ancestor of the giraffe is *Samotherium*, a deer-like creature with slightly longer necks. It has also been suggested that giraffes evolved from cervoids (superfamily: Cervoidea), which were deer-like animals with side toes, an anatomical feature absent in giraffes. Probably, these side toes may have been lost during evolution.[9]

The only extant giraffid besides the giraffe is the rare, forest-dwelling okapi (*Okapia johnstani*), which is confined to central Africa. It is also called the 'forest giraffe'. The okapi has distinctive black and white striped markings on its buttocks, thighs, and the tops of its forelegs, reminiscent of a zebra's pattern. It is the only species in the genus *Okapia*.[4] The okapi and the giraffe are the two living members belonging to the family Giraffidae. The primitive giraffe is thought to be a fast running, and somewhat large animal similar to okapi, measuring approximately 1.6 meter at the shoulder. Like the giraffe, there is no fossil evidence indicating evolution of okapi. Okapi is often regarded as a "living fossil" because it has remained essentially unchanged as per fossil records for several millions of years.[9] It is the closest and the only living relative of the giraffe.

In the absence of clear empirical evidence, evolutionary biologists have proposed various theories, linking giraffes to several dissimilar animals. Despite the abundance of fossil remains of related species, there is no conclusive evidence to support the existing speculations regarding the evolution of the giraffe. Meanwhile, these speculations have led to numerous controversies, and the evolution of the giraffe remains a debated and unresolved topic.[9]

Darwin's work

It was Charles Darwin's (1809 - 1882) five-year voyage on the *Beagle* that sparked his evolutionary thinking. The expedition covered South America and the Galápagos Islands off the coast of Ecuador. His one-month stay in the Galápagos Islands was probably one of the most significant and productive periods of his life, as it helped him understand the distribution of diverse animal groups. This was particularly striking in the Galápagos, where each island had its own unique yet closely related assemblage of species. The fauna characteristic of each island was distinct and appeared different from that of the mainland. In Galapagos islands, he observed finches with differently shaped beaks. These observations led him to believe that "present species resembled past species and that different species shared similar structures" and also that "one species had been taken and modified for different ends" indicating evolution as the cause for the formation of the species.[6] Darwin was profoundly influenced by reading an Essay on *'The Principle of Population'*, published by Thomas Malthus (1766-1834), a British economist. Malthus argued that while food supplies necessary to sustain a population increase arithmetically, populations themselves grow geometrically, resulting in inevitable food shortages. Famine, war, and disease, according to Malthus, act as natural controls to limit population growth. This idea inspired Darwin to ponder that the tendency of species to reproduce more offspring than available resources could sustain would lead to competition among individuals in animal populations. In this "struggle for existence," animals with favourable variations would have a higher chance of survival and reproduction, while those with unfavourable traits would be gradually eliminated through a natural selection process. Over time, this mechanism could lead to the emergence of new species. Alfred Russel Wallace, a naturalist who specialized in collecting various species of animals, independently arrived at a similar theory of natural selection, after also reading Malthus's work. Wallace shared his theory with Darwin, and in 1858, the two jointly published a short paper on natural selection in *The Journal of the Linnean Society*. However, the publication received little response from the scientific community, likely because it lacked substantial supporting evidence.[6] In 1859, Darwin published his landmark book, *On the Origin of Species*, which provided extensive evidence and documentation supporting the concept of evolution through natural selection.[26] This work was well-received by both naturalists and the general public, marking a pivotal moment in the history of evolutionary biology.

Criticisms

The publication of Darwin's book sparked enthusiasm among naturalists and made evolution a widely debated topic in academic circles. However, theologians and clergy of the Anglican Church accused Darwin of attempting to undermine belief in God, dismissing his ideas as a brutal philosophy designed to tarnish Christianity. One notable debate occurred between Bishop Samuel Wilberforce and Thomas Huxley, a passionate advocate of Darwinism. The discussion became personal when the bishop mockingly asked Huxley whether his grandparents were descended from monkeys. Huxley retorted that, if given the choice, he would unhesitatingly prefer to have an ape as his ancestor rather than a bishop who misused his position to oppose scientific progress.[6]

While the scientific community largely accepted the concept of evolution that all living beings evolved from a common ancestor through the development of favourable variations and their preservation by natural selection, there were differing opinions regarding the specifics of Darwin's process of natural selection.[7]

The concept of struggle for existence

Malthus's views on human population growth and its associated problems influenced Darwin, who incorporated some of these concepts into his theory. For example, Darwin envisioned a struggle for existence among individuals in animal populations, as a consequence of geometric population growth. While sudden population increases are uncommon, occasionally such eruptions happen, such as pest outbreaks. However, these are typically transient and have little impact on evolution. The dynamics of animal populations depend on various characteristics and ecological factors. For instance, a direct relationship exists between prey and predator populations. Every population has a self-regulating system, preventing its size from exceeding the habitat's carrying capacity.[27] Regarding the struggle for existence, it can be assumed that successful populations tend to avoid competition through various strategies, such as migrating to unexplored habitats or exploiting new food sources. This explains why a single host plant can serve as food for multiple insect species. For example, more than 72 pest species are reported for paddy, and over 109 pests for cotton.[28] Another example can be drawn from a study on the feeding behaviour of giraffes. Research conducted by Cameron and du Toit (2007) reveals that giraffes, by feeding primarily on the upper foliage of trees, leave the lower bushes and grasses available for other ungulate browsers sharing the same habitat. This behaviour helps reduce competition for food resources.[29,30]

In Darwinian theory, individuals within a population are tasked with competing for survival, with the fittest prevailing while others perish. However, in reality, individuals play no direct role in evolution beyond contributing desirable alleles to the gene pool. An individual organism cannot evolve into a new species or produce offspring of a new species simply by engaging in and winning the struggle for existence. In fact, it is the population that evolves into new species by shifting the frequency of favourable mutated alleles over time.[31]

Darwin's concept of heredity

Darwin had no understanding of the mechanism of heredity, which made it difficult for him to explain the variations observed among different animal groups. At that time, genetics as a branch of biology had not yet been developed. In fact, Mendel published his findings on the mechanism of heredity in garden peas in 1862, three years after Darwin published his book on evolution. Despite this, Darwin proposed a theory called *Pangenesis* to explain variability among animals.[6] According to this theory, each part of an organism releases minute particles called "gemmules" into the circulatory system. These gemmules, representing the organism's traits, are believed to reach the gonads, where they are multiplied and transferred to the offspring during reproduction. However, this theory was both unconvincing and unnecessary and was ultimately rejected by the scientific community.

It was August Weismann (1834 -1914) who disproved the theory of pangenesis through an experiment.[6,32] He amputated the tails of mice for 22 consecutive generations and demonstrated that the offspring in each generation were born with fully intact tails. This experiment conclusively showed that the inheritance of tail was not influenced by the presumed loss of "tail gemmules." Additionally, this experiment disproved the concept of the inheritance of acquired characteristics proposed by Lamark. Weismann also proposed an alternative theory of inheritance known as the Germ Plasm Theory. This theory postulates that hereditary factors for the entire organism are transmitted exclusively through the germ plasm; i.e., the reproductive tissues of the testes and ovaries. It further suggests that changes occurring in the somatoplasm (i.e., non-reproductive tissues) are not inherited. This implies that traits acquired through constant use or environmental influence in somatic tissues cannot be passed on to the next generation.[32]

Darwin’s evidence for natural selection

Darwin lacked examples of natural selection in action and presented examples that he himself said were “imaginary Illustrations”.[7] He, however, had some indirect evidence. For instance, selective breeding of pigeons produced diverse breeds, all descended from wild rock pigeons.[6] The problem with artificial selection is that it relies on human choice rather than natural processes. In this method, breeders select parents with desirable traits to produce offsprings while culling or eliminating those with undesirable traits. Through continued selection, offspring with the desired traits are consistently produced in almost all cases. Darwin claimed that natural selection could similarly produce significant effects comparable to or even greater than those achieved through artificial selection leading to speciation, given the longer time scales associated with evolution. Meanwhile, there is another issue with natural selection. Darwin, like most biologists of his time, subscribed to the concept of blending inheritance, which suggested that heredity is a mixture of maternal and paternal contributions, akin to the blending of two colours. Critics of natural selection argued that, according to this concept, new traits or adaptations arising through natural selection would gradually blend away with each generation of interbreeding, thus undermining the very mechanism of natural selection.[6] Furthermore, artificial selection cannot be equated with natural selection, as natural selection operates on populations with random mating and does not guarantee the inheritance of any specific traits in the offspring.

Industrial melanism

“Industrial melanism” demonstrated by Kettlewell in 1973, is considered the first scientific proof of natural selection.[33] In the industrial city of Birmingham, he identified two distinct forms of the peppered moth (*Biston betularia*) based on pigmentation: melanic (dark) and non-melanic (light) forms. Before industrialization, the light-coloured moths were more abundant, as they were well-camouflaged against the pale lichens on tree trunks where they rested. In contrast, the melanic forms were rare. Following industrialization, the number of melanic moths increased. For his experiment, Kettlewell captured a known number of both forms of moths, released them in both industrial and non-industrial areas, and later recaptured them. His findings revealed that the proportion of melanic moths was significantly higher in polluted industrial areas. This indicated that the melanic moths had a survival advantage there, as they were better concealed against darkened tree trunks, making them less noticeable to bird predators. Meanwhile, in non-industrialized areas, where trees were covered with pale lichens, the light-coloured moths remained better protected. In other words, natural selection favoured the melanic forms in industrial areas while favouring the non-melanic forms in unpolluted regions. In this experiment, the non-melanic moths which were camouflaged for a light background, were artificially exposed to predation in industrial areas, negatively impacting their survival. Therefore, it can also be argued that industrial melanism reflects an organism's adaptive ability to remain inconspicuous in its natural habitat rather than being solely an effect of natural selection.

Genetic variability and evolution

Morphological differences among organisms are, in general, referred to as variations. It is now known that morphological variations are the outward expressions of genetic variability. It is also a fact that genetic variability is a prerequisite for evolution and that evolution works on genetic variability i.e., without genetic variability there will be no evolution. The genetic variability is, in turn, caused by mutations. Mutations produce different variants of a gene and these are called alleles. Evolution happens when the frequency of individual alleles shifts to a particular pattern. In fact, any change in allelic frequencies through generations can be considered an indication of evolution. Allelic frequencies remain the same in nonevolving populations referred to as Mendelian populations. According to Strickberger a population with little or no variability may become extinct within a short period if exposed to harsh changes in environment or some ecological challenges.[6]

Continuous vs. discontinuous variations

A controversial topic in evolutionary biology was Darwin's view of evolution as a slow and gradual process driven by natural selection, often referred to as the gradualistic view. Even some staunch supporters of Darwinism disagreed with Darwin's emphasis on continuity in variation and the slow progression of evolution. While Darwin acknowledged the existence of large, discontinuous variations in natural populations, he regarded these as too rare to serve as the primary source of evolutionary change.[13]

Huxley and Galton argued that for natural selection to be effective, it must act upon occasional large, discontinuous variations.[7] This idea gained experimental support from Hugo de Vries (1848-1935), who observed sudden appearances of traits in his stocks of the evening primrose (*Oenothera*) that were previously exposed to radiation.[34] De Vries termed the mechanism responsible for these sudden changes as 'mutation'. He proposed that mutations in natural populations could produce abrupt variations in traits, providing raw material for evolution. This concept became known as the mutation theory of evolution, which introduced a sense of purpose and direction to evolutionary change.[34]

Mechanism of inheritance of traits

Further support for discontinuous variations came from Mendel's breeding experiments with the garden pea, *Pisum sativum*. Mendal's experiments in garden pea involved contrasting traits such as round vs. wrinkled seeds and axial vs. terminal flowers.[31] Mendel's work established a convincing mechanism for the inheritance of hereditary traits. According to Mendel's theory, hereditary traits are transmitted from parents to offspring through discrete units called "factors" (now known as alleles). Each trait is determined by a pair of factors, one inherited from the male parent and the other from the female. Traits differ in their expression, with some being dominant and others recessive. The combination of factors in a zygote is random, and the expression of traits follows predictable ratios based on the dominant and recessive nature of the factors. These ratios, known as Mendelian ratios, are derived following the rules of probability.[31]

Populations: The units of evolutionary change

Mendelian inheritance patterns soon became essential for studying population characteristics, such as allelic and genotypic frequencies. Mendelian ratios were modified and extended into a mathematical framework known as the Hardy-Weinberg equation, which facilitated the understanding of genetic composition in populations and the development of models to study changes in genetic equilibrium over successive generations.[31] By this time, populations were considered the fundamental units of evolution. As statistical and mathematical approaches expanded, the field of population genetics emerged as a critical and significant branch of evolutionary studies.[31]

Other objections

Evolution through successional changes within a single lineage is called phyletic evolution. Darwin's emphasis on phyletic evolution, i.e., the transformation of a single species into another, invited criticism.[6] Many evolutionists who supported Darwinism disagreed with this view, as it failed to explain the splits and divisions within an ancestral lineage that lead to the emergence of more than one species. Palaeontology also provides evidence supporting the origin of many new species during evolution, rather than the mere transformation of one old species into a new one. Darwin did not address the question of how a newly evolved species could be considered distinct, if it arose solely from gradual transformation. He also failed to explain how a new species could possibly evolve in the same geographical area occupied by the original species. Additionally, he overlooked the role of isolation between groups and the sterility of hybrids, both of which were crucial for maintaining unique adaptations in the process of speciation.[6]

Eldredge and Gould analysed fossil data from various vertebrates and molluscs and observed long periods of fossil uniformity interrupted by brief periods of rapid speciation. They termed these periodic bursts of evolutionary activity as punctuated equilibrium.[35,36] According to Gould, in such cases, the evolutionary trend resembles climbing a flight of stairs rather than rolling something up an inclined plane. Macromutations are probably the cause for the rapid occurrence of speciation, a process referred to as macroevolution. Evolution through punctuated equilibria can be considered a form of macroevolution. Although punctuated equilibrium is often viewed as contrary to Darwin's gradualistic model of evolution, there is now a consensus among evolutionists that both gradual and rapid changes occur during the evolutionary process.[6]

Limitations of natural selection

Darwin and his supporters were unable to provide a precise definition for natural selection. It may be perceived as a virtual phenomenon that deals with the challenges in the survival of an organism. Natural selection acts as an external force on variations, selecting only the favourable ones. But, in the evolutionary concept involving natural selection, the adaptive ability inherent in the organism is not adequately considered as a cause of evolution. According to Strickberger, natural selection can result in the exclusion of a significant number of non-optimal individuals, even in long-established populations.[6] He states, "If we consider genetic perfection as the elimination of all deleteriously inferior gene combinations, there is little doubt that most, if not all, populations are imperfect." The loss of genetic variability due to natural selection may be particularly evident in the early stages of evolution, as selection favours advantageous traits by eliminating individuals with less favourable characteristics. For example, consider the evolution of the giraffe according to the theory of natural selection. The ancestral population of giraffes initially had short necks, and over time, some individuals developed slightly longer necks. These long-necked giraffes were then selected through natural selection. As a result, the short-necked individuals decreased in number, as they were eliminated from the population. In subsequent generations, the long-necked variants became more prevalent, eventually outnumbering the original short-necked ones. This process of eliminating a significant portion of the original population would inevitably lead to a loss of variability within the population.[6]

Another limitation of natural selection is that it addresses challenges in the present environment but cannot predict future advantages. It is also unlikely that natural selection acts simultaneously on multiple traits for a specific purpose; instead, it primarily focuses on individual traits. Evolution is thought to occur incrementally, as chance events which may lead to useful adaptations. Darwin argued that giraffes evolved through gradual accumulation of small, random changes over long periods.[7,13]

Neo-Darwinism

In the first decades of the twentieth century, evolutionists recognized Mendelian heredity as a regular system of inheritance in natural populations and mutations as the source of variation. It appeared to them that Mendelism and Darwinism were complementary and that a synthesis of these two concepts would provide a better understanding of the evolutionary process. This idea came to be known as Neo-Darwinism or the synthetic theory of evolution. Neo-Darwinism views evolution as a consequence of changes in the frequencies of alleles introduced into the population gene pool through mutations. Among the various forces driving these changes, natural selection is considered the most significant, though not the only, factor. Advocates of Neo-Darwinism include R.A. Fisher, Sewall Wright, and J.B.S. Haldane, who developed quantitative models to study the distribution of gene frequencies in Mendelian populations.[7] They analysed the effects of various factors, such as selection, mutation, dominance, epistasis, population structure, and polymorphisms, on gene frequencies. While they arrived at similar conclusions regarding most quantitative aspects of evolution, they held differing views on the mechanisms by which natural selection operates. Neo-Darwinism also allowed for the reinterpretation of many unresolved concepts of Darwinism from the standpoint of genetics.[6,7]

Evolution without natural selection

At the beginning of the post-Mendelian period, evolutionary studies became more scientific and less conceptual due to rapid advancements in genetics. New theories emerged that explained evolutionary mechanisms without the involvement of natural selection.

Genetic drift

Sewall Wright (1889-1988), a renowned population geneticist, for the first time proposed that evolution could occur without selection in small, isolated populations.[37,38] In such cases, chance plays a crucial role in shifting allelic frequencies randomly over several generations, eventually leading to either the fixation or elimination of specific alleles. Since this process operates without selection, it does not take into account whether the alleles involved are beneficial, harmful, or neutral. Genetic drift reduces genetic diversity within a population, as certain alleles may be completely lost. This phenomenon is most effective in smaller populations where mating is random. The "bottleneck phenomenon," occurs when a population experiences a drastic reduction in size due to sudden catastrophic events or natural calamities like floods or droughts.[6] A consequence of such a population crash is a smaller gene pool with potentially different allelic frequencies compared to the original population. A closely related concept is the "founder effect," observed when a small group of individuals from a larger population migrates to a new place or by other means establish a new population elsewhere. The new population often has significantly different allelic frequencies when compared to original population due to the limited genetic diversity of the founding members. Populations shaped by the bottleneck phenomenon or the founder effect are typically smaller, creating favourable conditions for genetic drift to occur.[6]

Neutral theory of molecular evolution

The genome comprises two major components: a functional component and a nonfunctional component. The functional component consists of the coding sequences of nucleotides in genes responsible for protein synthesis and the sequences associated with the spatiotemporal regulation of gene expression. The nonfunctional component includes noncoding DNA, such as introns, tandem repetitive sequences, junk DNA, and transposable elements. Mutations in the functional DNA are often unfavourable or may even be deleterious. Meanwhile, mutations in the nonfunctional DNA do not impose constraints related to any specific function affecting the organism's survival, thereby permitting changes that do not cause deleterious effects. Even within the functional component of DNA, single amino acid substitutions may not always have harmful effects. For example, the human alpha chain of haemoglobin shows 75 differences when compared to the beta chain. Moreover, because an amino acid is specified by more than one codon, a point mutation in the codon of a gene may not always result in amino acid substitution. In such cases, the mutated codon may simply specify the same amino acid as the original codon.[6,31]

Kimura and his collaborators, as well as King and Jukes, independently proposed the neutral theory of evolution. According to this theory, much of the genetic variability in populations arises from mutations that are neutral with respect to selection.[39] Since neutral mutations are not subject to selection, the frequencies of mutated neutral alleles and the fixation of such alleles occur through random genetic drift, provided the conditions for drift are met. As natural selection is not involved in these changes, evolution by this mechanism is often referred to as "non-Darwinian evolution." The neutral theory of molecular evolution is supported by the extensive and widely observed degrees of enzyme and protein polymorphisms. Neutral mutations also explain the accumulation of "junk DNA" in the genome.[39]

Molecular clock and developmental evolutionary biology

Studies involving changes in base sequences of nucleic acids (DNA and RNA) and amino acid sequences in proteins form the foundation of molecular evolution. It has been revealed that proteins evolve at constant rates. Hence, the time scale required for changes in these molecules can be used to construct molecular clocks to estimate divergence times between species. In other words, nucleotide differences in DNA or amino acid changes in proteins between different species can be used to establish molecular phylogenetics.[6] Phylogenetic trees constructed on the basis of such data are found to be quite accurate and often agree with trees established using traditional criteria.

Developmental genes, such as the homeotic genes in *Drosophila*, are known to play an important role in the determination of embryonic cells and pattern formation. Homeotic genes contain a highly conserved sequence of nucleotides known as the homeobox, which is present in many species. The homeobox is also found in mammalian genes, and these genes are referred to as *Hox* genes. Developmental genes, including homeotic genes, have provided significant insights into embryonic development and evolution. A relatively new area of study focusing on the role of developmental genes in evolution is gaining importance, and this field is known as developmental evolutionary biology.[31] Studies on developmental genes may help answer how genes involved in early development contribute to large morphological differences between species. Not much is known about whether altered activity of regulatory genes during embryonic development can drive rapid, large-scale modifications in anatomy and morphology that may provide advantages in a changing habitat, as may have occurred in the evolution of the abnormally long neck in giraffe.[23]

Conclusion

According to Darwin, the giraffe evolved into its present form through the accumulation of individual random changes preserved by natural selection. However, major evolutionary changes due to macroevolution, believed to have occurred in giraffes, may require a comprehensive set of functionally coordinated adaptations.[35] While the elongation of the giraffe's neck has provided certain advantages such as access to food sources unavailable to most other browsers and an improved field of vision, these benefits may not be the reason for its evolution. Despite these advantages, giraffes faced several challenges that necessitated extensive anatomical and physiological modifications. They have successfully overcome these challenges and thrived for the past one million years since their appearance. Such an outcome is plausible only if there is a coordinated blueprint or a more structured framework for evolutionary changes, as these modifications are interdependent. Several pertinent questions remain unanswered. If evolution is a random process, it is unclear how natural selection could be presented with an integrated package of adaptations necessary to produce a highly modified animal like the giraffe.[11] Similarly, how could natural selection favour a modification that requires several corrections or multiple adjustments? Last but not least, considering the vast possible combinations of variations, how can natural selection identify and favour the best? Therefore, given the above-mentioned complexities, it appears that evolution of neck in giraffe cannot be fully explained on the basis of any single theory.

An examination of the history of science reveals several instances where certain theories and concepts, postulated by acclaimed philosophers and thinkers, persisted for long periods and hindered scientific progress. For example, Karl Linnaeus's contributions to taxonomy are invaluable. He developed a system of classification for animals and plants based on morphological similarities and dissimilarities. To support this concept, he proposed that each species has a fixed morphology that does not change, a concept known as the "fixity of species." [40] This may be appealing to taxonomists since classification is done based on the characteristic morphological features of a species. Meanwhile, the very idea of "fixity of species" rules out the possibility of evolution. Regarding Darwinism, the theory of natural selection was proposed without valid scientific evidence and at a time when no information about genetics or hereditary mechanisms was available. As a result, the theory has inherent flaws. It is, therefore, not reasonable to show too much inclination towards a century-and-a-half-old theory to interpret modern findings, particularly those related to evolutionary genetics. Evolutionary biologists must distance themselves from outdated concepts that lack scientific validation and adopt a new framework grounded in modern genetics. Similarly, textbooks for undergraduate and postgraduate students often give undue importance to the pre-modern, classical evolutionary theories. A common example is the use of the girraffe's neck elongation to explain evolutionary theories. While there is nothing wrong with using this example to illustrate these theories, it should not be presented in a manner that implies "one theory is correct, and the other is wrong".

Postscript

The perspectives of the author on certain issues are shared in this paper, which are subject to discussion and debate.

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