

NECK ELONGATION IN GIRAFFES: FOSSIL EVIDENCE AND EVOLUTIONARY PERSPECTIVES

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Abstract

The evolution of the giraffe's remarkably elongated neck has long fascinated biologists and remains one of the most debated examples of morphological adaptation. Two primary hypotheses dominate this discussion: the high-browsing hypothesis and the sexual selection, or "necks-for-sex," hypothesis. The high-browsing hypothesis proposes that neck elongation evolved as an adaptive response to ecological pressures, enabling giraffes to access foliage beyond the reach of other herbivores and thereby reduce interspecific competition during periods of food scarcity. In contrast, the sexual selection hypothesis suggests that elongated necks evolved primarily through male-male competition, as males use their necks and heads as weapons during combat to establish dominance and secure mating opportunities. Fossil records and comparative anatomical studies provide partial support for both hypotheses, indicating that neck elongation occurred gradually and may have served multiple functions over evolutionary time. However, the fossil evidence remains incomplete, limiting definitive conclusions about the primary selective pressures involved. From a theoretical perspective, early Lamarckian ideas emphasized the role of environmental demands and use-based trait modification, while Darwinian natural selection and sexual selection frameworks highlight heritable variation and differential reproductive success as key drivers of morphological change. A synthesis of ecological and sexual selection perspectives suggests that giraffe neck elongation likely resulted from the combined influence of feeding advantages and reproductive competition rather than a single selective force. Such a multifactorial explanation aligns with modern evolutionary theory, which recognizes that complex traits often arise through interacting selective pressures. Despite significant advances in behavioral ecology, paleontology, and biomechanics, important questions remain regarding the functional anatomy, developmental pathways, and energetic costs associated with extreme neck elongation. Further integrative research incorporating fossil data, biomechanical modeling, and behavioral studies is needed to fully resolve the evolutionary origins of this iconic trait.

INTRODUCTION

The elongated neck and limbs of the Giraffe (*Giraffa camelopardalis*) set it apart from other mammals (Williams 2016). Together with its long neck, the

giraffe's long legs greatly contribute to its overall size. A giraffe's height is greatly influenced by these anatomical characteristics, which allow an adult male

to reach an impressive height of five meters (Dagg 2014). The fossil record for the current species is weak, and there are no progressive examples of fossil giraffes with necks that get longer over time (Danowitz, Domalski et al. 2015). The vegetation changed from tropical to open-woodland savannah toward the end of the late Miocene (six million years ago) due to a change in the climate (Janis 1993). This change would have been beneficial to browsers. Because this would have been different in the current giraffe subspecies, more research is required to ascertain how adaptation to this arid climate favored browsers with longer necks and larger mouths (Pretorius, de Boer et al. 2016). The study found that giraffoids have a wider range of headgear than other ruminants, and that intraspecific conflict behaviors that were favored by their environments may have led to the development of unusual head-neck morphologies in various giraffoid lineages (Wang, Ye et al. 2022). Compared to other browsers, giraffes can travel great distances within their home ranges and eat a wider variety of plants (Mills, Bester et al. 1990). Contrasting Darwin's (right) and Lamarck's (wrong) theories of evolution. In order to avoid competition with other mammals during dry spells and to feed on higher vegetation, giraffe ancestors developed longer necks over millions of years. This led to a slow transition from a short-necked animal that resembled an antelope to the long-necked giraffe of today (Holdrege 2005).

Hypothesis of long neck

There are two main theories as to how the long necks of giraffes evolved. One theory holds that giraffes developed long necks in order to browse high in tree canopies (Wilkinson and Ruxton 2012). According to the "necks-for-sex" theory, giraffes evolved as a result of sexual selection between rival males (Simmons and Altwegg 2010). Compared to more curved necks, giraffes' head-neck arrangement places more strain on their vertebrae. In addition to its functional importance for movement, the giraffe's cervicothoracic transition's abnormal shape may be related to the neck's posture because of its excessive length (Müller, Merten et al. 2021).

Like many common classroom clichés, the simple equation "short-necked giraffes + natural selection +

time = long-necked giraffes" is both physiologically and historically incorrect (Switek 2017). Compared to the few species that have been previously documented, allometric exponents seemed unremarkable, suggesting that neck elongation was more significant during evolution than leg elongation (van Sittert, Skinner et al. 2015). According to one theory, known as "sexual selection," their shape changed as males established sexual dominance with their heads and necks. This idea is supported by the fact that males spend more money on head and neck development than females do (Mitchell, Van Sittert et al. 2009).

They had higher survival rates because their longer necks made it simpler for them to reach higher acacia tree levels. The majority of publications portray giraffes consuming acacia trees, erroneously implying that this is their main food source. According to Simmons and Scheepers, this explanation is so compelling that both students of giraffe behavior and evolutionary scientists accept it implicitly (Simmons and Scheepers 1996). Due to interspecific competition and the nutritional demands of pregnancy and lactation, the giraffe's long neck and legs were initially evolved by natural selection to give it a competitive advantage in browsing. Later, male-to-male competition and sexual selection led to an even greater increase in neck mass (Cavener, Bond et al. 2024).

Fossil Evidence of Neck Elongation

The head-to-neck ratios of juvenile and adult giraffes are different. The head hardly doubles in size from juvenile to adult, but the neck grows nearly 4.5× (about four times) longer (Colalillo and Solounias 2023). An osteological study of foetal and adult giraffe vertebrae concluded that substantial cervical lengthening occurs after birth (Van Sittert, Skinner et al. 2010). Despite extensive research on the modern giraffe neck, there is a lack of osteological evidence to support the fossils and the evolutionary changes to the neck. The palaeotragines (c. 12 Ma) exhibited giraffid cervical elongation, according to a study that compared the vertebral lengths of extinct giraffids and contemporary ungulates (Badlangana, Adams et al. 2009).

In order to maintain overall functional integration, specialized adaptations of skeletal components require compensatory changes in other skeletal components. The evolutionary elongation of the giraffe's neck and legs, for instance, involved repositioning the neck to a more posterior position above the forelegs and reducing the trunk in order to preserve balance and locomotion (Mitchell 2021). As is typical of many long-limbed ungulates, particularly giraffes, brachiosaurus could readily lower their necks to feed at shoulder level, drink, and occasionally access desirable food items, albeit with some discomfort (Paul 2017).

The two fossils discovered with giraffes might have been deer or cattle, or other animals with short necks and cloven hooves. Evolutionists estimate that 12–15 million years ago, giraffids with long legs but unelongated necks coexisted with giraffes with short necks and legs (Gaitan 2015). Giraffe epiphyseal plates may have a special ossification and fusion mechanism due to the elongation of the front part of the vertebra (Danowitz and Solounias 2015).

Evolutionary Theories of Neck Elongation

Several evolutionary theories have been proposed to explain the adaptation of the long giraffe neck; however, few studies examine the fossil cervical vertebrae (Danowitz, Vasilyev et al.).

Lamarck's theory

By continuously stretching their necks, giraffes developed longer necks, which they subsequently passed on to their offspring, according to Lamarckian theory (Bergman 2002). Living things' interactions with their environment have a direct impact on how they evolve, according to Lamarck. The evolution of an organ toward greater or lesser complexity depends on whether it is used or not (Quaglio, Fraga et al. 2019). The fact that acquired qualities are not inherited challenges Lamarck's theory (Lönnig 2006). According to Lamarck, a species' physical structures would be altered by use or lack thereof, but it would not become extinct (Kampourakis and Zogza 2007).

He suggested that the giraffe stretched its neck to reach leaves higher up on the branches. The giraffes' current length is the result of many generations of

neck stretching because they grew longer as a result of their frequent neck stretching, and their offspring also had longer necks (Deweese 2005). Lamarckian natural philosophy was considered an example of agapism, or evolution marked by the development of habits, even though it contained some mechanistic elements. However, differentiating between these evolutionary types is more of a classification problem because they are all interrelated (Švorcová, Lacková et al. 2023).

Darwin's theory

The Darwinian perspective is slightly different but more accurate: When competition for leafy plants increased, those early giraffes with slightly longer necks were marginally better able to feed themselves by reaching high-growing leaves (Barash 2015). Lamarck's giraffe is comparable to a Darwinian giraffe, whose populations have continuously included individuals with extremely short necks among giraffes with longer necks (Minelli 2020).

In an ancestral population, there were giraffes with slightly longer necks than their counterparts. Due to their ability to reach higher branches, these giraffes were able to reproduce more successfully because they were able to continue consuming an undiscovered food source, whereas smaller giraffes perished due to competition (Switek 2010).

Between the ancestral and modern giraffes, there had to be more than just variations in neck length (Black). Many people think that the evolution of the giraffe's long neck is a perfect example of forage-competition-based evolutionary biology (e.g., Darwin 1871) (Cameron and du Toit 2007). Darwin's theory is less popular among biologists. Thus, they synthesize the modern synthetic theory of evolution (Neo-Darwinism) as an alternative explanation of sexual and natural selection (Ahad 2011). A peculiar prehistoric giraffe relative, however, suggests that early neck evolution may have been influenced by both fighting and feeding (Tamsiea 2022).

Sexual selection theory

It is believed that the tallest giraffes with the longest necks are the most successful breeders and, therefore, have the best chance of transferring their traits to the next generation (Simmons and

Scheepers 1996). Since females hardly ever do this and only do it with males, it shouldn't be selective in females. This mechanism of sexual selection is not well supported by the fact that, when scaled for gender body size, there are no discernible differences between the necks of male and female giraffes (Bercovitch and Deacon 2015).

Giraffes may be able to engage in high browsing and/or male competitive behaviors due to the increased neck flexibility provided by their unique first thoracic vertebra (Gunji and Endo 2016). No sex differences were found for giraffes with the same body mass (Mitchell, van Sittert et al. 2017). While testing sexual selection-based hypotheses can be difficult, particularly since there is no one reliable method to detect sexual selection, we argue that it is not impossible; in fact, there are now several instances where sexual selection is evidently supported (Knell, Naish et al. 2013). Even if the specific geometric pattern was nonadaptive, reproductive isolation; facilitated by sexual selection and genetic drift; may have solidified regional diversity in unique coat patterns if local populations were constrained in their dispersal and developed unique pelage profiles (Bercovitch and Deacon 2015).

Feeding theory

In the wild, giraffes, both male and female, usually eat at their best rate, which is about 60% of their maximum feeding height (Young and Isbell 1991). A significant number of giraffes' dorso-ventral osteological range of motion is attributed to their long necks, which enable a range of feeding activities. The osteological range of motion for both adult and neonatal giraffes include every feeding position seen in the wild (Vidal, Mocho et al. 2020). Longer necks give giraffes an advantage. They are able to consume the higher branches. Natural selection will favor longer-necked giraffes if this eating advantage enables them to survive and procreate slightly better than shorter-necked giraffes (Kottak 2000).

By expanding the feeding envelope, neck elongation is thought to have increased feeding efficiency and produced trophic niches that other herbivores could not access (Bates, Mannion et al. 2016). Despite being categorized as a leaf-dominant browser, the

giraffine *Bohlinia attica* can browse on higher foliages than *H. duvernoyi*. All things considered, the reconstructed diets lend credence to the notion that heavier grazing practices are linked to smaller premolars, but not to higher dental crown height (Merceron, Colyn et al. 2018).

Conclusion

The evolutionary development of the giraffe's neck remains a complex topic with interrelated explanations. Darwinian selection supports high browsing advantages, while sexual selection emphasizes male competition. Fossil evidence suggests gradual cervical elongation, though gaps remain. Juvenile and adult skeletal structures indicate significant postnatal neck growth. Contrasting Lamarckian and Darwinian theories illustrate broader evolutionary debates. Despite recent insights, uncertainties about ecological and sexual selection interplay persist. Future research should explore genetic, developmental, and functional aspects to refine our understanding of this unique evolutionary trait.

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