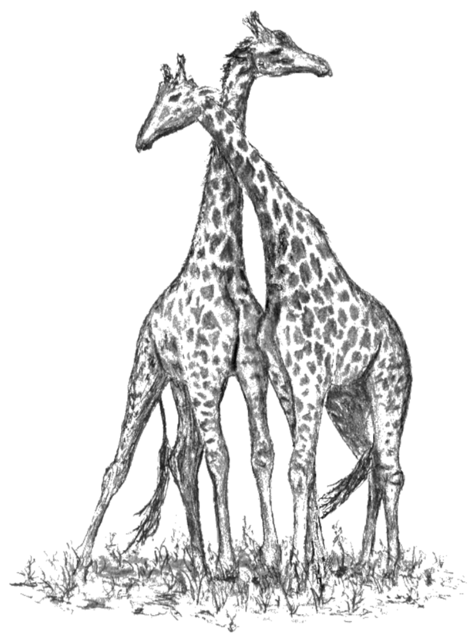
The
Giraffe's Long Neck

From Evolutionary Fable to Whole Organism



Craig Holdrege

Nature Institute
Perspectives
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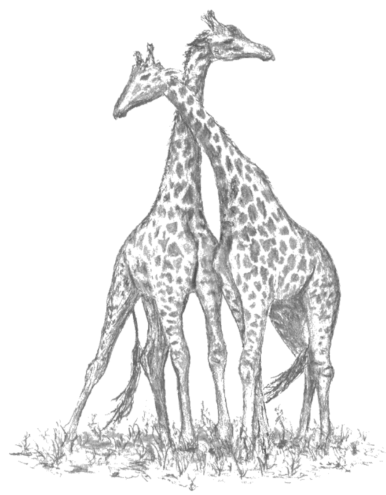

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Contents

Acknowledgments

My studies of the giraffe have extended over a good number of years. A 2002 trip to Botswana, where I was able to observe giraffes again and again, brought new focus to my interest in the giraffe. This monograph is the result of the ensuing work.

As part of my research I spent numerous hours in museums observing and measuring bones. My thanks to *Jean Spence* at the American Museum of Natural History in New York and *Michi Schulenberg* at the Field Museum in Chicago for facilitating my visits to these great collections.

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Introduction

A lone giraffe bull stood at the edge of the scrubby bush forest that opened into a grassland. It was August, the beginning of spring, but also the middle of the dry season in the southern African savannah. The grasses and forbs were yellowed and brittle. Many trees and bushes had no leaves, though some still bore fruit, and others were just beginning to flower.

The giraffe didn't seem bothered by our presence, although we were off the main tourist track. We were quite close and its towering height was striking. Long narrow legs carried its barrel-shaped, beautifully brown-and-white patterned body high above the ground. Its back sloped downward, extending into the tail with its long strands of wavy hair that nearly reached the ground. Towards the front the body took on more bulk and sloped steeply upward, merging into the massive, skyward-reaching neck.

From its lofty perch, the giraffe watched us calmly with dark, bulging eyes. It was not excited, nor was it aggressive. When it turned its head to face us directly, we could see fine, out-curving eyelashes encircling attentive eyes.

We observed the animal for a good while. It was feeding, but not on the leaves of trees and bushes, which we'd grown used to seeing giraffes eat. There were no trees or bushes within its reach, and its head was not lowered to the ground grazing. But it was chewing on a hearty meal, part of which was sticking out of its mouth. Imagine a giraffe smoking a giraffe-sized cigar and you get an inkling of the scene. The giraffe's meal was a sausage tree fruit,[1] which really does look like a sausage (or an over-sized cigar). Sausage trees hang full of them at this time of year. They are about one to two feet long, two to three inches in diameter, and can weigh up to twenty pounds.

About six inches of the fruit were protruding, so the other foot or so was in the giraffe's mouth cavity. Chewing with circling motions of the lower jaw, every now and again the giraffe would raise its head in line with its neck and gulp, as if trying to swallow the fruit. But the fruit never moved. We were concerned that it might be stuck, since, at the time, we didn't know that giraffes do eat these fruits during the dry season. But the animal didn't look concerned and was apparently in no rush; with a sausage fruit as its meal it didn't need to wander around. I don't know how long we were there, but eventually we moved on, wondering whether the giraffe succeeded in getting the long fruit through its long mouth and down into its long throat.

Everything about the giraffe seems built around lengthening—from its tail hairs to its long eyelashes, from its long legs to its long neck and head. Coming across a giraffe embodying elongation to the fullest in eating that long fruit of a sausage tree, was an unexpected gift.

* * *

In the 1980s I taught a college-preparatory high school course on evolution in Germany. Although I was teaching at an independent Waldorf school, the curriculum for the final year of high school (thirteenth grade) had to conform to state guidelines. One of the topics involved comparing and contrasting

1. The sausage tree (*Kigelia africana)*, a member of the Jacaranda family (Bignoniaceae) to which trumpet vine and catalpa belong, grows in southcentral and southeastern Africa.

Lamarck's view of evolution (the wrong one) with Darwin's (the right one). An expedient way to do this was to use the giraffe and its long neck as an example. How would Lamarck and Darwin each explain how the giraffe's neck evolved? Textbooks sometimes discussed this example, so I had the material I needed to introduce, explain, and finish off the problem of Lamarckianism versus Darwinism in one three-quarter-hour session, with a review in the next class. Since I was always under time pressure to cover all the material, this example was efficacious and had the added advantage that it stuck in the students' minds.

I don't know how many times I taught this example, but I do remember that both the students and I had a hard time taking it too seriously. It was clear, at least in a subterranean way, that the giraffe was just a handy convenience to make a theoretical point. With knowing smiles, we moved on to more serious matters.

In too willingly following authority ("the curriculum"), I had not taken Lamarckianism seriously enough and had hardly given the giraffe the time of day. I was teaching about a caricature—not about the giraffe and not about evolution. How could I possibly teach about an animal's evolution if I knew next to nothing about that animal and was only using its long neck to make a point? When I think about this today, I have to cringe and extend my inner apologies to my students at that time, to Lamarck, and, of course, to the giraffe.

It may be that a need for redemption later led me to become fascinated with the giraffe and to study it in much greater detail. This booklet is a result of that study. In essence, it is a conversation in three parts. Chapter 1 begins with a conversation with evolutionary ideas about the giraffe's long neck. In Chapters 2 and 3, I converse with the giraffe itself. And in

Chapter 4, the conversation returns to the question of evolution, but from the perspective of the giraffe as an organism.

My aim in undertaking such a study was to gain a comprehensive picture of the giraffe. One facet of the work was to look more carefully into the "textbook" explanation of how the giraffe evolved its long neck. The story goes something like this: giraffe ancestors evolved, by chance, somewhat longer necks, a characteristic that allowed them to feed on higher vegetation, and avoid competition with other mammals during droughts; this increased their survival rate so that over millions of years a short-necked antelope-like creature evolved gradually into today's long-necked giraffe. When you compare this standard story with the reality of giraffe biology, behavior, and ecology, it soon becomes clear that the story does not hold water. Neither do attempts to explain the giraffe's unique form by appealing to other Darwinian survival strategies. In a sense, Chapter 1 clears away the layers of oversized thickets that have hidden the giraffe—despite its long neck—from view for so long.

The inadequacy of attempts to explain the giraffe makes clear why we need to study an organism more thoroughly *before* we begin to interpret its evolution. It's all too easy to craft a tight and coherent explanation of something if the something one is explaining is not the thing itself but a reduced, already theory-adapted take on the phenomena.

Chapters 2 and 3 form the core of what I call a whole-organism study. All scientific inquiry is guided by ideas, and I have chosen a very broad idea to guide my study—the idea of organism. We all know that in an organism, be it an amoeba, a dandelion, an earthworm, or a giraffe, all parts and functions are interconnected and work together within the context of the whole creature. When some part of an organism functions in isolation or out of context, we know something is wrong (such as when we have a nervous twitch, or when a beaver in a zoo gnaws repetitiously on the metal barrier of its enclosure). In a healthy organism, the parts always stand in meaningful relation to the whole. Or we could also say, the whole lives in and through the parts (cf. Bortoft 1996).

But to know *that* this is the case is not to know concretely *how* it is the case. I wanted to get to know the giraffe as an organism—its unique features within their specific context. So the guiding idea of the organism has been, in fact, a question: Can you show me, giraffe, how you are a unified and integrated creature?

The problem with such an undertaking is that in gathering data about the giraffe (or any other organism) we take it apart. We look at its blood circulation, its feeding behavior, its fossil record, its skeletal morphology, its mating behavior, and so on. Moreover, all of these areas of investigation have their own methodologies, assumptions, and biases that one has to get to know. The danger is that we end up with manifold parts considered from varying perspectives while the animal as a whole—the basis of the entire undertaking—has slipped unnoted between our fingers.

It is an extra step, one not usually taken in science today, to attend to how and in what way the *parts* one discovers are actually *members* of the whole organism, to use Kurt Goldstein's terms (Goldstein 1939/1995; especially chapter nine). This is the holistic approach I take in Chapters 2 and 3. I portray and, I hope, paint a rich picture of the giraffe and its characteristics. If I give you a glimpse into the giraffe's unified nature—its unique way of being and how it lives in its world of the African savannah—then I will have succeeded. I know all too well that I have only begun to penetrate the surface of deeper connections that hold sway in the giraffe. But this beginning is itself immensely satisfying and has important implications for the way we think about evolution.

In Chapter 4, I return to the question of giraffe evolution, but now against the background of its biology as a whole organism. The evidence from the fossil record is intriguing, but alone cannot solve the problem of giraffe evolution. The biggest issue, once we have gathered as many facts as we can, is how we think—how to adequately conceive of—evolution as a process. The whole-organism perspective makes it clear that the organism itself has essentially been left out of most thinking about evolution, replaced by genes and survival strategies. But if we're only talking about the evolution of genes and strategies, then we're talking about abstractions and not reality. Bringing the organism itself back into our thinking about evolution makes everything more complex, not a welcome message if the goal is to have a neat conception of things that works and subsumes all the facts. But if we want to touch reality with our ideas, then we will be happy to acknowledge that getting to know a creature like the giraffe in an intimate way entails confronting and breaking through the limitations of our conceptions. In fact, what could be more exhilarating than seeing before us a long path, just asking to be trod, leading further into such a deep and complex matter as the nature of an organism and its evolution?

Chapter 1

Evolutionary Stories Falling Short

(or Why Evolutionary Science Needs a Holistic Foundation)

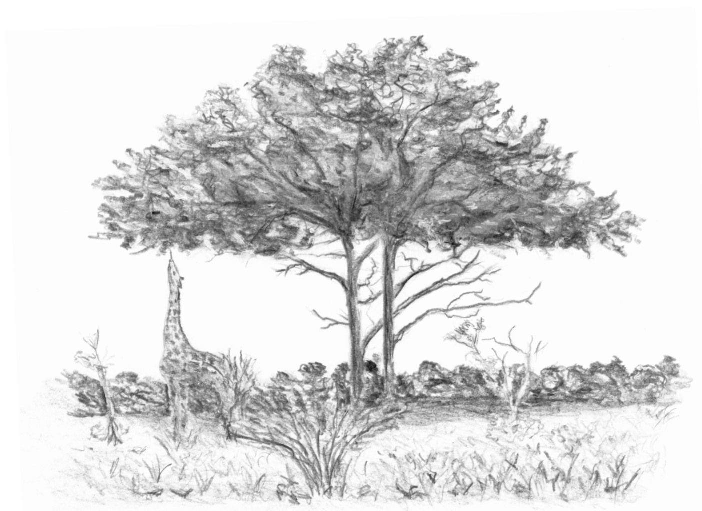


Figure 1. Giraffe in a "classic" feeding position, extending its neck, head, and tongue to reach the leaves of an acacia tree. (Tsavo National Park, Kenya; drawing by C. Holdrege after a photo in Leuthold and Leuthold 1972.)

Lamarck and Darwin

Once scientists began thinking about animals in terms of evolution, the giraffe became a welcome—and seemingly straightforward—example. It is as if the giraffe's long neck were begging to be explained by evolutionary theorists.

One of the first evolutionary thinkers, Jean-Baptist Lamarck, offered a short description of how the giraffe evolved in his major work, *Philosophie Zoologique*, published in 1809:

> It is interesting to observe the result of habit in the peculiar shape and size of the giraffe: this animal, the tallest of the mammals, is known to live in the interior of Africa in places where the soil is nearly always arid and barren, so that it is obliged to browse on the leaves of trees and to make constant efforts to reach them. From this habit long maintained in all its race, it has resulted that the animal's forelegs have become longer than its hind-legs, and that its neck is lengthened to such a degree that the giraffe, without standing up on its hind-legs, attains a height of six meters. (Quoted in Gould 2002, p. 188)

In Lamarck's view, we must imagine a situation in the past, in which the best food for browsing mammals was higher up in trees, the lower vegetation having been eaten by other animals. The ancestors of the giraffe—which we should imagine like antelopes or deer—needed to adapt their behavior to this changing environment. As Lamarck wrote, "Variations in the environment induce changes in the needs, habits and modes of life of living beings…these changes give rise to modifications or developments in their organs and the shape of their parts" (quoted in Gould 2002, p. 179). So Lamarck imagined that over generations the habit of continually reaching for the higher browse produced in the giraffe's ancestors a lengthening of the legs and neck.

A little over sixty years later, Charles Darwin commented on giraffe evolution in the sixth edition (1872) of his seminal book, *Origin of Species*:

> The giraffe, by its lofty stature, much elongated neck, fore-legs, head and tongue, has its whole frame beautifully adapted for browsing on the higher branches of trees. It can thus obtain food beyond the reach of the other

> Ungulata or hoofed animals inhabiting the same country; and this must be a great advantage to it during dearths…. So under nature with the nascent giraffe the individuals which were the highest browsers, and were able during dearth to reach even an inch or two above the others, will often have been preserved; for they will have roamed over the whole country in search of food…. Those individuals which had some one part or several parts of their bodies rather more elongated than usual, would generally have survived. These will have intercrossed and left offspring, either inheriting the same bodily peculiarities, or with a tendency to vary again in the same manner; whilst the individuals, less favoured in the same respects will have been the most liable to perish…. By this process long-continued, which exactly corresponds with what I have called unconscious selection by man, combined no doubt in a most important manner with the inherited effects of the increased use of parts, it seems to me almost certain that an ordinary hoofed quadruped might be converted into a giraffe. (Darwin 1872, pp. 177ff.)

In many respects this is a classic formulation of how Darwin viewed evolution: every species consists of individuals that show considerable variations. Under certain environmental conditions particular variations will be most advantageous. Natural selection weeds out the unadapted and the better adapted survive. These variations become dominant in the species and so it evolves. In the case of giraffes, times of drought and arid conditions give an advantage to animals that can out-compete others by reaching the higher, untouched leaves. They form the ancestral stock of the animals that evolve into giraffes.

Interestingly, Darwin also believed in the "inherited effects of the increased use of parts." Evidently, he thought that repeated use by giraffe ancestors of their somewhat longer necks to reach high vegetation would increase the likelihood of the longer neck being inherited by the next generation. Darwin felt this was key to explaining evolution, since it provides a mechanism for anchoring a novel trait in the hereditary stream. Otherwise a new characteristic might arise in one generation and disappear in the next. This kind of "Larmarckian" view—that the activity of the organism affects its evolution—may have made sense to the founder of Darwinism, but it is certainly not a popular idea among mainstream Darwinists today.

The Long Neck as a Feeding Strategy

The idea that the giraffe got its long neck due to food shortages in the lower reaches of trees seems almost self-evident. The giraffe is taller than all other mammals, can feed where no others can, and therefore has a distinct advantage. To say that the long neck and legs developed in relation to this advantage seems compelling. Why else would the giraffe be so tall? You find this view presented in children's books, in website descriptions of the giraffe, and in textbooks.

But because this explanation is widespread does not mean it is true. In fact, this "self-evident" explanation retains its ability to convince only as long as we do not get too involved in the actual biological and ecological details. Various scientists have noticed that this elegant picture of giraffe evolution dissolves under closer scrutiny. Here are a few examples of my and their objections.

1) Since the taller, longer-necked, evolving giraffe ancestors were also larger and heavier, they would need more food than

the animals they were competing with. Wouldn't this counterbalance their advantage in times of dearth? Would they really have any advantage over smaller members of the same or other species? Moreover, it is absurd to assume that *only* the leaves on high branches were available to the giraffe during a drought. Had this been the case, the multitude of browsing and grazing antelope species in Africa would all have gone extinct (or never evolved in the first place). So even without growing taller the giraffe ancestor could have competed on even terms for those lower leaves.

2) Male giraffes today are up to one meter taller than female giraffes; newborn and young giraffes are much smaller. As this sexual dimorphism manifested in the evolution of the giraffe, the males would have been able to reach the higher branches. Under conditions of food shortage, females and young animals would have died, and the species would have gone extinct (Pincher 1949).

3) If giraffes evolved by eating high foliage during times of drought and maximal competition for food, one would expect that giraffes today do the same in similar circumstances. Males do usually feed at greater heights than females, but the results of one study show a surprising spread (Ginnett and Demment 1997). Male giraffes fed nearly half of the time at heights of almost five meters, that is, in the "classical" long-necked giraffe posture. In stark contrast, females fed around seventy percent of the time at belly height or below, which the theory demands they should not be doing. These researchers did not report on the seasons in which they made these observations, so their results are of little help in discerning whether, for example, males feed at greater heights mainly during droughts.

A variety of other studies show that giraffe feeding habits vary according to place and time (reviewed in Simmons and

Figure 2. Giraffe feeding at about shoulder height—the most prevalent height at which giraffes feed. (South of Moremi Game Reserve, Botswana; drawing by C. Holdrege.)

Scheepers 1996). The best "fit" to the theory comes from a study in Niger (Ciofolo and Le Pendu 2002), where giraffes coexist in an agricultural habitat with cattle and humans. There, giraffes feed above the height that cattle can reach, and males usually feed at a height of over four meters while females feed at heights between two meters (neck horizontal) and four meters (neck fairly upright).

In East Africa, giraffes have been studied quite extensively (Leuthold and Leuthold 1972; Pellew 1984). They move seasonally, and in the dry season tend to seek out lower valley bottoms and riverine woodlands. There they usually feed from bushes at or below shoulder height (about two and one half meters in females and three meters in males). Fifty percent of the time they feed at a height of two meters or less, which overlaps with the feeding zone of large herbivores such as the gerenuk and the kudu (see Figure 2). During the rainy season, when there is abundant browse at all levels, giraffes are more likely to feed from the higher branches, browsing fresh, protein-rich leaves. Other studies also show that giraffes do most of their feeding at about shoulder height, with their necks positioned nearly horizontally (Young and Isbell 1991; Woolnough and du Toit 2001).

So the studies indicate that most giraffes are not using their long necks the way the theory demands. And they use them even less to reach heights in the dry season, when the theory demands they should need them most!

4) There are other ways to reach the high foliage of trees. Goats, for example, are known to climb into trees and eat foliage (see Figure 3). Why didn't tree-climbing leaf-eaters (folivores) develop in the savannah? They would have had the advantage of feeding at all levels easily and been in that respect more adaptable than the highly specialized giraffe. The long-necked gerenuk, an antelope, often stands on its hind limbs and browses, reaching heights of two meters and more. The much larger and heavier elephant even stands sometimes on its back legs and extends its trunk to reach high limbs—but no one thinks that the elephant developed its trunk as a result of selection pressures to reach higher food.

In summary, there is nothing in these observations that shows a compelling link between leg and neck lengthening and feeding on high limbs. Just because giraffes have long necks and long legs and *can* reach food high in the trees does not mean that a need to reach high browse was a causative factor in the evolution of those characteristics. Evolutionary theorist Stephan Jay Gould (1996) as well as giraffe researchers Graham Mitchell and John Skinner (2003) reach a similar conclusion. Mitchell and Skinner state, "The presumptions of historical unavailability of browse and of browse bottlenecks as the selective pressures for neck and limb elongations are highly doubtful and probably false" (p. 69).

Figure 3. A goat does not require a long neck to feed on twigs and leaves of an oak tree. (Drawing by C. Holdrege after a photo in Butzer 2000.)

Clearly, both Darwin's and Lamarck's conceptions of giraffe evolution were highly speculative. The idea that giraffes developed longer legs and necks to reach higher food seems plausible, even compelling, as long as we do not (1) think the idea through to its logical conclusion and (2) take into account essential observations of giraffe behavior and ecology. In the end, the idea is neither compelling nor based on fact.

Alternative Explanatory Attempts

Pincher (1949), after critiquing Darwin's explanation, suggests that the "most extraordinary feature of the giraffe is not the length of the neck but the length of the forelegs." By developing long legs, the giraffe has acquired a huge stride so that it can move relatively fast for its size, which has left the giraffe with only one predator—the lion. Pincher therefore explains the "excessive length of its forelegs as the effect of natural selection acting continually through the hunter-hunted relationship, as in the case of hoofed mammals generally." The neck, in turn, followed the lengthening legs so that the giraffe could still reach the ground to drink.

It is strange that Pincher is able to critique Darwin's view so clearly and yet doesn't recognize that he is proposing the same type of inadequate explanation. The giraffe ancestor could just as well have developed greater bulk or more running muscles, both of which would have aided in avoiding predators. The fact is that despite its size and long stride, the giraffe is still preyed upon by lions. And as one study of one hundred giraffes killed by lions in South Africa showed, almost twice as many bulls were killed as cows (Pienaar 1969; cited in Simmons and Scheepers 1996). The longer stride of bulls evidently doesn't help them avoid lions better than the shorter legged females. Who knows whether their long stride may in some way make them more vulnerable? Another speculative idea into the wastebasket.

Brownlee (1963) speculates that the lengthening of the limbs and neck gives the giraffe a relatively large surface area, which should allow it to dissipate heat. This would be advantageous in the hot tropical climate since the largest animals would have been best able to survive heat waves, so natural selection would encourage the tendency toward lengthening.

As in the other suggested explanations, the central question is whether Brownlee's idea is rooted in reality. Because of its long legs and neck, the giraffe appears to have a large surface area. But surface area alone is not important; it is the relation of the heat-producing volume to surface area that is crucial. A small animal has a small body volume in proportion to its surface area, while in a large animal the volume is proportionally large.[2] The giraffe is a very large animal with a barrel-shaped torso. Although its neck is long, it is also voluminous; only the lower parts of the legs, which carry relatively few blood vessels, would act to enlarge the surface area substantially. Krumbiegel (1971) estimates that the ratio of volume to surface in the giraffe is 11:1, compared, say, to a smaller, long-necked antelope, the gerenuk, which has a ratio of 4.7:1 (similar to the human). In other words, despite appearances, the giraffe still has a very large volume in relation to its surface area and its unique form provides no grounds to think that it evolved in relation to dissipating heat.

More recently, Simmons and Scheepers (1996) proposed that sexual selection caused the lengthening and enlarging of the neck in males. These scientists relate their ideas to known facts and concrete observations—a happy contrast to the other hypotheses we've discussed. They describe how male giraffes fight by clubbing opponents with their large, massive heads; the neck plays the role of a muscular arm. The largest (longest-necked) males are dominant over other male giraffes and mate more frequently. Therefore, selection works in favor of long necks. This explanation would also account for why males have not only longer, but proportionately heavier heads than females.

This hypothesis seems consistent with the difference between male and female giraffes. At least it gives a picture of how the males' longer neck can be maintained in evolution. But it doesn't tell us anything about the origin of neck length-

2. Assuming for the sake of explanation a spherical body, the two-dimensional surface grows as a function of the square of the radius, while the volume—being three-dimensional—grows as a function of the cube of the radius. Therefore the proportion of volume to surface area grows as a function of the radius. For example, a sphere with a radius of 2.5 cm (about one inch) has a volume-to-surface ratio of 0.8:1. A much larger sphere with a radius of 50 cm (about twenty inches) has a volume-to-surface ratio of 16.7:1.

ening in giraffes per se—the neck has to reach a length of one or two meters to be used as a weapon for clubbing. How did it get that long in the first place? Moreover, the female giraffe is left out of the explanation, and Simmons and Scheepers can only speculate that female neck lengthening somehow followed that of males. In the end, the authors admit that neck lengthening could have had other causes and that head clubbing is a consequence of a long neck and not a cause.

Does the Giraffe Really Have a Long Neck?

All the above explanations of the evolution of the giraffe's long legs and long neck are unsatisfying. Each of the scientists sees problems in other explanations, but remains within the same explanatory framework when putting forward his own hypothesis. No one sees the necessity for stepping outside the framework and looking at the difficulties of the overall approach. In each case the scientist abstracts individual features (long neck, long legs, large surface area) and considers them in isolation from the rest of the organism. The individual feature is then placed into relation to *one* purported causal factor in the environment (drought, heat, predator avoidance, male competition). The link of individual feature to environmental factor is supposed to explain the evolution of that feature.

But this procedure is highly problematic. The giraffe's neck carries out a variety of functions—it allows feeding from high branches, serves as a weapon in males, brings the head to elevated heights that give the giraffe a large field of view, is used as a pendulum while galloping, and so on. Virtually all structures and organs in the animal body are multifunctional and interact dynamically with other multifunctional structures and organs. When we pick out a single function and focus solely on it to explain a multifunctional organ, the explanation can only be inadequate. It is comparable to believing you have accurately portrayed a richly nuanced, multicolored landscape with charcoal. It just does not work.

I sometimes wonder why no one has maintained that the giraffe has, in reality, a *short* neck. If you observe a giraffe drinking, or, as they occasionally do, grazing close to the ground, then you know what I mean (see Figure 4). Giraffes do not drink often, but when they do, they have to either splay their forelegs to the side or bend them strongly at the wrist joint. Both procedures take time and are awkward. But only in this way can the giraffe get the tip of its mouth down to the surface of the water. Looked at from the perspective of drinking, the giraffe has a short neck. Antelopes and zebras reach the ground without bending their legs, and the long-legged elephant has its trunk to compensate for its short neck. Only the giraffe and its rain forest relative, the okapi, have necks so short relative to their legs and chest that they must splay or bend their legs.

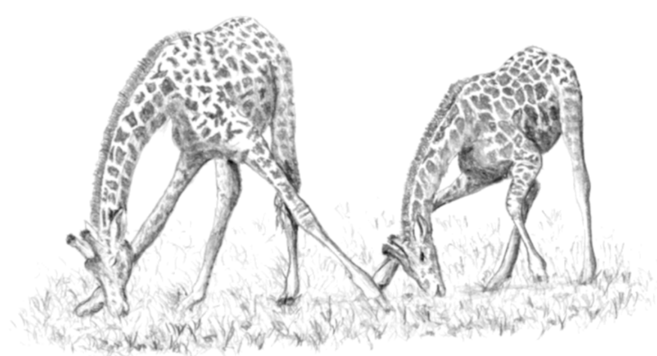


Figure 4. "Short-necked" giraffes grazing. Giraffes can reach the ground with their mouths to drink or graze only by splaying their front legs (left) or splaying and bending their forelegs (right). (Drawing by C. Holdrege after a photo in Dagg and Foster 1982.)

So why hasn't the giraffe become famous for its manifestly short neck? Why don't we have evolutionary hypotheses explaining how the giraffe got its short neck? The reason is that the giraffe's neck, in other respects or from other perspectives, *is* long. No other mammal has such a long neck in absolute terms or in relation to the length of its torso. We all have seen (in life or in pictures) and been amazed by the standing giraffe, its long neck sailing skyward, in comparison to which the ungainly, short-necked drinking giraffe appears a most unfortunate creature.

Whether the neck is long or short depends on our perspective and on the behavior or anatomical context we are focusing on. We understand the giraffe only when we take various perspectives and let it show different aspects of its being. The moment we focus solely on the long neck—and on it solely in terms of a food-gathering or some other strategy—we've lost the reality of the giraffe.

Reality is richer than such explanations. The explanation may be in and of itself coherent and logical, but what it explains is not the thing itself but a specter of it—the isolated aspect that has been abstracted from the whole organism. In reality, the organism as a whole evolves; all its parts are multifunctional, facilitating its interactions with its complex, changing environment. If we don't consider all partial aspects within this larger context, we can only have inadequate explanations void of life.

Another consequence of the usual way of explaining is that the organism itself is atomized into individual characteristics, each having its own explanation. Each part takes on a quasi-reality of its own, while the whole organism—which brings forth and gives coherence to the parts—degenerates into a kind of epiphenomenon, a mere composite of the surviving parts that "really" count.

In summary, the whole project of explaining the evolution of an animal by abstracting from the whole leads to unsatisfying, speculative ideas on the one hand, and to a conceptual dissolution of the unity of the organism on the other. A more adequate understanding requires that we first investigate the organism as a whole and how its members interrelate and interact within the context of the whole organism and its environment. This holistic understanding can then form the *starting point* for thinking about the evolution of the animal. The evolutionary biologist Dobzhansky's famous statement that "nothing in biology can be understood except in the light of evolution" (1973) is a grand claim, which I believe is, in the end, true. But we have a lot of work to do before we get there, and we should not be satisfied with short-cut evolutionary "explanations."

If evolutionary thought is to have a solid foundation, we must firmly ground it in holistic understanding. As it is, stories of the evolution of traits seem compelling until you look for their context and foundation in the world and discover a pool of quicksand. As Simmons and Scheepers remark about Darwin's idea of giraffe evolution, "It may be no more than a tall story."

Chapter 2

The Unique Form of the Giraffe

First Context—The Giraffe as an Ungulate

> [In Africa] there lives an animal which the Greeks call Camelopardalis, a composite name which describes the double nature of this quadruped. It has the varied coat of a leopard, the shape of a camel and is of a size beyond measure. Its neck is long enough for it to browse in the tops of trees.

This is one of the first written descriptions of the giraffe, penned about 104 BCE by a Greek scholar, Agatarchides (quoted in Spinage 1968a, p. 41). During the Roman era and in

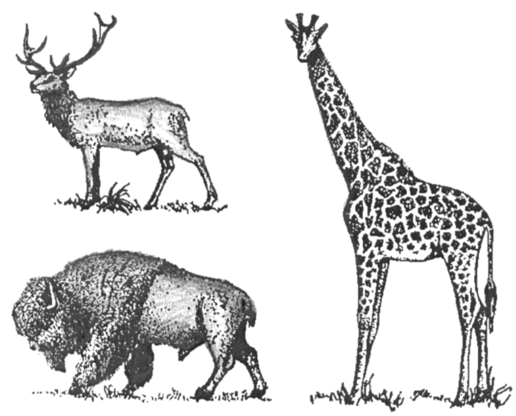


Figure 5. Despite their divergent morphologies, the elk (wapiti), bison, and giraffe all belong to the group of the even-toed, ruminant hoofed mammals. (Slightly altered, from Schad 1977, p. 177.)

Persia and Europe of the Middle Ages, the giraffe was variously described, but always as a composite creature. So Abu Bakr Ibn al-Fuqih around 906 CE:

> The Giraffe has the structure of a camel, the head of a stag, hoofs like those of cattle and a tail like a bird. (Quoted in Spinage 1968a, p. 54)

In 1759, the giraffe received its scientific name *Giraffa camelopardalis*. Starting around this time and extending through the nineteenth century, natural historians (they weren't yet called scientists) in England, France, and Germany undertook detailed comparative studies of the anatomy and morphology of animals. It was the golden age of comparative anatomy. On the one hand these natural historians wanted to gain an exact picture of the physical structure of every known animal and, on the other hand, they were interested in patterns and order in nature. Animals may contrast greatly in external shape and appearance but on closer examination reveal similarities in body plan and anatomical structures.

Despite its odd shape and great size, comparative anatomists recognized that the giraffe clearly belonged to the hoofed mammals, the ungulates. They had discovered two main groups of ungulates: the even-toed or cloven-hoofed (Artiodactyla—bovines, pigs and hippos, deer, antelopes, and camels) and the odd-toed (Perissodactyla—horses and zebras, rhinos, and tapirs). Since the giraffe's feet end in two toes, it was easily identifiable as a member of the Artiodactyla and it was found to share even more characteristics with the deer and cattle (bovid) families. To name a few: it has a four-chambered stomach and chews its cud (ruminates); it has horns; and it has no incisors or canine teeth in the upper jaw.

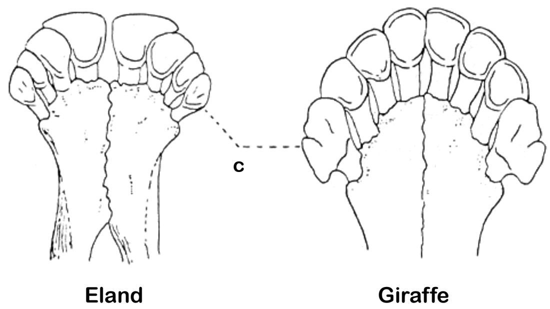


Figure 6. The lower jaw of the giraffe and the eland (a large African antelope), viewed from above. The large canine (c) in the giraffe has two lobes, a characteristic that only members of the giraffe family possess. (From Grassé 1955, p. 661.)

But the giraffe also has characteristics that distinguish it from the deer and cattle families, so that it is placed within its own family within the ruminant ungulates. For example, the giraffe's horns are skin-covered and lie above the parietal bones, unlike either cattle horns or deer antlers. Another important diagnostic feature is the lower canine, which in giraffes has two lobes, clearly distinguishing it from the single-lobed canine in all members of the deer and cattle families (see Figure 6). Unlike the deer and cattle families, which are diverse and species-rich, the giraffe family has only two living members—the giraffe and the okapi of the African rain forest (which we'll learn more about later).

Knowing that the giraffe is a ruminant, even-toed ungulate provides one starting point for understanding it better. But this knowledge has to become more than simply fitting the giraffe into an abstract biological scheme. Qualitatively, the more you know about the characteristics of the giraffe and of other ungulates—antelope, zebra, buffalo, etc.—and learn to view the characteristics in relation to each other, the more the different animals begin to illuminate one another. The unique characteristics of the giraffe speak all the more strongly when viewed in the light of its zoological relatives. The long (or short) neck, the long legs, the large eyes, the particular gait—all become expressions of the unique creature we are trying to understand.

From the perspective of comparative anatomy, the giraffe is in no way a "composite" creature. Like every other living being, it has its own integrity. But the giraffe is also part of a larger web of relations that allow us to understand it better. In the giraffe we find the characteristics of ruminant ungulates evolved in a singular fashion. It is this singularity within its broader contexts that I hope to illuminate.

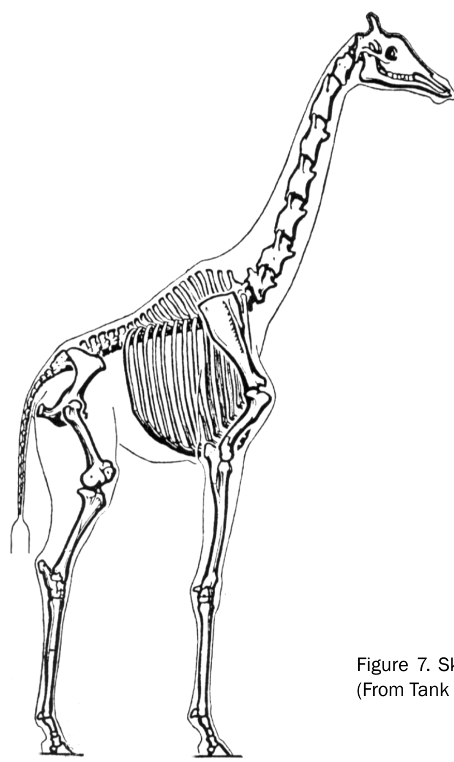


Figure 7. Skeleton of a giraffe. (From Tank 1984, p. 111.)

Soaring Upward

Charles Darwin identified a key to open up a holistic understanding of the giraffe when he remarked on its "lofty stature, much elongated fore-legs, head, and tongue." It's not only the giraffe's neck that is long. We find remarkable elongation in other features.

The Legs

The giraffe has the longest legs of any animal. The ungulates are typically (but not always—think of pigs and hippos) long-legged mammals. This elongation arises primarily through lengthening of the lower (distal) part of the fore- and hind legs (see Figures 7 and 8). Compared with the human skeleton, the ungulates stand on their tiptoes, which are covered with a hoof

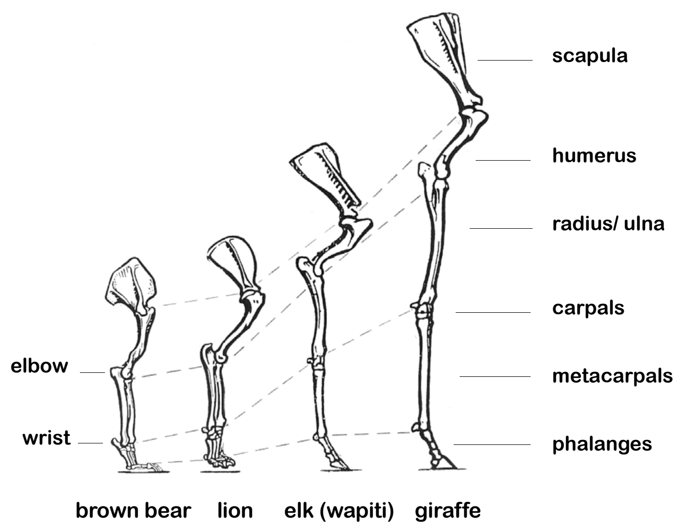


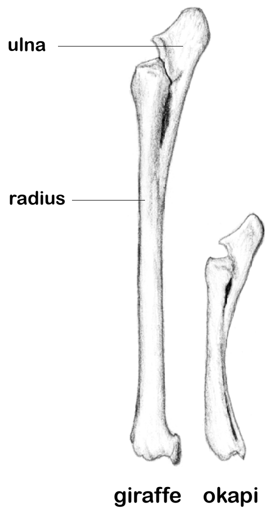
Figure 8. The foreleg of different mammals; the humerus in each animal has been drawn to the same length. This comparison shows that the lengthening of the giraffe's foreleg is most pronounced in the lower (distal) segments of the leg: radius/ulna and metacarpals. (Original figure; drawings of individual legs from Tank 1984.)

(thickened toenail). The bones of the toes and feet are very long so that the heel (hind legs) and wrist (forelegs) are high off the ground. The lower leg bones (ulna and radius in the front; tibia and fibula in the back) are usually fused and long. The elbow (front) and knee (back) joints are high up, so that the relatively short upper (proximal) leg bones (humerus in the front; femur in the back) are taken up into the body.

The giraffe takes the lengthening of the leg bones to an extreme. The adult giraffe's heel, for example, can be one meter above the ground. The impression of lengthening is emphasized even more because the form of the upper part of the leg remains visible, which is not the case in most other ungulates. In zebras, deer, and antelopes the upper part of the leg is hidden from view by a flap of skin that reaches from the knees and elbows to the torso. The upper leg appears to be part of the torso. Since the giraffe does not have this flap of skin (neither do the relatively long-legged and long-necked camels and llamas), the upper leg is clearly visible.

The giraffe's leg bones are not only long, but also straighter and more slender than those of other ungulates (van Schalkwyk et al. 2004), increasing the character of upright lengthening (see Figure 9). Normally in mammals, when the limb bones lengthen they also become proportionally larger in diameter. But this is not the case in the giraffe. The diameter of the limb bones is smaller than it "should" be. The giraffe compensates for its slender bones by making them sturdier and reducing the diameter of the marrow cavity (see Figure 10).

In all ungulate species except the giraffe, the rear legs are longer than the forelegs. The giraffe, in contrast, has slightly longer forelegs than hind legs. Stephen Jay Gould (1996) and, more recently, Mitchell and Skinner (2003) claim that the giraffe's forelegs only appear to be longer than the hind legs.



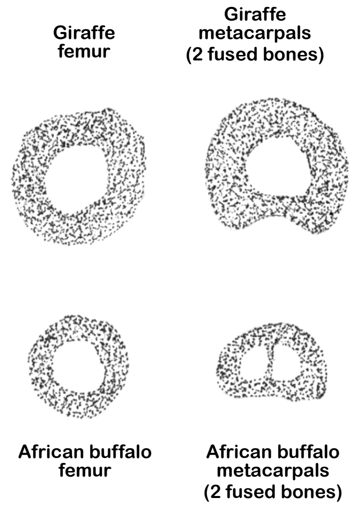


Figure 9. The ulna and radius in the giraffe and okapi, drawn to scale. These two bones are part of the lower leg and fused together. Functionally they form one stable bone. The giraffe's radius is especially straight and sleek in form. Total length of actual bones: 93 cm in the giraffe and 50 cm in the okapi. (Drawing by C. Holdrege.)

Figure 10. Cross sections of the femur and metacarpals in the giraffe and the African buffalo (*Syncerus caffer*). Both animals weigh about the same. See text for further description. (Drawing after photo in van Schalkwyk et al. 2004, p. 313.)

But when one measures the lengths of the individual bones of the forelegs and the hind legs, the forelimbs are clearly longer (see Table 1 and also Colbert 1935). It is not a matter of "mere appearance." The tendency toward lengthening is stronger in the front part of the body.

The length of the forelegs is accentuated by the fact that the humerus rests fairly upright on the vertically oriented lower leg (the fused ulna and radius). In other ungulates the humerus is more horizontally inclined. This vertical orientation is continued into the very long and narrow shoulder blade (scapula).

Similarly, the hind leg—though not as long—has a fairly upright femur. Although the giraffe's pelvis is relatively short, it is, characteristically, oriented more vertically than in other ungulates. Thus the limbs of the giraffe are not only longer in absolute terms, but the bones' vertical orientation increases their upward reach even more.

Table 1. These data show that the giraffe's forelegs are longer than its hind legs. The length of the three longest bones in the forelimb and hind limb were measured in a total of 21 specimens; in all cases the forelimb was longer than the hind limb.

Source of Data	Harris (1976)*	Holdrege (original)
Sample size	14 specimens from Kenya National Museum, Nairobi	7 specimens from the American Museum of Natural History, New York
Sex	all males	male, female, unknown
Length of forelimb bones (humerus, radius, metacarpus)	mean: 210 cm (range not reported)	mean: 192 cm (range: 177 cm to 210 cm)
Length of hind limb bones (femur, tibia, metatarsus)	mean: 196 cm (range not reported)	mean: 180 cm (range: 167 cm to 193 cm)
Length difference	mean: 14 cm (range not reported)	mean: 12 cm (range: 6 cm to 17 cm)
Ratio of forelimb length to hind limb length	107.1: 100	106.7: 100

* The data from Harris 1976 were modified to give the length of the radius and not the combined length of the radius and ulna, which he reports. The proximal end of the ulna extends on average 11 cm beyond the proximal end of the radius (my data), which articulates with the humerus. This amount was subtracted from his reported radius/ulna lenghts in order to give a truer picture of overall limb length.

The Neck

The neck follows the same principle as the legs—upright lengthening (cf. Kranich 1995, pp. 138–46). It is an astounding fact that all mammals (with just two exceptions, the sloth and the manatee) have seven neck (cervical) vertebrae. Birds with long or short necks have varying numbers of neck vertebrae, but not mammals. Whether the neck is very short (dolphins) or long (giraffe), there are seven cervical vertebrae. In the virtually neckless dolphin, the seven neck vertebrae have fused to make one short bone that links the head to the torso. Neck lengthening in mammals is achieved through lengthening of the individual neck vertebrae. This is, again, taken to an extreme in the giraffe. In the adult male an individual neck vertebra can be over 30 cm (12 inches) long! Although its limbs are already so long, the giraffe has a significantly longer neck in relation to its limbs than other mammals (see Table 2).

In comparison to other ungulates, the giraffe's neck vertebrae are not only longer, but also more uniform in shape

Table 2. Neck length (seven cervical vertebrae) is given as a percentage of limb length (three longest bones of each limb, excluding phalanges). The giraffe's neck is proportionately much longer in relation to the limbs than that of the okapi and elk, even though the giraffe has longer legs than any other mammal.

Species	*Length of neck relative to length of forelimb (forelimb = 100)*	*Length of neck relative to length of hind limb (hind limb = 100)*
Elk	66.4	55.2
Okapi	62	61.4
Giraffe	84.7	91.3

(Note: Sample size was seven specimens of each species; each specimen was measured and the mean length in each group of seven was used to establish the ratios; original data.)

(Lankester 1908; see Figures 11 and 12). The sixth neck vertebra in other ungulates has a unique shape that sets it apart from the other neck vertebrae. But, as Lankester observed, in the giraffe it is very similar to the third, fourth, and fifth neck vertebrae. The seventh neck vertebra in the giraffe is also similar to the rest, while in other ungulates the seventh cervical has become like the first thoracic (rib-carrying) vertebra. Moreover, the first true thoracic vertebra in the giraffe articulates with the vertebrae in front of and behind it in the manner of a *neck* and not a thoracic vertebra. More recently, Solounias (1999) found that the shape of the first rib-carrying vertebra in the juvenile giraffe is virtually identical to that of the seventh neck vertebra in the adult or juvenile okapi. In addition, the confluence of nerves that serve the shoulder and foreleg (brachial plexus) forms around the first rib-carrying vertebra in the giraffe and around the seventh neck vertebra in the okapi.

These seemingly esoteric anatomical details are eminently revealing. The first rib-carrying vertebra in the giraffe has, in effect, become an eighth neck vertebra. In other words, the tendency to form neck vertebrae extends down into the torso of the giraffe, while in other ungulates the tendency to form thoracic vertebrae extends up into the neck. In the giraffe, the neck has truly become a dominant element in the formation of the spine.

This dominance is also visible in the "extraordinary" development (as the eminent nineteenth century comparative anatomist Richard Owen put it) of the primary ligament of the neck, the ligamentum nuchae. In mammals, this elastic ligament extends from the head over the neck to the neural processes of the vertebrae between the shoulders. It helps support the head and neck, anchoring them to the torso, and at the same time its elasticity

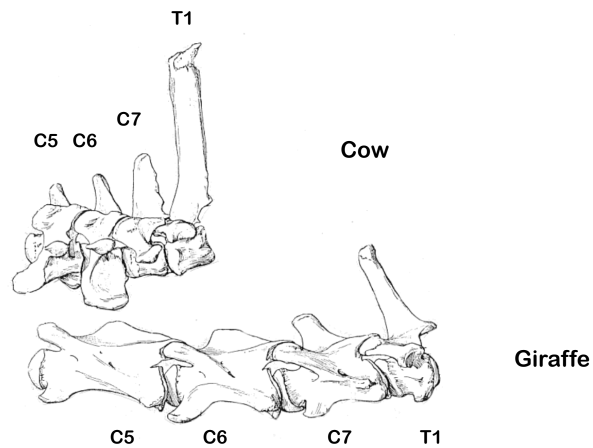


Figure 11. The last three neck (C5, C6, C7) and first thoracic or rib-carrying vertebra (T1) in the domestic cow and the giraffe. The giraffe's neck (cervical) vertebrae are both long and uniform in shape. (From Lankester 1908, pp. 321 & 323.)

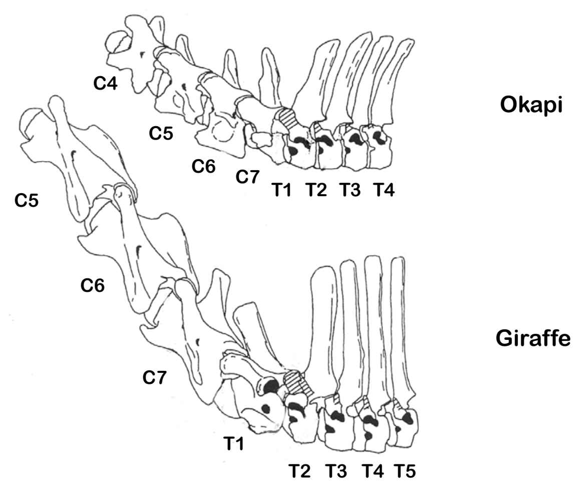


Figure 12. The last neck and first thoracic vertebrae of the okapi and giraffe. In the giraffe, the first thoracic vertebra (T1) has essentially become part of the neck. (Slightly altered from Solounias 1999, p. 264.)

allows movement of the head and neck. It is most developed in longer-necked mammals, so it is not surprising that it becomes the dominant spinal ligament in the giraffe. What astounded the comparative anatomists of the nineteenth century in their investigations was that the ligament in giraffes also has striated fibers, that is, muscle-type fibers that allow active contraction (as opposed to the fibers in other ligaments, which contract only in response to previous stretching). Describing this ligament, anatomist J. Murie allows himself to express his awe in an otherwise quite dry anatomical study:

> For several reasons this most remarkable body of contractile tissue has been looked upon with the eye of wonder as well as curiosity. Its immense length, volume, and resiliency give it a conspicuous character, added to which it is unique in the ultimate fibre being striated. (Murie 1872)

Since the giraffe's enormous neck is involved in every movement of the body, this unique ligament that is also a muscle plays a key role in the giraffe's ability to finely adjust the position and movement of its neck. (See also Chapter 3.)

The dominance of the neck becomes drastically apparent when one compares the length of the neck to the length of the body (thoracic and lumbar part of the spine). The giraffe's neck is 129 percent of the length of the body, while in the white-tailed deer it is 48 percent and in the horse 52 percent (Slijper 1946). This extreme difference is related not only to the lengthening of the giraffe's neck, but also to the shortening of its body. The giraffe's sacrum—the last section of the vertebral column before the tail—is, for example, very small and short.

Table 3. Length of the limbs as a percentage of body length (thoracic/lumbar spine); i.e., length of the body equals 100. The bison's limbs are about the same length as its body, while the giraffe's are more than twice the length of its body. (Data from Slijper 1946)

Species	*Length of forelimb relative to body length (length of body = 100)*	*Length of hind limb relative to body length (length of body = 100)*
Bison	93.5	113.8
Elk	121.5	151.1
Giraffe	225.5	210.0

In other long-necked mammals, such as the horse and zebra, the camel, the llama, or the gerenuk (a very long-necked African antelope), the body is relatively long and horizontally oriented. These mammals also have relatively long legs. Only in the giraffe, where neck and leg elongation is taken so far, do we find a correlative *shortening* of the body (see Table 3). As Goethe suggested,

> We will find that the many varieties of form arise because one part or the other outweighs the rest in importance. Thus, for example, the neck and extremities are favored in the giraffe at the expense of the body, but the reverse is the case in the mole.… Nothing can be added to one part without subtracting from another and vice versa. (Goethe 1795; in Miller 1995, pp. 120–121.)

The shortness of the giraffe's torso is accentuated by its diagonal orientation. The neck seems to continue down into and through the body into the legs, whereas in other longer-necked ungulates, the horizontal orientation of the body is clearly demarcated. In the giraffe, the body appears as a continuation of the neck. The contrast between the stringently horizontal spine of an elk (wapiti) and the upward sloping spine of the giraffe vividly illustrates this difference (see Figure 13).

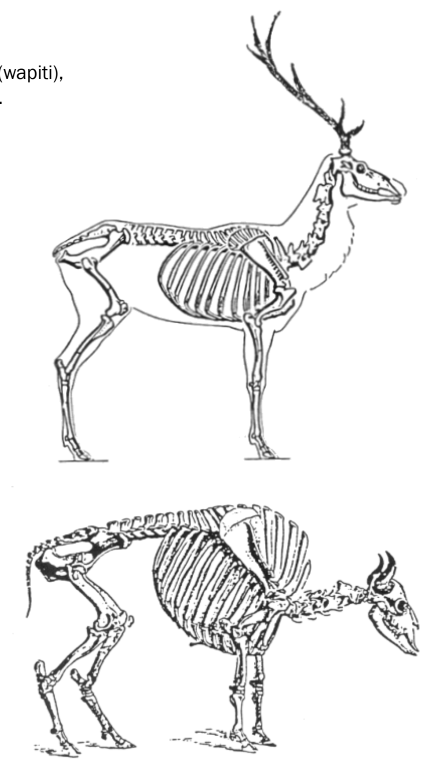
A Comparison

We can learn a great deal about formative tendencies and how different characteristics are interconnected in shaping an animal by carefully comparing the skeletons of the bison, the elk, and the giraffe shown in Figure 13. The bison has especially short forelegs, a downward sloping thoracic spine and holds its

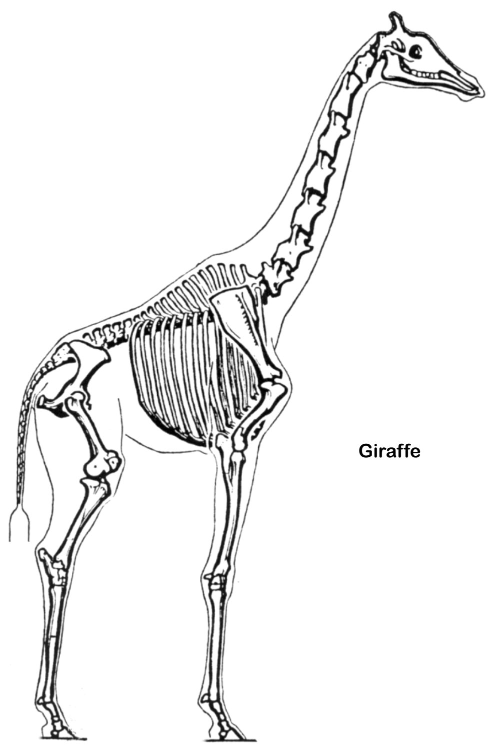
Figure 13. Skeletons of the elk (wapiti), bison, and giraffe, drawn to scale.

Elk (Wapiti)

Bison



head close to the ground. The elk has longer legs and a longer neck that allows the head to rise above the height of the body and also to reach the ground. The bison's limb bones are about the same length as its body, while the elk's limbs are twenty (foreleg) to fifty (hind leg) percent longer than the body (see Table 3; body length is measured as the sum of the length of the thoracic and lumbar regions of the spine). The giraffe's legs are more than twice the length of its body and its neck no longer mediates easily between reaching up and down as in the elk. Its head remains primarily at or above the height of the shoulders, just as the bison's head remains below shoulder height.



Giraffe

The bison's head is held low to the ground, and its rib cage also slopes toward the ground. The neck connects to the body at about the level of the joint between the humerus (upper leg bone) and the shoulder blade. In the elk, with its horizontal spine, the neck attaches higher up, at about the middle of the shoulder blade. Finally, in the giraffe, the neck attaches at the top of the long shoulder blade. From this already substantial height, the neck soars upward. In other words, the giraffe's neck gains increased height by its high origin in the body.

This relation between neck and body sheds light on why, from the perspective of reaching the ground and drinking, the giraffe has a *short* neck. If its forelimbs were shorter and its neck originated lower down, say, closer to the top of the humerus, it would be able to reach water without splaying its legs. It could drink straight-legged like other "reasonable" mammals. But then it would no longer be a giraffe! You cannot have a soaring neck and expect it to reach the ground as well. It is the configuration of the whole body that gives the giraffe such a great height, to which its long neck contributes. But this very configuration makes the giraffe's neck *short* when it returns from the heights to make contact with the earth and water.

The Head

The head also reveals a tendency toward lengthening. A male giraffe's skull can be about 60 cm (two feet) long. The jaws are long and slender; the front part is specially elongated and there is a large gap (diastema) between the molars and the incisors in the lower jaw (see Figure 14). Just as the legs lengthen primarily in the end-most (distal) members, so also does the

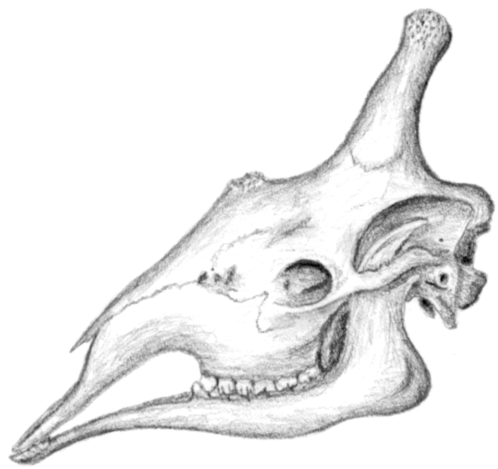


Figure 14. Side view of the skull of an adult giraffe from Botswana. Probably a male because of its large size (length of skull: 72 cm [29 inches]) and the massive horns. (Specimen #24290 from the American Museum of Natural History, New York; drawing by C. Holdrege.)

skull. In his study of giraffe anatomy, Richard Owen remarked on "the prolongation and extensibility of the hair-clad muzzle.... The form of the mouth of the Giraffe differs from every other ruminant...in the elegant tapering of the muzzle" (Owen 1841, pp. 219–220).

The joint between the skull and the neck is also uniquely formed in the giraffe, allowing the giraffe to extend its head upward in line with the neck. In this way the giraffe reaches even greater vertical heights.

The tongue puts the finishing touch on lengthening. It is long, slender, and flexible and can extend forty to fifty cm (16–20 inches) *beyond* the mouth (see Figure 15). So when we read that a giraffe is four or five meters high, we must remember that it can expand this length another meter by raising its head and extending its tongue.

Figure 15. A captive giraffe reaches with neck, head, and tongue to gather browse. (Photo by Mark Riegner.)

What Counts: The Configuration of the Whole

When we say that the giraffe has a long neck, and perhaps add that its legs are also long, we're not saying anything false. But such statements suggest that everything else in the giraffe is "normal" (i.e., "typical ungulate") and the long neck is just a matter of extension. In this vein biologist Richard Dawkins writes,

> If an okapi mutated to produce a giraffe's neck it would be … a stretching of an existing complexity, not an introduction of a new complexity. (Dawkins 1996, p. 103)

Dawkins is arguing that one could imagine, fairly simply, the evolution of an okapi-like animal into a giraffe, since this would be just a matter of altering a pre-existing organ. But what he overlooks is that the configuration of the whole animal—in relation to the long neck—is altered. You cannot simply get a giraffe by elongating an ungulate ancestor's neck. The whole animal is differently configured. The "story" is elegantly simple, but has little to do with reality. Long legs and long neck are only the two most glaring instances of what we discover to be an overall formative principle in the giraffe—vertical lengthening, which we also see in the head, tongue, and in the way the neck attaches to the body. This tendency correlates with a shortening in the horizontal (short body and pelvis)—and even these shortened parts become more vertically oriented than in other ungulates. The giraffe soars upward.

Mediating Extremes: The Giraffe's Circulatory System

When you survey the scientific literature on giraffe biology, you come across a large number of articles on its circulatory system. Scientists have long thought that the giraffe's large body, long legs, and long neck must place special demands on its circulatory system. As the title of one article asks, "How does the giraffe adapt to its unique shape?" (Mitchell and Skinner 1993).

One phenomenon that has long fascinated scientists is the giraffe's high blood pressure—at the level of the heart nearly twice that of most other mammals (see Table 4). This pressure is continuously and actively modulated and maintained by the rhythmical contractions of the heart's muscular walls (especially the thick-walled left ventricle) and other large arteries below the level of the heart. The primary internal sense organ for perceiving changes in blood pressure in mammals (the carotid sinus) is located not far from the heart in the carotid artery of the neck, which brings most of the blood to the head.

The giraffe's carotid sinus is highly elastic and finely innervated with sympathetic nerve fibers (Kimani and Mungai 1983, Kimani and Opole 1991). We must imagine that through this internal sense organ the giraffe's body can perceive blood pressure fluctuations and then, through changes in heart rate, dilation of vessels, etc., finely modulate its blood pressure in the whole circulatory system.

There are large pressure differences in different parts of the giraffe's body (see Table 4). The pressure is, on average, remarkably high in the giraffe's lower legs and near average (for mammals) in the head and upper neck. One primary factor in this pressure gradient between head and limbs is the giraffe's great height and the effects of gravity that come with having such a large body. Think for a moment of the giraffe as a column of fluid: the pressure in the legs would be much higher than the pressure in the head, just by virtue of the weight of the fluid itself. (Imagine the pressure we feel in our ears at the bottom of a 10-foot-deep pool, where we have a 10-foot-high column of water resting on us. The higher the column is, the greater the pressure, which is called gravitational or hydrostatic pressure.) An animal has to deal with such physical forces. And because of its great vertical length, hydrostatic forces play a more significant role in the giraffe's life than they do, say, in the life of small animals or even large animals that are essentially horizontally oriented.

But the giraffe is not a static column of fluid; it is a living, active being. Its blood courses through the body and the body itself changes its positions (standing with raised neck, neck lowering, lying, etc.) and moves at varying tempos. When the giraffe moves, its blood pressure fluctuates radically. For example, each time its forefeet hit the ground while running, the arterial blood pressure (measured in the neck) drops rapidly

Table 4. Blood Pressure in the Giraffe

Height (in meters)	*Hydrostatic pressure in a water column (mm Hg)*	*Mean arterial pressure in Giraffe (mm Hg)*	*Venous pressure in Giraffe (mm Hg)*
4: level of head	0		
3.5: upper neck	40	100 (+/-21)	16 (jugular vein)
3			7 (jugular vein)
2: heart level	150	185 (+/-42)	0 (right atrium)
1: ankle joint			
0: lower foot	300	260 (range 70 to 380)	150 (range: -250 to +240)

This table shows that the giraffe's blood pressure varies significantly depending on the height of the body part in which the measurements are taken (left column) and whether the blood was flowing through an artery (third column) or a vein (fourth column). The pressures in a four-meter-high standing column of water are given as a comparison (second column).

Scientists generally express blood pressure in millimeters of mercury (mm Hg). Mercury, a metal, is a very dense fluid at room temperature, so the pressure of 1 mm Hg is equal to that of a 13.6 mm high column of water. If you want to know the pressure at the bottom of a column of water expressed in mm Hg, you measure the height in millimeters and divide the number by 13.6. Most of us are used to stating blood pressure with two numbers, such as 120/80, which is a typical blood pressure in a resting human, with the first number expressing the higher pressure when the left ventricle contracts (systolic pressure) and the lower number expressing the lower pressure when the left ventricle relaxes (diastolic pressure). Scientists often use, for simplicity's sake, only one number, the mean arterial pressure, which is simply halfway between systolic and diastolic pressures.

Even taking into account that the blood pressure in a resting animal can vary greatly, measurements of blood pressure in giraffes suggest that the mean pressure is significantly higher than in most other mammals. The mean arterial pressure at the level of the heart in a standing giraffe is 185 mm Hg (±42; Mitchell and Skinner 1993). In contrast, the mean arterial pressure (resting) in mammals as different as cattle, dogs, and mice is between 100 and 120 mm Hg. In humans the average mean pressure is 100 mm Hg.

Note the large blood pressure oscillations in the giraffe's feet, which arise when it walks and runs. Arterial pressure in the feet can go from 70 to 380 mm Hg while the venous pressure in the feet varies between minus 250 (!) and plus 240 mm Hg. These extreme changes pose a major riddle.

Sources for data: Hargens et al. 1987, Mitchell and Skinner 1993.

(van Critters et al. 1966, Warren 1974). Even during normal walking, blood pressure in the feet varies significantly (Hargens et al. 1987). Evidently, the dynamics of the giraffe's circulation are intimately related both to its overall vertical length and to the movement of its limbs.

So what happens when the giraffe brings its head down to ground level to feed or drink? We know that pressure in the neck artery rises significantly, but backflow of blood to the head through the jugular vein is prohibited by valves that close when the head sinks below body level. But how the giraffe prohibits too much arterial blood from rushing to its brain and then maintains constant blood flow to the brain when again it lifts its head four meters high after drinking, remains a riddle. Biologists have long wondered why a giraffe doesn't get dizzy or faint when it lifts its head. (Think of our tendency to black out when we get up rapidly after lying down.) There is some evidence that vessels below the head constrict when the giraffe raises its head, keeping blood from dropping away (Mitchell and Skinner 1993). But one thing is sure: giraffes lift their heads rapidly and show no signs of dizziness or fainting. They maintain their quiet, attentive demeanor.

The center of the circulatory system, the giraffe's heart, lies high above the ground (about two meters). Only the elephant has an equally elevated heart. But, in contrast to the elephant, the giraffe's blood courses from the heart another two meters upward through the long neck vessels to the head and back again. The giraffe's heart, therefore, mediates a much larger vertical span than in other mammals, whose dominant orientation of blood flow is horizontal. In the giraffe, as we have come to expect, vertical orientation predominates. This is even mirrored in the shape of the heart itself, which can be over two feet long (!) and is positioned fairly upright within the chest cavity. In contrast, the massive heart of the elephant is much more compact and nearly as broad as long, indicative of its compact body.

In the 1950s, South African scientists did autopsies on a few adult wild giraffes (Goetz et al. 1955). They examined the hearts and found them to weigh between 11 and 13 kg (around 25 lbs). If one takes the average weight of an adult giraffe to be between 800 and 1,000 kg, the heart weight makes up about 1 to 1.5 percent of the giraffe's total body weight, considerably higher than in most mammals. For example, in the bison, which weighs about the same as the giraffe, the average heart weight is 6.5 kg (or 0.65 percent of its total body weight).

What's interesting is that the few measurements that have been made of heart weights in captive (zoo) giraffes suggest that the heart may be on average significantly smaller in zoo animals, weighing around 4 to 7 kg. In "fact sheets" about the giraffe in books and on animal and zoo websites, you often find the description of the large heart and then the interpretation (stated as though it were a fact) that this is because the heart has to pump so much blood "uphill" to the brain.[3] But if zoo giraffes have on average hearts that are comparable in size to those of other large mammals and are significantly smaller than in wild giraffes, this explanation falls by the wayside. The task of pumping blood uphill would present the same challenge to wild and to captive giraffes.

As we have seen, the giraffe's blood pressure and blood flow fluctuate strongly in relation to activity. In contrast to most

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3. There is an ongoing controversy in the scientific literature about the flow of blood to the brain and just how much pressure is actually needed to get the blood to the brain. I will not touch upon that unsolved problem here. (See the articles by B. S. Brook, Henry Badeer, James Hicks, Alan Hargens and T. J. Pedley in the bibliography.)

captive giraffes, which move very little, wild giraffes spend most of their days wandering through the savannah. One can easily imagine that the heart—as a muscular organ—responds to that greater activity by growing larger than in zoo giraffes. A larger heart means not only a larger muscle to maintain and modulate blood pressure, but an increase in the heart's volume as well, allowing more blood to flow through the heart (as happens in well-trained human athletes). We can think of the "big-hearted" giraffe as the giraffe moving through its wild natural habitat.

The special nature of the giraffe's circulatory system is further revealed in morphological and functional differences found above and below the heart. Its lower leg arteries have tiny openings and proportionately very thick muscular walls (see Figure 16). We must imagine that these vessels are continuously counteracting high gravitational pressure, with their muscular walls acting as a kind of "limb heart" that modulates pressures in the legs. This effect is increased by the tight skin of the legs that helps prevent swelling (edema), which would occur were the vessels thin-walled and embedded in a loose, expandable matrix.

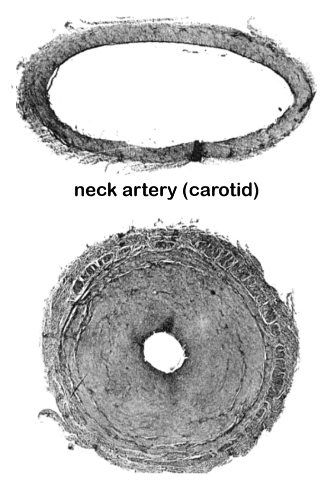


Figure 16. Cross sections of a neck artery and a lower leg artery in the giraffe. Both arteries have the same outer diameter. (From Goetz and Keen 1957, p. 552.)

Above the heart, different relations reign. In contrast to the leg arteries, the neck arteries, such as the carotid artery, have wide openings, and are thin-walled and elastic. While the leg vessels carry fairly small amounts of blood—the lower legs and feet are virtually skin, tendons, and bones—the neck arteries bring large amounts of blood to the head. They also do not actively contract, as do the leg arteries; rather, they take in the pulsations created by the heart and gradually even them out (the so-called "windkessel" effect). Blood flow and pressure become even more uniform when the blood spreads into a network of tiny blood vessels below the brain called the carotid rete mirabile. As a result, the arterial blood flow to the head is much steadier than the pulsating flow in the lower part of the body.

The brain needs—and receives—a constant, steady, and even flow of blood despite changing conditions. The radical fluctuations observed in blood flow and pressure in the lower legs is unthinkable in the brain, which can easily be damaged when, through injury or disease, it receives too little blood even for a short time. From a physiological perspective, the brain is the organ than needs the greatest degree of constancy. (It swims, for example, almost weightless in cerebrospinal fluid and thus is not subject to gravitational forces.) Although the giraffe's head is perched so much higher above the heart than in other mammals, the average arterial pressure in the neck beneath the brain is about the same as in other mammals. Evidently, this pressure is needed to help maintain constant blood flow to the brain.

The contrast in the circulatory system between the neck and head on the one hand and the legs on the other is mirrored in the bony structures of these body parts. The leg bones are the densest bones in any four-legged animal, dealing the most with gravity in carrying the animal's weight. Carrying the body so high above the ground, the giraffe's long, sleek legs are subject to special strains. Just as the leg arteries have small openings and thick walls, the leg bones gain strength by laying down extra bone and reducing the size of the marrow cavity within the bones. This makes the bones stable, but they remain sleek, since the overall diameter remains small. In contrast, the long neck vertebrae are much less dense. A kind of expansive lightness extends into the elevated head: the weight of the giraffe's skull is about half that of the skull of a cow with nearly the same body weight (König 1983). Through its lofty head, with its senses of sight and hearing, the giraffe opens itself to the broader surroundings that its long and sturdy legs carry it through.

Chapter 3

The Giraffe in Its World

In the Landscape

There is nothing like seeing a giraffe in its natural habitat—dry savannah grassland with both loose stands of trees and thickets of thorny bushes. When a giraffe moves across an open grassland, you can see it from far away. It is conspicuous like no other animal. After spotting an individual or group of giraffes in Botswana, I would take my binoculars to view more closely. Invariably I found the giraffes already looking at me (or at least at the Land Rover I was perched in). The giraffe has the largest eyes among land mammals. Since its eyes are set at the sides of a head that rises four to five meters above the ground, the giraffe has a very large field of view. It is keenly aware of moving objects in its visual field. In viewing the giraffe from afar, you have the impression of a lofty creature sensitive to the happenings within its broad horizon.

When you leave the open grassland and wind your way slowly through wooded and bush areas, you often come upon giraffes at very close distance without any preparation. Among trees, the giraffe seems to disappear into its habitat—a stark contrast to its visibility in the open landscape. At least two features of its appearance allow it to blend in this way. First, with its long upright legs from which the neck branches off at an angle, the giraffe's form follows the lines of the tree trunks. When as observers we are close to the ground looking horizontally, what we see (or rather overlook until they are very close) are the narrow legs that meld in among the many trunks of the acacia or mopani trees. The second factor is the giraffe's uniquely patterned coat. Despite the variety of coat patterns in different populations and subspecies of giraffes, all have in common the brown (varying from reddish to black) patches separated by white spaces or lines. When a giraffe is among trees, this dark-light pattern is similar to the mottled pattern of brightness and shade that plays among the branches and leaves. So with its unique shape and coat pattern, the large giraffe recedes into its wooded environment.

It is also the case that the giraffe does not make much noise, either while feeding (browsing off the trees and bushes) or after it notices you. It may stand and watch you from on high for a moment, swing its head and neck around and then amble off. Rarely it makes a snorting sound during such encounters, but

Figure 17. A lone giraffe walks across an opening in the savannah of Botswana. (Photo: C. Holdrege.)

that is usually the limit of its minimal aggressiveness. In contrast, an elephant may tread silently, but it snaps off branches while feeding, and trumpets loudly and makes a mock charge when surprised.

Sensing

With its "lofty stature" (Darwin), the giraffe commands a large overview. It's not surprising that the sense of sight plays a dominant role in the giraffe's life. It can see fellow giraffes, and also predators such as lions, from far away. The giraffe's vision is keen—as already mentioned, a giraffe usually sees you before you see it. Experiments in captivity indicate that giraffes also see colors (Backhaus 1959).

As we might expect, vision plays an important role in communication between giraffes:

> Staring seems to be a favorite form of giraffe communication. There are what look to human observers like hostile stares, come-hither stares, go-away stares, there's-an-enemy stares. When giraffes spot lions in the grass, a steadfast gaze alerts dozens of other giraffes that may be scattered over a square mile of savanna. Giraffe mothers stare at other adults to warn them away from calves. (Stevens 1993, p. 10)

The dominant role of vision goes hand-in-hand with a reduction in importance of the sense of smell, so central in most other mammals:

> The sense of smell recedes in importance and is limited to scents in rising air currents…. The unique body of the giraffe causes the sense of smell to play such a small role.

> Scent-marking of territory falls away … [and] scent glands are lacking. Extensive visual communication compensates the lack of olfactory communication. Tail movements serve as signals. (Krumbiegel 1971, p. 52)

With its body high off the ground and the head resting even farther up on the long neck, the giraffe distances itself from the rich world of smells near the ground, a world in which most other mammals are immersed. It is a telling fact that the end of the giraffe's nose and muzzle is dry, in contrast to the moist nose and muzzle of most other ruminants.

Recently, researchers have discovered that giraffes communicate with infrasound—very low tones inaudible to the human ear (von Muggenthaler et al. 1999). It's not yet clear how they use this capacity in the wild. But observations in zoos show that when some giraffes are kept inside and out of view of other giraffes that are outside, they communicate with infrasound. The visible cue for a human observer is when the giraffes throw back the head and neck, extending the head upright. At this moment they create the deep tones and immediately thereafter the giraffes outside react. Sometimes the head and neck throws are also accompanied by "a 'shiver' or vibration extending from the chest up the entire length of the trachea" (ibid.). It may be that air moving up the neck is producing the infrasound tones.

Other large mammals, such as the elephant and rhino, as well as the giraffe's nearest relative, the okapi, are known to produce infrasound. Since these animals are morphologically so different from each other, the question arises whether infrasound tones are produced in different ways in each species. It would certainly be reasonable to think that the long neck plays a key role in the giraffe's infrasound tone creation, especially since they always extend their heads upward, effectively lengthening the neck, when they produce the tones.

Since the giraffe is such a visual animal, one can imagine that the use of hearing and infrasound come more into play when vision is limited at night or by vegetation and topography. In those conditions giraffes can keep in contact with each other by sending out and receiving infrasound tones.

Floating over the Plains

One of the most striking things about giraffes is the way they move. Karen Blixen describes the strange quality of their movement beautifully in *Out of Africa*: "I had time after time watched the progression across the plain of the giraffe, in their queer, inimitable, vegetative gracefulness, as if it were not a herd of animals but a family of rare, long-stemmed, speckled gigantic flowers slowly advancing."

An adult giraffe can weigh up to 1,100 kg, yet its movement appears almost weightless. The giraffe has two different gaits—the ambling walk and the gallop. In contrast to most ungulates, the giraffe walks by swinging its long legs forward, first both legs on one side of the body and then both legs on the opposite side. This type of stride is called an amble, and the giraffe has it in common with okapis, camels, and llamas. In contrast, other ungulates walk by simultaneously moving the left front and right rear legs and then the right front and left rear legs.

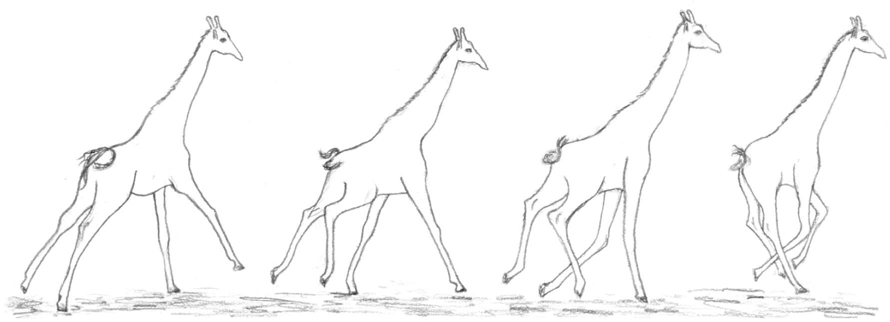
The amble has a flowing, rhythmical quality and the giraffe's body and neck softly swing side to side, counterbalancing the one-sided movement of the legs.

The giraffe's legs are longer than any other mammal's, which gives it a very long stride. And since its forelegs are longer than its hind legs, its gait is unlike that of any other mammal. Its rear leg touches the ground about 50 cm (20 inches) in front of the spot from which it lifted its front leg. Because the giraffe is so large, the movement of the legs seems to be almost in slow motion. And with its center of gravity so high, and its attentiveness concentrated in the elevated head, the giraffe seems to sweep along, hardly in contact with the earth. It treads on the earth, but it certainly does not appear to be of the earth. As Jane Stevens describes, "I watched as a group of seventeen floated along the edge of a yellow-barked acacia forest" (Stevens 1993, p. 6).

The unearthly quality of movement intensifies when the giraffe accelerates into a gallop (see Figure 18). Its stride lengthens even more and when its fore- and hind legs are widely spread and the forelegs reach far forward, the neck becomes more horizontal. The feet then come close together and at this phase of the gallop the neck reaches its most vertical position. The faster the giraffe moves, the more its neck moves down (forward) and up (back). A giraffe can attain a speed of 55–65 km/hr. The long swinging movements of both the legs and neck and the rhythmical expansion and contraction (spreading out in thrusting forward and contracting into the vertical while landing) are a fascinating sight. The impression that you are watching an animal in slow motion is accentuated during the gallop.

Dagg and Foster describe the mechanics of the giraffe's gallop in more detail:

> The power and weight of the giraffe are more in the forequarters than in the hindquarters, so that the main



a b c d

Figure 18. A galloping giraffe. a): The most extended phase of the gallop as the left foreleg has reached the ground. b): The right foreleg reaches the ground. c): The right foreleg is on the ground and the hind legs swing in. d): The legs are bunched together and the neck is at its most upright as the right hind leg approaches the ground. (Drawings by C. Holdrege after photos in Dagg and Foster 1982, pp. 100–101.)

> propulsion for each stride comes from the forelegs. By pressing forward at the beginning of each stride, the neck moves into line with the power stroke. The neck facilitates the movement by shifting the center of gravity of the giraffe's body forward and more nearly over the forelegs. At the end of each stride or leg swing, as the hooves touch the ground again, the neck moves backward in order to slow down the forward momentum of the body and enable the giraffe to keep its balance. (Dagg and Foster 1982, p. 102)

In other words, the pendulum motion of the neck helps to propel the giraffe forward and aids in maintaining balance. No other mammal's neck plays such a role in forward movement! And in no other mammal do the forelegs give the main propulsive force, a task usually taken on by the rear legs. Thus the giraffe's unique form of motion arises out of the interplay of its unusual characteristics—its long neck, short body, high center of gravity, and long legs.

The neck not only plays a role in walking and running, but also is absolutely necessary in aiding a giraffe to stand up, as biologist Vaughan Langman describes:

> A giraffe, unlike most other mammals, is totally reliant on its head and neck to rise from lying on its side. In order to get off the ground, it must throw its head and neck toward its legs and use the force of the throw to bring [the giraffe] to its stomach. To come up to a standing position requires another throw of the head and neck, this time back toward the tail; once again it is the momentum of the head-neck throw which makes it possible for a giraffe to stand. (Langman 1982, p. 96)

As all these examples show, the giraffe's neck, which stands out so conspicuously in a morphological sense, also takes on a prominent role functionally in its movement.

Figure 19. A giraffe rising from the lying position. (Drawings by Jonathan Kingdon 1989, p. 328; reprinted by permission from Elsevier.)

"Necking"

> Movement and counter movement appear rhythmical and synchronized, imparting the sinuous grace of a stylized dance. (Estes 1991, p. 205)

Imagine a grouping of younger and older male giraffes. One animal starts moving closer to another, until the two are perhaps four to five meters apart. He raises his neck and head into an erect posture, emphasizing his height and uprightness. (We might say, anthropomorphically: emphasizing that he's a *real* giraffe.) If the other male responds similarly, they begin walking toward each other, stiff-legged and with legs splayed. They come to stand facing in the same direction, body next to body. They begin leaning and rubbing flanks, necks, and heads against one another. Both giraffes stand with splayed forelegs. One will swing his neck out to the side and swing it back, making contact with the other's neck. The partner responds with the same kind of neck swing. So ensues the "rhythmical and synchronized" dance that Estes characterizes (see Figure 20).

This "necking behavior," as it is dryly named, can either stop after awhile or transform into a more forceful sparring (Coe 1967). In this case the blows with the head and neck become much more powerful, and the slap of contact can be heard far away. When the two giraffes stand side-by-side, but facing in opposite directions, the blows tend to be more violent. Necking bouts may last only a few minutes when one male is clearly dominating the bout. But when the partners are more evenly matched they can last for more than half an hour, and some have even been described as going on for hours. Rarely is a giraffe hurt in these necking bouts; usually one simply stops "necking" and wanders off.

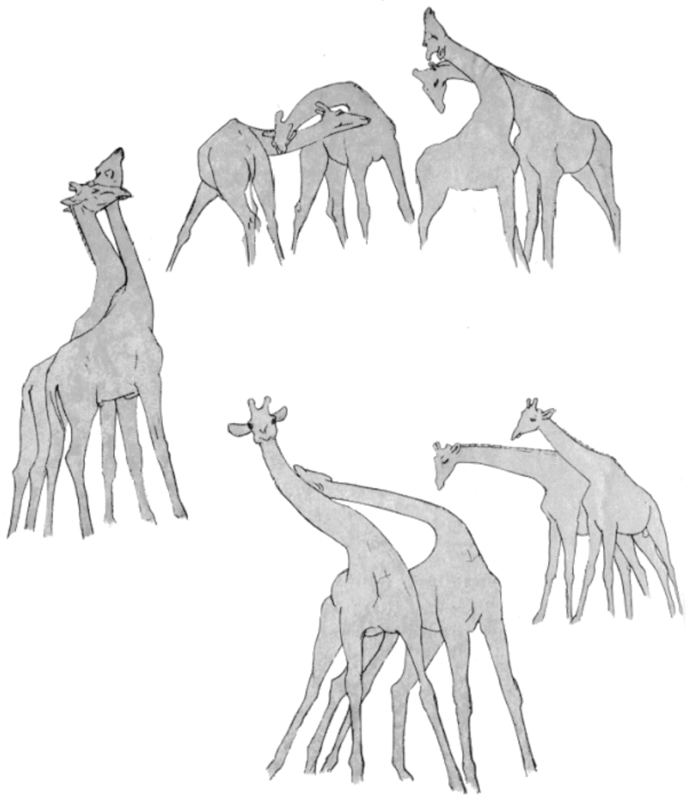


Figure 20. "Necking" giraffes. (Drawings by Jonathan Kingdon 1989, p. 332; reprinted by permission from Elsevier.)

Sparring and dominance bouts among males are known in many ungulate species. What is characteristic about this behavior in the giraffe is that the neck plays such a central role. The broad, undulating sweeps of the neck have, as Estes has expressed it, a "sinuous grace." The character of the giraffe comes very clearly to expression in this remarkable form of behavior.

Lofty—and at a Distance

Giraffes are not solitary animals. They live in herds of varying sizes, often between ten and fifty animals. But as biologist Richard Estes puts it,

> The giraffe is not only physically aloof but also socially aloof, forming no lasting bond with its fellows and associating in the most casual way with other individuals whose ranges overlap its own. (Estes 1991, p. 203)

Giraffe herds are more accurately described as loose groupings, since their composition continually changes. Groupings rarely stay the same for more than part of a day. In one case, a female giraffe was observed on 800 consecutive days and was only found twice in a group that remained the same for twenty-four hours. As Estes remarks, with regard to herd structure and composition, "variability is the only rule" (Estes 1991, p. 204).

In some instances researchers have observed more long-term relationships. For example, in the Nambian Desert some females show up with other females about one-third to half of the time (reported in Milius 2003). That's of course nothing like the bonding between individuals in elephants, but shows that, perhaps in relation to particular habitats, giraffe groupings can be something other than random mixing.

When giraffes are in groups, they tend to keep at a physical distance from each other, remaining within eyesight but often not closer than twenty feet. They reduce these distances when feeding together from the same trees or shrubs. Under these circumstances one can see giraffes closely grouped, although rarely touching each other.

Touching and rubbing are also not typical forms of giraffe social behavior. They occur usually only between cow and calf, between "necking" males (see above), and before and during mating. Otherwise giraffes prefer distance. You don't see giraffes lounging around with necks resting on the backs of fellow herd members—a typical sight among zebras.

So while there is grouping and some social interaction, giraffes have a kind of self-contained quality. This finds a different expression in their relation to heat. Even on hot days when shade is available, you will often find giraffes in the open. Only when the temperature went over 54° C (129° F) were giraffes observed actively seeking the shade of trees (Dagg and Foster 1982, p. 65).

It is interesting in this connection that giraffes rarely drink. I have discussed (Chapter 1) their awkward manner of splaying their forelegs to reach down to drink water, as if their ungainly posture were telling us about their lack of need to drink. They take in substantial amounts of water from the leaves and shoots they browse. Giraffes also do not bathe in watering holes or rivers and rarely swim. If you picture a giraffe immersed in water, it's hard to imagine how it could keep its balance with its high center of gravity. The giraffe is definitely not adapted to life in water!

The quiet, sensitive aloofness of the giraffe stands out more when we contrast it to the elephant. Elephants live in tightly bonded family groups with the members in close physical contact. They rub up against each other and caress and slap each other with their trunks. They are continually pulling in the scents of their surroundings through their trunks. An elephant will smell you before it sees you; its eyes are definitely not its dominant gateway to its surroundings. Elephants also love water and, when they can, bathe every day. Elephants are about

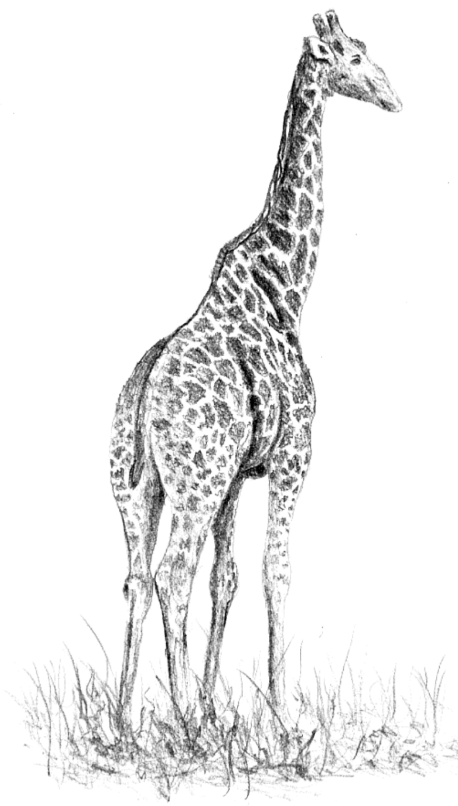


Figure 21. A lone male giraffe in Botswana. Note that the tail is missing its long hairs, which were probably lost when it was grabbed by a lion. (Drawing Craig Holdrege.)

contact and immersion; giraffes maintain more distance. Although giraffes and elephants often inhabit the same area, qualitatively they live in very different worlds.

The Developing Giraffe

When people first started reporting about the cow-calf relationship in giraffes, they painted a picture of the all-too-aloof mother. Young calves were often found alone with the mother nowhere in sight for many hours. Over the years, field biologists have gained a fuller picture of the cow-calf relationship (see, for example, Estes 1991, Langman 1982, Pratt and Anderson 1979). A giraffe's gestation period is about fourteen to fifteen months. Usually one calf is born, dropping to the ground from the considerable height of about two meters. It stands up on its long spindly legs within an hour and then begins suckling. The newborn giraffe is nearly two meters high—just high enough to reach the mother's udder! Since observers find young calves at all times of the year, reproduction appears to be largely independent of the seasons.

Although the calf soon has the ability to stand for longer periods of time and to walk considerable distances, it does not follow its mother while she feeds. The mother leaves the calf in a spot where it is inconspicuous and then wanders off to feed, sometimes going as far as fifteen miles. From this behavior the anthropocentric picture of the cold, unconcerned mother arose. But she returns to the calf two to three times during the day and stays with it at night. When she returns, she nudges the calf, licks its neck and the calf begins suckling. When it is done suckling, she leaves again to feed. This pattern continues for about one month.

Then different mothers with calves congregate and leave the calves together in crèches during the day. This pattern can go on for six months or more, although the calves already begin supplementing milk with browse after a month. After the "crèche phase," the calf stays close to the mother until it is about one and a half years old and then separates for good. A female giraffe becomes pregnant for the first time around four years of age, while males begin mating at about seven.

Calves grow very quickly in the first six months of life, shooting up as much as one meter during this time. After a year the growth rate slows markedly. The adult height of four to five meters is reached after about three to four years.

At birth the legs are—compared to the adult's—disproportionately long and the neck is disproportionately short. At this time, therefore, the giraffe's neck does not appear particularly long. But during the phase of growth, the neck catches up and lengthens considerably faster than the legs. All of the giraffe's other anatomical structures and physiological functions are caught up in this remarkable growth and transformative process.

Feeding Ecology

Giraffes browse primarily on the leaves and twigs of trees and bushes. Rarely do they splay their legs and reach down to feed on forbs; they almost never feed on grasses. Where there is only grassland you don't find giraffes, and desert-dwelling giraffes in Nambia browse along river woodlands (Fennessy et al. 2003). Acacia trees and bushes are one of the giraffe's primary sources of food, so unsurprisingly you are likely to come across giraffes in acacia woodlands and thickets. But giraffes are by no means only narrow acacia specialists (like the koala in Australia, which is bound to eucalyptus trees). Different research groups have found that giraffes feed on forty-five to seventy different species of trees and shrubs (Leuthold and Leuthold 1972; Pellew 1984; Ciofolo and Le Pendu 2002).

Giraffes are selective feeders; they don't just eat what is right around them. They wander around—up to twenty kilometers per day—feeding on different trees and bushes. They prefer a number of relatively rare species and will browse them more intensively than the much more prevalent acacias that quantitatively make up the largest part of their diet. But even with acacias they are selective, preferring, when they are available, the young shoots and leaves, and in some species the flowers. Because they pick out their food, giraffes spend more time feeding, in relation to their body weight, than, say, their large, unselective grazing cousin, the African buffalo. In this respect giraffes are more like the impala, a relatively small antelope. Giraffes eat about 500 pounds of browse per week, and up to 75 pounds per day. (A large adult male can weigh nearly one ton.)

As mentioned in Chapter 1, giraffes shift their feeding grounds according to the seasons. In East Africa, they are more on the plateaus in acacia savannahs during the wet season, while in the dry season they wander through the valley bottom woodlands that have more fresh browse. Giraffes also have a marked daily rhythm. During daylight they feed or move around, often to find food. Feeding is concentrated in the hours after dawn and before dusk, with a pause during midday. During the day they also ruminate. A giraffe grinds its food using circling motions of the jaw and then swallows it. The movement of the food through the long esophagus is outwardly visible as a bulge racing down the skin of the neck. Soon thereafter the bolus (as the ball of partially digested food is called) shoots back up the esophagus, and you see another wave, this time moving up the neck: a remarkable sight. A giraffe usually stands while ruminating during the day. Its very large salivary glands secrete saliva to moisten the cud (Hofmann and Matern 1988).

After the sun sets, giraffes feed less frequently. Pellew (1984) found that they feed much more often on moonlit nights than on moonless nights, which suggests that they orient visually when seeking browse. During the dark hours they spend more time ruminating, often while lying down. They also sleep lying down, with their necks curved around and their heads resting on their flanks.

As the nineteenth century British comparative anatomist Richard Owen remarked, "the peculiar length, slenderness and flexibility of the tongue are in exact harmony with the kind of food on which it is destined to subsist" (1841, p. 219). Dagg and Foster describe vividly the browsing giraffe:

> When browsing, a giraffe reaches out with its long dark tongue, wraps the tip about a branch (often heavily thorned), and draws it gently in between its extended lips. Then it closes its mouth and pulls its head away, combing the leaves and small twigs into its mouth with its extra-wide row of lower front teeth.[1] Twigs, leaves, pods, fruit, galls and ants are all chewed together in the tough mouth. (Dagg and Foster 1982, p. 82)

Young shoots have a lighter, fresh green color—a color giraffes probably recognize and use to select just those shoots. The thorns on these shoots are still green and flexible, but giraffes have no problem feeding on more mature shoots with sizable thorns. (Autopsies of wild-killed giraffe stomachs reveal leaves, twigs, seeds, and thorns up to three and a half centimeters in length; Hofmann 1973, p. 119.) The tongue's upper surface is thick-skinned and covered with small recurved spines, giving it a sandpaper consistency. The inside of the mouth is also clothed with a tough epidermis. So the giraffe's discriminating, facile style of feeding, with the dexterous motion of the agile tongue, is infused with an underlying toughness.

1. Giraffes—and all other even-toed hoofed ruminant mammals—have *no* top front teeth (upper incisors).

Hofmann describes giraffes feeding on longer-thorned acacia species "with remarkable skill and care, using the extremely mobile tongue in conjunction with the soft lips" (ibid.). In the process they not only tear off leaves but also break off thorns, which pass through the well-protected mouth, down the esophagus and into the stomach, where they are at least in part digested. Nonetheless giraffes prefer younger, soft-thorned shoots. In a field experiment scientists removed thorns from branches of acacia trees (*Acacia seyal*) and found that giraffes browsed these de-thorned branches significantly more intensively than they did the naturally thorned branches (Milewski et al. 1991).

Although giraffes are clearly predisposed to selective feeding, they do survive quite well in zoos where they are fed much more fiber-rich, low protein diets. (Young leaves have a higher protein content than old leaves.) Hofmann and Matern (1988) performed autopsies on zoo and wild giraffes and found remarkable differences in the first two, largest, chambers of the stomach (the rumen and the reticulum). The zoo giraffes had significantly larger chambers, which could hold about 150 liters (nearly 40 gallons) as compared to an average of 105 liters (nearly 28 gallons) in wild giraffes. This change correlates with the increased amount of roughage in the feed of zoo giraffes. Grass-eating (grazing) ruminants, which ingest more roughage, have proportionately larger stomachs than broad-leaf-eating browsers. So it is not too surprising that when giraffes are fed more like grazers, their stomach enlarges to accommodate the digestion of high-roughage feed.

But with the increase in stomach volume in zoo giraffes, the absorptive surface also decreases, which is shown through the small size and number of the papillae that make up the inner lining of the rumen. Wild giraffes, in contrast, had much larger and more numerous papillae, so that their absorptive surface was in fact nine times larger. This allows for the intensive digestion of the fresh material they feed on, which passes much more quickly through the digestive system than roughage-rich fodder.

This remarkable adaptation of the stomach to the food a giraffe eats shows that the giraffe is not physiologically or anatomically set in its ways. It is flexible and can adapt to changing conditions.

The Intertwined Existence of Acacia and Giraffe

In their classical umbrella form—a broad, spreading crown branching off from a single erect trunk—acacias help define the savannah landscape in which giraffes thrive. We have seen how giraffes live off acacias as a primary source of food, but the interaction between these two very different organisms goes deeper.

Acacias in Australia—which is home to nearly one thousand species—are thornless, whereas virtually all of the approximately 130 species in Africa bear thorns. Since there are no large herbivores in Australia that browse acacias, it's obvious to think that African acacias might have developed thorns in response to the browsing of giraffes and other browsers. Field biologists have made observations that support this view, noting that acacia branches above the height of giraffe browsing have fewer and shorter thorns than the branches accessible to giraffes (Milewski et al. 1991). When giraffes and elephants were excluded from areas of acacia woods in field experiments, the new shoots developed *shorter* thorns (Young and Okello 1998). Browsing may not explain the origin of thorns in African acacias, but it is certainly evident that the length and extent of thorns is influenced by browsing, with giraffes playing a primary role.

It is a simple matter to picture thorn formation as an adaptive response that keeps browsers from feeding on a tree, thereby increasing its survival chances. The interesting thing is that giraffes feed on acacias even when they are densely packed with thorns. The coevolution of thorn formation and giraffe browsing does not lead these two organisms to sever their interaction. Maybe thinking of thorns solely as weapons to deter browsing is too narrow a view. Although we don't yet know it, there may be more to thorns than pricks a mouth.

Similarly ambiguous is the evolution of stinging ants that live exclusively on the whistling thorn (*Acacia dreparalobium*) in East Africa. These ants build their nests in the bulbous swellings at the base of modified thorns; only this species of acacia has these swellings that can provide such a home for ants. The ants live from the nectar produced in the acacia's leaves. When an antelope or a giraffe browses on a branch, the ants swarm out and sting it. Again, thinking simplistically of "stinging ants as acacia protectors," you might say that the stings ward off the browsers. In fact, one study showed that trees with more active ants had more foliage than those with less active colonies. Moreover, young giraffes browsed less on trees with more active ants. But the ants had no apparent effect on the browsing behavior of adult giraffes (Madden and Young 1992). Once again, reality is more complex than simple (and convenient) explanations.

When we view thorns and ants exclusively as defensive mechanisms, we assume the acacia and the giraffe are antagonists, each busily shaping the survival of its own species. We view species as separate entities that interact on the basis of competition. But species are not separate entities; every species lives from and provides life to many other kinds of organisms. When we view species interaction in terms of coexistence, where each species, through its own life, supports the life of other species, we transcend the narrow terms of competition and individual species survival that constrain so much of ecological and evolutionary thought today.

Scientists in South Africa observed that giraffes browsed acacias near water holes more intensely than trees far away from such water sources (DuToit 1990a). Acacias grow new shoots after the onset of the rainy season (one or two times a year). The scientists observed that the shoots from the more heavily browsed trees grew back very rapidly, and grew longer, which compensated for the intense browsing. In contrast, the lightly browsed acacias grew smaller shoots, so that the net shoot extension was the same in both habitats. In other words, giraffe browsing stimulated growth of the acacias in relation to the degree of browsing—a wonderful example of dynamic balance (which is disturbed when the habitat is too small for the number of giraffes living in it). This interaction is an example of a widespread phenomenon in plants known as compensatory growth (see McNaughton 1983).

The heavily browsed acacias reacted to giraffe feeding in another, perhaps more surprising way. The leaves that grew in the rainy season after browsing were richer in nutrients and contained significantly less condensed tannins, which make leaves less palatable. Tannins are formed after cessation of leaf growth, while nutrient-rich phosphorus and nitrogen compounds are formed during growth. Stimulated by browsing, the acacia leaves remained in a more juvenile state, which is exactly the type of leaf giraffes prefer!

Of course, a population of herbivores can become too large for a habitat and damage it. Usually this happens when human beings limit the movement and therefore the home range of the animals. For example, in the Ithala game reserve in South Africa, five giraffes were introduced in 1977 and their population increased to around 200 by 1999. Giraffes browse intensively in a relatively small area (they cannot navigate the steep slopes in the preserve); here one species of acacia has disappeared altogether (Bond and Loffell 2001).

Let me mention one more example of the intertwined biology of giraffes and acacias. The flowers of knob thorn (*Acacia nigrescens*) are an important source of food for giraffes in the late dry season in southern Africa, when many trees have lost their leaves (Du Toit 1990b). The flowers of this species grow bunched on stalks (they have a "bottle brush" form) and stand beyond the fairly small, curved thorns. Most of the flowers are sterile, consisting only of pollen-producing stamens and lacking the pistil out of which fruits and seeds form. Therefore, giraffe browsing has little to no effect on the reproductive capacity of the tree—what the tree offers in abundance the giraffe takes.

Giraffes unintentionally "collect" pollen on their mouths and skin while feeding on the flowers. Since they can wander up to twenty kilometers in a day, mainly in search of food, the South African biologist Du Toit, who has studied giraffes extensively, suggests that giraffes might be important pollinators for this species. This hypothesis has to be investigated more closely, but it at least points to one more facet of the richly interwoven lives of giraffes and acacias.

In conceiving abstractly of discrete organisms, we think of giraffe and acacia as separate entities, which of course they are *physically* when the giraffe is not feeding. But the fed-on acacia is not the same after giraffe browsing. It may form more and longer thorns, but it may also produce longer shoots, take more minerals out of the soil, and form nutrient-rich substances in its leaves, while suppressing leaf-aging as indicated in less tannin formation. In this way the giraffe has become part of the acacia. Then, when it feeds again, the giraffe feeds on something that is connected to its own activity. The apparently clear boundary between organisms dissolves, and we are led to picture organisms as participating *in* each other, rather than standing *next to* each other. We can only truly understand the giraffe when it is viewed as part of this concrete web of life.

Summing Up

Before we return to the question of giraffe evolution in the next chapter, let me briefly summarize what I have presented in the last two chapters. I have tried to bring the giraffe into view as a whole organism in relation to its environment. This approach involves building up a more comprehensive picture of the animal than we normally have when our aim is to explain this or that feature. But an encyclopedic gathering of information about the giraffe is not the same thing as a cohesive picture. Going beyond a consideration of facts we discover how the various features of the organism are interconnected. Our eyes are opened to how the organism is truly an organism and not a collection of parts, an artifact, which it becomes in our analytical mode of investigation. So I have done my best to show connections—how, you could say, the parts speak the same language.

It's not by chance that all people who study the giraffe are brought back again and again to its long neck. What we have seen is that the long neck is the most vivid and perhaps extreme manifestation of an overall tendency toward vertical elongation in the giraffe. We see this feature not only in the neck but also in its long slender legs, in its long head, its long tongue, and even its long heart. The vertical orientation of the body is increased by the shortness of the rump, which slopes upward into the neck. Vertical elongation reveals itself most prominently in the front part of the animal; the giraffe is the only hoofed mammal with longer forelegs than hind legs. The forelegs extend into the long and sleek shoulder blade. Because the neck also emerges high up on the trunk, its upward reach is extended even more. This augmented elongation makes it impossible for the giraffe to reach the ground with its head without spreading or bending its forelegs. Truly, the giraffe has a one-sided, but highly integrated morphology.

With its long strides the giraffe ambles through the savannah. When it transitions into a gallop the neck helps propel the animal forward. Similarly, when standing up, the giraffe throws its neck upward to help lift its body from the ground. And in male neck sparring, the sinuous beauty and power of the neck shows in yet another way the dominance of this organ in the life of the giraffe.

E.-M. Kranich points out that the neck is the organ in an animal that frees the head from its close connection to the unconscious vital processes of the rump. Thereby the head becomes a more autonomous center of sensation and perception (Kranich 1995 and 1999). With its long neck, the giraffe carries its head significantly higher above the rump than does any other mammal, opening itself to a wide surroundings through its large eyes and keen vision. It is a calm, silent sentinel. With its overviewing eyes, it lives more like a bird surveying its surroundings from on high than like so many of its mammalian relatives that bathe, head-lowered, in the near-ground world of scents. Characteristically, the giraffe has a dry snout and not the moist snout of a typical mammal, upon which airborne scents can dissolve.

Giraffes communicate with one another largely through vision, much less through touch and smell. While giraffes do associate with one another, infraspecies relations are usually loose and changing.

Like other browsers, the giraffe spends much of the day feeding, selectively browsing on an array of trees and bushes, but with a decided preference for acacias. Its elongated neck, head, and tongue give the giraffe a uniquely large vertical span within which it can browse (four meters). It can also reach far in front of its body using the neck as an immense arm to gather food at a distance. And, of course, at times the giraffe reaches with neck, head, and tongue in line to great heights to feed. With its flexible and yet tough tongue, it reaches out to enwrap, if possible, young and tender leaves. But it is also impervious to woody, pointed thorns. The ingested acacia becomes part of the giraffe, and giraffe browsing affects, in turn, the growth of the acacia. Through such interrelationships we see that the giraffe as an organism is part of the larger organism of the environment.

Against this background I return to the question of evolution.

Chapter 4

The Giraffe and Evolution

Thinking about Evolution

The idea that organisms evolve began to take hold of human minds in the decades before and after 1800. This spurt in interest was not because a wealth of new evidence for evolution was suddenly laid out. Rather, individual thinkers and scientists began viewing geological, biological, and historical processes in terms of development and transformation (cf. Teichmann 1989, Eisely 1961). What had previously been looked upon in biology as separate entities—species, genera, etc.—related ideally in a "great chain of being," became in the minds of early evolutionary thinkers members of an unbroken stream of evolutionary transformation. Johann Herder wrote in 1784:

> Compounds of water, air, and light must have arisen before the seed of the first plant-organization, like the mosses, could arise. Many plants must have arisen and then died before an animal-organization became. Also insects, birds, water and nocturnal animals must have preceded the advanced animals of the land and day. (quoted in Teichman 1989, pp.13–14; transl. CH)

The idea of evolution shed light on things; it was revelatory. And what more does the human mind seek in the search for knowledge than ideas that illuminate the nature of the world we are investigating? This revolution in human thought was not bound to any particular theory. Whether promoted by materialists or individuals who believed in a spiritual foundation to the world (like Herder), by scientists or philosophers, the idea of evolution caught on. The intuition that things evolve was the wellspring for new ways of viewing the natural world and human history. Specific interpretations and explanations of evolutionary processes came second. Differing views of evolution arose, depending on the perspective of the individuals. Some were spiritual, others materialistic; some were teleological, others emphasized randomness; some placed structure in the foreground, others function.

After the publication of *Origin of Species* in 1859, Darwin's cogent and well-argued theory of evolution became, over time, *the* theory of evolution. Most of us today, when we hear the term "evolution," think immediately of the Darwinian theory of evolution: random mutation and natural selection drive the evolution of species. We probably don't even know that there always have been and still are other ways of interpreting evolutionary phenomena.[1] In the United States, it seems, one must be either a Darwinist or a Creationist (i.e., someone who doesn't believe in evolution). Recently some scientists have propounded what they call "intelligent design" as an attempt to wed spiritual and evolutionary views (see Meyer 2004); they are, by and large, pushed into the creationist camp by Darwinians. The battle between Darwinists and Creationists, fought on both sides with religious fervor, has led to unfortunate oversimplifications and to an unwarranted polarization of perspectives. This dichotomizing is, to my mind, counterproductive

1. I have cited a few examples in the bibliography: Berg 1922/1969; Bowler 1988; Goodwin 2001; Goodwin and Webster 1996; Gutmann 1995; Ho and Saunders 1984; Kranich 1999; Riedel 1978; Verhulst 2003.

and shuts down our thinking about some of the true riddles of evolution.

So what can we do? We can step back and look more openly at the phenomena themselves and the challenges they present to us. What emerges is a many-faceted picture of evolution that leads to new kinds of questions. In my own studies of evolution I have found so many doors closed through narrow ways of viewing that I have come to see the most important step entails opening up some of those portals and letting in fresh air. This approach may not provide the safe surroundings of a closed, coherent system, but it is invigorating.

Okapi and Giraffe

The skin of an unknown, horse-sized mammal from the central African rain forest (the Ituri Forest of Congo-Zaire) was sent to Europe in 1900. The skin was dark brown, almost black in areas, but had zebra-like stripes on the legs and rear quarters. Was it a rain forest zebra? From the skin alone there was no telling. Since it had been acquired from the pygmies living in the forest, they were asked about the animal. They insisted that it has paired hooves and not a single hoof like a zebra's. They also described its large donkey-like ears and the small, spiked-shaped and hair-covered horns the male carries. So it was definitely not a zebra.

Soon a skull of the animal arrived. The horns were like those of a giraffe and the skull had two-lobed canines in the lower jaw, which only giraffes possess. So this newly discovered mammal was a member of the giraffe family! The new species was called okapi, after the pygmies' name for it, and then given the scientific name *Okapia johnstoni*.

Based only on the skull and the skin, artist P. J. Smit, under the guidance of anatomist and British Museum of Natural History Director Sir Ray Lankester, painted a reconstruction of the okapi that proved to be an almost exact likeness to the living animal. This is a remarkable example of how careful examination of a limited number of parts coupled with a broad and deep knowledge of the anatomy and morphology of comparable animals can lead to a picture of the whole animal.

This "extraordinarily handsome animal" (Spinage 1968a, p. 153) was seen alive by Europeans only twice before 1906. For most of the twentieth century, scientists could observe the okapi only in zoos, until in the last few decades field researchers began to learn more about this shy and elusive animal's life history and ecology (Lyndaker et al. 1999, Hart and Hart 1989).

Figure 22. An okapi (*Okapia johnstoni*). (Drawing by Jonathan Kingdon 1989, p. 338; reprinted by permission from Elsevier.)

The okapi has aroused additional interest because its skeletal structure is very similar to that of fossils discovered in Asia and Africa. It quickly became known as a "living fossil," although that label is controversial among specialists. The question arose, Does the okapi give us a glimpse of the ancestor of giraffes?

Clearly, the okapi does not have the giraffe's characteristic long neck and short body. Both its neck and body are more like those of an antelope or deer than the giraffe's. In its overall form, the body is less specialized than the giraffe's. But it does have long legs. While in other ungulates the rear legs are significantly longer than the front legs, in the okapi they are nearly the same length. This is a step in the direction of the giraffe. Moreover, the okapi, like the giraffe, splays its forelegs when grazing near the ground. As another feature of elongation, the okapi also has a long, pointed, and flexible tongue. So in some respects we can see in the okapi the nascent giraffe. But to know more, we must turn to the fossil record.

Fossil Giraffids

The fossil record is a picture in the present of life in the past. We find traces of life in fossilized bones, imprints, and other fossilized body parts and can build up pictures of animals, plants, and habitats of the past. Of course these pictures are always subject to alteration, and at times our fantasy will take flight. The skins of animals, for example, are almost never found, yet reconstructions usually present animals in full color and patterning. We need to be careful that our pictures remain tentative and open.

With this in mind, let's look at the fossil history of the giraffe family, known to scientists as the "giraffids" (Giraffidae). (I draw here primarily from Bohlin 1926, Churcher 1978, Colbert 1938, Harris 1976, and Mitchell and Skinner 2003.)

If the evolution of the giraffe had progressed as Darwin envisioned, one would expect to find fossils of many intermediate stages of animals with successively longer necks and legs between the giraffe ancestor—a small deer- or antelope-like animal that perhaps resembled the okapi—and the fully evolved giraffe. But this is not the case.

Fossils of giraffes—perhaps not the same species as today's *Giraffa camelopardalis*, but clearly giraffes—can be found in Africa and Asia in the layers of the lower Pliocene and the upper Miocene, geological periods that directly precede the last ice age (the Pleistocene period). In these strata, one finds fully developed giraffes—some smaller, some larger and more robust—along with other, now extinct, members of the giraffe family. That these other fossils belong to the giraffe family and not, say, to the deer or cattle families, can be seen in such diagnostic characters as the bilobed lower canine teeth and the horns.

Two groups (subfamilies) of giraffids coexisted with the early giraffes in Africa, the Palaeotraginae and the Sivatheriinae. The former were generally deer- to elk-sized animals with long legs and body proportions resembling the okapi. The sivatheres consisted of massive, in some cases, elephant-sized animals that were much stockier than other giraffids. *Sivatherium maurusium* resembled an elephant-sized moose (see Figure 23). It even had spreading horns that resemble antlers. In both subfamilies there was a wide array of horn forms. Neither the palaeotragrines nor the sivatheres had the unusual limb proportions, the short torso or the overly elongated neck of the giraffe.

So there were three quite distinct groups of giraffids: the large, long-legged, short-bodied, and long-necked giraffes; the

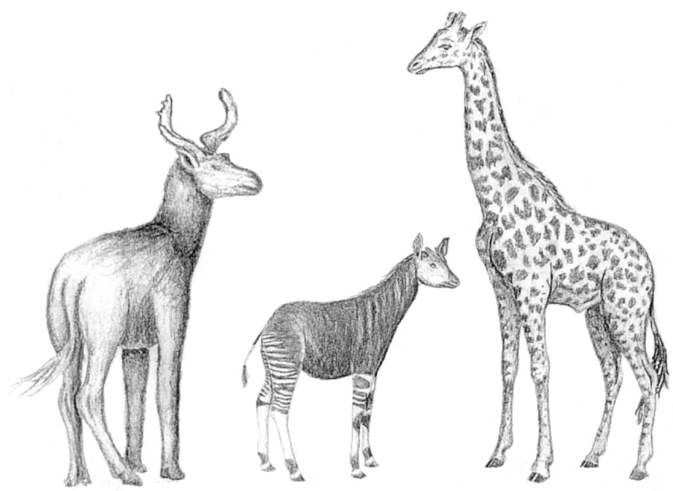


Figure 23. Representatives of the three members of the giraffe family: a reconstruction of the extinct Sivatherium, the okapi, and the giraffe. The drawings are to scale. (Drawings by C. Holdrege after Churcher 1978 [Sivatherium], Kingdon 1989 [okapi], and Skinner and Smithers 1990 [giraffe].)

massive sivatheres; and the more "typical" ungulate group to which today's okapi belongs. What is the origin of the three giraffid subfamilies?

The remains of the first giraffids are found in the lower layers of the early Miocene fossil record of Africa. One species, *Canthumeryx sirtensis* (formerly called *Zarafa zelteni*), resembles a "lightly built deer or antelope, with generally slender proportions and light build to all parts" (Churcher 1978, p. 514). It is generally viewed as the most "primitive" giraffid, since it is both an early representative and its body is not highly specialized. It comes the nearest to being the basal species of giraffids from which others might have evolved. Because, however, it coexisted with a relatively small sivathere, it is not considered to actually be at the base of giraffe family evolution. That origin, as is so often the case when one arrives near the base of an evolutionary tree or bush of a given group of animals, remains dark. Interestingly, the giraffe family evolved later than other ungulate families.

Before giraffes appeared, one finds many fossils, both in Africa and Asia, belonging to the okapi-like Palaeotraginae subfamily. There is diversity among these fossils, which has led paleontologists to speak of three different genera (*Giraffokeryx, Palaeotragus,* and *Samotherium*). All have quite long limbs and the forelimbs are about the same length as the hind limbs. The proportions of the lengths of individual bones in the limbs resemble those of the okapi much more than those of the giraffe. However, some species (e.g., *Palaeotragus germaini*) have somewhat elongated neck vertebrae that resemble in morphology giraffe vertebrae. Arambourg, who examined these fossils (see Churcher 1978), saw this species as a parallel development within the Palaeotraginae to what was developing, perhaps at the same time, in the—still unknown—ancestors of the giraffe.

The fossils of the first giraffes have been found in Europe (Greece) and Asia (in the layers of the upper Miocene and lower Pliocene). Up until now, fossils of giraffes in Africa have been found only in more recent layers. These earliest known remains of a giraffe (called *Bohlinia* or *Orasius*) closely resemble modern giraffes, both in size and shape. Key features of the skull are very similar to the present-day giraffe and limb length and proportions "agree fully with *Giraffa*," writes paleontologist Bohlin, who described the fossil remains in detail (Bohlin 1926).

What the fossil record does not show are intermediate forms linking early okapi-like animals—the presumed ancestors of giraffes—with the giraffe and its specialized morphology. The fossils tell no clear-cut story. Three quite distinct subfamilies evolved with considerable variation within these groups. But if you're looking for the gradual transition of one form into another, a picture suggested by Darwin's view of evolution via the accumulation of small variations over long periods of time, the fossil record is disappointing. One might argue that this is an artifact of the incompleteness of the fossil record. And of course no one can predict what still might be found.

A Temporal Pattern of Development

Increasingly paleontologists recognize that the lack of intermediate stages between related groups is a *typical pattern* within the fossil record. In many groups of animals, the fossil record is characterized by the development of various distinct subgroups that coexisted over long periods of time. In other words, a new group (family or genus) evolves rapidly and then exists for a longer period of time characterized by small evolutionary modifications. The German paleontologist Otto Schindewolf, one of the first to recognize this gestalt of the fossil record, spoke of two evolutionary phases: typogenesis, in which the new group appears, and then the much longer period of typostasis, when the group evolves in small increments without radically new characteristics developing (Schindewolf 1969).

In 1972, American paleontologists Niles Eldredge and Stephen Jay Gould formulated basically the same idea, describing evolution as a process of "punctuated equilibrium" in which long periods of relative morphological stability are punctuated by evolutionary innovations (Eldredge and Gould 1972; Gould and Eldredge 1993). This picture certainly fits the current fossil-based evidence of evolution within the giraffe family better than a gradualist one. It seems likely that the main thrust of giraffe evolution occurred in a condensed period of time, followed by a longer period, extending to the present day, with relatively little change.

If we look around us at developmental processes today we also find that major changes usually occur rapidly. Embryonic development is the example par excellence. The most significant events in biological development occur in a short period of time within the overall span of the organism's life. In the first nine weeks of human embryonic development, for example, all the organ systems develop out of a tiny one-celled fertilized egg—the small (about one inch-long) embryo has a brain, heart, liver, stomach, and so on. These organs then differentiate further until birth and beyond. Never again does our body go through such rapid, all-encompassing transformation—nine months in a lifetime of perhaps sixty to eighty years.

Postnatal development is also characterized by periods of greater stasis and ones of more rapid change—growth spurts, puberty, and menopause, to name a few. Even in a period of rapid change, such as the fast growth of infants, growth is not evenly distributed but occurs in bursts. For example, researchers found that the growth of infants ranged between 0.5 and 2.5 centimeters over a sixty-day period, but most of this growth occurred during single nights—up to 1.65 centimeters in a night! (Lampi et al. 1992).

There are other phenomena of development that we can observe intimately, but tend to overlook. I mean the development of knowledge. Just think of when we have an "Aha!" experience, a new insight that sheds bright new light on things. Such new insights are of course usually borne out of strenuous efforts—perhaps longer periods of time in which nothing "comes"—and then at once a new insight is there. It does not simply grow gradually in incremental steps by adding on to past knowledge; it is a new idea that reorganizes our past knowledge, revealing new relationships and connections—and giving rise to new questions. Our body of knowledge takes on a new gestalt.

In these examples we see both the temporal dynamics of a developmental process and the fact that when rapid changes occur they affect the whole system and not just some isolated part. The metamorphosis of a tadpole into a frog is a wonderful example of such an all-encompassing organic transformation. The fish-like, fin- and tail-bearing, gill-breathing, herbivorous tadpole totally transforms in a short period of time into a strong-legged, tailless, lung-breathing carnivore. Every organ goes through dramatic changes as the frog develops by the reorganization of everything that was previously "tadpole."

This points us to another feature of such transformations: they leave no remnants. The whole system reorganizes. This makes sense, since we are dealing with an organism in which all parts (as members) are interconnected. Major developmental steps are not about incremental additions to a preexisting stable structure that remains essentially unchanged.

So if an organism evolves as an organism, and not as a collection of parts, then the pattern in the fossil record indicating that major evolutionary steps occur rapidly is actually not so surprising. It is a time gestalt or pattern on a large scale that we find everywhere within developmental processes we can directly perceive today—dynamics involving phases of accelerated change and phases of greater stability. From this perspective of viewing major steps in evolution (often called macroevolution) as a developmental process, the "gaps" in the fossil record appear as a consequence of a rapid reorganization that leaves no remnants, no physical tracks.

I am certainly not suggesting that one day an okapi-like animal gave birth to a fully developed giraffe. How a new animal group in the past arose remains a huge riddle. Here we come up against a boundary of our present-day understanding. I prefer to acknowledge that boundary and not begin theorizing and speculating about how, in concrete terms, this process might have taken place. All possible "mechanisms" that purportedly explain macroevolution end up replacing the true complexity of the matter with a simplified scheme. It's more fruitful, I believe, to be conscious of the boundary, hold back on speculative explanations, and continue to explore the rich contexts within which evolution occurs.

An Overriding Morphological Pattern

We have just seen how the fossil record of the giraffe family indicates a time pattern within more general developmental processes. While researching the giraffid fossil record, I was struck by another type of overriding pattern that German biologist Wolfgang Schad has found in living mammals and described in great detail (1977; see also Riegner 1998). Schad found that many groups of mammals fall quite naturally into three subgroups. For example, three ungulate families (the so-called pecorans) have horns or antlers: the cattle, deer, and giraffe families. Similarly, the odd-toed ungulates also fall into three families: the rhinoceroses, tapirs, and horses (which include zebras). What's interesting is not so much the numerical pattern but that within each of the groupings you find a biological polarity mediated by an intermediate form.

We have already seen this pattern in Chapter 2 when I compared the bison, elk, and giraffe. The bison is a member of the bovid family (which includes the cow, yak, sheep, goat, and antelope). On the whole these are weighty, compact, and bulky animals. Think of the bison with its short legs and heavy, low-to-the-ground head. In contrast, the giraffe is tall and sleek with long neck and legs. The deer family, represented by the elk, has a more balanced, intermediate form. In a related way, within the odd-toed ungulates, the rather unspecialized tapirs represent a mediating form between the massive rhinoceros and the relatively long-necked and long-legged, swift-footed horses and zebras.

What's intriguing is that this pattern of morphological extremes with an intermediate group is reiterated within each group. So within the bovids you have the cattle group (bison, cow, yak) on one side and the fleet-footed, sleek antelopes on the other, with sheep and goats in between. Similarly in the deer family, there are the more petite deer species such as the European roe deer or the somewhat more robust American white-tailed deer on the one hand and the large, bulky moose on the other hand: the elk (wapiti) represents a middle form within this group.

After I had studied the giraffe family fossil record for some time, it came to me that this pattern was showing itself again within this group. There are, as we have seen, three groups of giraffids. The sivatheres, which are extinct, were large, sometimes huge, animals. Proportionately they have the shortest legs and neck of all giraffids. But they often have massive antlers resembling those of the moose, which we just saw also falls to one pole of its family. The long-legged giraffe represents the other pole with its long neck separating its head from its shortened body. The okapi-like fossils form an intermediate group with less extreme specializations.

It would lead us too far afield to go into a large number of examples here to show all the variations, iterations, and nuances of this threefold pattern as they show themselves in form, coat patterns, physiology, and behavior. Since Schad's groundbreaking study, others have found a similar pattern not only in mammals, but also in dinosaurs, birds, insects, and other groups of animals.[2] Of course this is not the only kind of morphological pattern to be discovered, and you have to be cautious that you don't end up fitting everything into a neat scheme that no longer does justice to the phenomena. We need to hold such patterns in as flexible and open a form as possible.

But acknowledging such overriding morphological patterns has important consequences for how we think about evolution. Finding patterns that encompass many groups of animals indicates that we need to go beyond a focus upon a given species or genus to understand evolution. The threefold pattern suggests, at a macroevolutionary level, the evolution of a kind of "super-organism" that differentiates into extremes (poles) and a middle form within a given class, family, or other systematic group. This notion is, for our standard ways of thinking about evolution, quite radical. But it is one suggested by the order of the phenomena themselves. The problem is that we have to stretch our thinking beyond the idea of wholly self-contained organisms and begin to see each species, genus, or family as embedded within a larger organismic context that encompasses many animals.

The Ecological Perspective

When we look at the ecological relationships between organisms today, it is clear that the lives of species are intimately intertwined. Because it is impossible to understand any organism in isolation, ecologists have found it necessary to take concepts that

2. Suchantke (2002) gives examples within different groups of animals; Riegner (1998) describes the pattern in mammals; Lockley (1999) gives examples in dinosaurs.

were originally conceived of in connection with individual organisms and expand them to refer to larger ecological categories. They use terms such as "ecosystem genetics" and "community heritability" to express how a whole ecosystem evolves with the individual species being members or organs within the larger system (see, for example, Whitham et al. 2003).

The giraffe evolved within the context of a savannah environment (Mitchell and Skinner 2003). We have seen how in present times the giraffe is intimately interwoven with its savannah habitat in Africa. It lives, for example, from the acacia, which is modified by the giraffe and in turn affects the giraffe. We can only envision evolution as coevolution. No creature evolves by itself as if in a vacuum. Just as we can see that the giraffe evolves as a member of an organic threefold pattern with respect to other animals, so also we can see that its evolution is nested within an environment, a larger organism, that in the end encompasses the whole earth. Goethe, who was an eminently ecological thinker, expressed this view already in the 1790s:

> We will see the entire plant world, for example, as a vast sea which is as necessary to the existence of individual insects as the oceans and rivers are to the existence of individual fish, and we will observe that an enormous number of living creatures are born and nourished in this ocean of plants. Ultimately we will see the whole world of animals as a great element in which one species is created, or at least sustained, by and through another. (Goethe 1790–1794; in Miller 1995, p. 55f.)

When I stood for the first time in the savannah of southern Africa surrounded by lions, hippos, giraffes, impalas, and elephants, I was awestruck and gripped by a powerful thought that I can only express in the form of a question: "Where did all these animal forms come from?" I was experiencing how each of these species is unique. To use Goethe's phrase, I was seeing each as "a small world, existing for its own sake" (in Miller 1995, p. 121). And yet it was just as palpable that the African savannah is their womb and sustenance. They all belong together in this landscape.

Savannah-like conditions exist in other parts of the world, but only Africa sustains such a diversity of large mammals. What was and is at work specifically on this continent? This question of the specific qualities of the different continents and bioregions looms large. It goes much deeper than the sum of climatic and geological factors. Similarly, the question of the unique quality of each animal encompasses more than the sum of genetic and environmental factors.

Nested Contexts

In the previous sections I have tried to show that we can begin to understand the evolution of the giraffe only if we view it within larger contexts. One context is the fossil record of the giraffe family. It points to a temporal pattern that initially is surprising: there is no series of connecting links between the different subfamilies, showing how the giraffe might have gradually evolved in a step-by-step fashion. Rather, the three subfamilies appear as quite distinct groups. The major evolutionary innovations apparently occurred quite rapidly (macroevolution), while over longer periods of time smaller variations within a given group arose (microevolution). This pattern appears to be widespread in the fossil record of other organisms and is also typical of the way developmental processes occur today. In this sense the giraffe's evolution is part of a more general evolutionary or developmental trend.

A second context is a morphological one: the threefold pattern of differentiating into two extremes and an intermediate group. We find this pattern not only in the giraffe family but also in many other groups of animals, both vertebrates and invertebrates. It is an overriding morphological pattern of which giraffe evolution is a part.

A third context is ecological. All life is interconnected, and the evolution of any organism is bound up in the evolution of others. Evolution at this level entails the modification of already existing forms and relates mostly to microevolutionary processes.

The fourth context—and I know it may sound strange putting it like this—is the giraffe itself. It has been the main focus of this booklet. We can view the giraffe as evolving within the context of more encompassing patterns—as we have seen in the threefold differentiation that occurs within myriad systematic groups. The giraffe family, within the order of the even-toed ungulates, shows a distinct tendency toward limb lengthening. But the tendency toward vertical lengthening that plays itself out to an extreme in the giraffe, with the whole body form and structure being reorganized in relation to the disproportionate lengthening of the neck, cannot be deduced from the overriding pattern. No one could predict that the giraffe would evolve in just the way it has.

Similarly, we cannot derive the giraffe's unique qualities from environmental interactions. As Mitchell and Skinner point out, the giraffe's "physiological adaptations … subserve the needs imposed by their anatomy rather than the needs imposed by their environment" (2003, p. 64). They view the giraffe as a unique case because of its extreme specializations.

But actually they are directing us to a reality that holds for all organisms, namely the primacy of the coherence of the organism itself. You have to think about the organism in its own terms and then see the manifold relations to the environment.

Back to the Whole Organism

I argued in the first chapter that any adequate concept of evolution needs to be based on some understanding of the organism as a unitary whole. If we don't have at least an educated inkling of what an organism truly is, it becomes all too easy to explain the organism away through neat evolutionary stories. With these stories we "educate" our high school and college students, and the public via the popular press.

The explanations we discussed in the first chapter of how the giraffe evolved its long neck now appear almost laughable in light of a richer, contextualized knowledge of giraffe biology, ecology, and the fossil record. The inevitable shortcomings of such evolutionary stories have to do with focusing on particular characteristics ("long neck") and considering them in isolation from the rest of the organism. You then take a next step and pick out a particular function (selecting it from the various functions that any part of an animal has) and consider it from only one narrow perspective: how it contributes to the animal's survival. The trait ("long neck") becomes a survival strategy ("allows survival during droughts"), and on this basis you build your picture of evolution.

Both the trait ("long neck") and the particular survival strategy are products of a process of abstraction from a complex whole. Therefore we can think them clearly and establish a clean and transparent explanation that seems to work—it makes sense that the long neck evolved in relation to survival and feeding habits. Unfortunately—and it is the price we pay when we operate with abstractions—we have lost the giraffe as the whole, integrated creature it is. We're not explaining the giraffe, we're explaining a surrogate that we have constructed in our minds. The animal has become a bloodless scheme. For this reason evolutionary stories are usually woefully inadequate. The way of viewing evolution and the organism is simply too narrow, too one-sided, and too unaware of its own limitations.

Anthropologist and historian of science Loren Eisely points to the central perspective that is largely missing in the Darwinian approach:

> Darwin's primary interest [was] the modification of living forms under the selective influence of the environment.... Magnificent as his grasp of this aspect of biology is, it is counterbalanced by a curious lack of interest in the nature of the organism itself.... It is difficult to find in Darwin any really deep recognition of the life of the organism as a functioning whole which must be coordinated interiorly before it can function exteriorly. He was, as we have said, a separatist, a student of parts and their changes. He looked upon the organism as a cloud form altering under the winds of chance and it was the permutations and transmutations of its substance that interested him. The inner nature of the cloud, its stability as a cloud, even as it was drawn out, flattened, or compressed by the forces of time and circumstance, moved him but little. (Eisely 1961, pp. 341–342)

In a sense, Darwin's gift of seeing how organisms change in relation to their environment kept him from acknowledging the organism in its own right. In and of itself this is not a problem. The problem arises when a one-sided approach becomes the only approach. Since Darwin, the main body of evolutionary science has followed this narrow and one-sided pathway. With the focus on genes and traits as survival strategies, the organism itself has been virtually lost from view.

Recognizing this problem, I have attempted in this study to give a many-sided picture of the giraffe. My aim has not been to "explain" in any narrow sense (which would entail reducing complex phenomena to underlying mechanisms). Rather, I've tried to present a comprehensive picture and let it stand as such. Such a picture brings us closer to the giraffe and its uniqueness, revealing the broader contexts of which the giraffe is a member, and also showing us what we don't yet know.

My central aim has been to bring the giraffe as a whole organism into view—to show the interconnectedness of its features and how we can begin to grasp it as an integrated whole. When we take the organism seriously, we gain knowledge of its integrity. This is what I have attempted with respect to the giraffe and its long neck. Yes, a giraffe can reach great heights to feed. This ability is remarkable, but it does not explain the neck. When we study the giraffe more in detail and the neck within the context of the whole animal, we discover an overriding tendency toward vertical lengthening that comes to fullest expression in the neck. This tendency shows itself in the legs, in the head, and in the shortening of the body. It becomes a key to understanding much that is unusual and special about the giraffe: the way it stands up, walks, and runs; the way it can reach so high; the way it awkwardly spreads its legs to drink; the way males spar with their rhythmically batting necks; its sensory focus in the overviewing eye. All these characteristics reveal the inner coherence of the organism. The picture of a specialized creature emerges with its unique—and one-sided—characteristics.

Even a nascent understanding of this holistic character of the giraffe transforms our image of what it means to be an animal. The giraffe is not a composite; it is not put together puzzle-like out of separate components. Its "long neck" is not a discrete trait added onto an already existing edifice.

From this perspective, the animal is an end in itself and irreducible. Typical evolutionary "explanations" ignore this quality of the organism and go to great lengths to reduce all evolutionary processes to genetics and environment. By so doing they forget the organism as the context of action and reaction for both genes and environmental cues. Unless you presuppose a center of cohesive activity that is the evolving organism itself, you're dealing with an abstraction.

The pillars of contemporary Darwinism—genetic mutation, gene recombination, and natural selection—therefore appear as modifying, regulatory factors and not as the driving forces of evolutionary innovation. They presuppose the "organism as a functioning whole … coordinated interiorly before it can function exteriorly," to use Eisely's expression. The whole organism—conceived in broadest terms—is the context for both genes and natural selection and is not a mere effect of their actions. It is the crucial font of evolutionary innovation.

Placing the holistic gestalt of the organism back into the center of evolutionary considerations has enormous implications. We can no longer look at animal evolution as the outcome of the interaction of causal mechanisms. We are always led back to beings that evolve in relation to other beings and to the many inorganic forces of nature. Beings interact and coevolve; yet each evolves in its particular fashion. No being is reducible to something else. This is a central riddle of life on earth, of development, and in the end, of evolution.

* * *

A towering giraffe ambles over a grassland, its long tail swishing back and forth while its deep black eyes glisten alertly. Its gaze encompasses a broad horizon high above the sea of ground-level smells in which other mammals live. The short body carried high by its long slender legs surges up into the grand neck from which the giraffe looks mostly down upon the world. Moving into the trees and bushes its clear gestalt dissolves among the patches of dark and light. It lowers its neck, extends its long tongue and enwraps a branch, stripping off the young leaves. It prunes the bushes and small trees from above and, occasionally, stretches its neck, head, and tongue upward to reach the lower branches of a large acacia tree, pruning it from below.

When we get too close the giraffe moves off and breaks into a gallop. It spreads its long legs and brings them back together in long strides. With its head held high, the neck undulates slightly to and fro. This ethereal movement stops and the giraffe stands. Its gaze spreads into the world around it.

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