TEXT BY ROBERT E. SIMMONS

TALL TALES

Or how the giraffe got its neck

Giraffes have long fascinated and intrigued us. Centuries ago, kings and emperors gave them as gifts and their extraordinary height and long necks have inspired countless myths and legends. Some 150 years ago Darwin suggested that these lofty creatures evolved to take advantage of the leaves at the tops of trees – a suggestion that has become the accepted explanation for the animal's remarkable morphology. A chance encounter with male giraffes doing battle, however, set biologist Rob Simmons thinking about alternative theories for how and why the world's tallest animal came to be.

The giraffe is an oddity by any yardstick. Its Latin name (camelopardalis) suggests that it is a cross between a camel and leopard. Often given as a gift between kings and emperors to impress and astound, this lofty creature has inspired an abundance of legends – mostly early attempts to explain the origins of its height and especially long neck. Despite the ingenuity and mastery of the spoken word, almost all of these tales were works of art, not science, and have been discarded by modern-day biologists seeking to understand the strange and inexplicable. And yet there is one tale that persists. In Charles Darwin's own words, it is clear how he believed the world's tallest animal came to be:

JEAN PATRICK SURAUD

Clubbing using the neck and head is a fighting style unique to giraffes

MARTIN HARVEY

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'With the nascent giraffe, the individuals which were the highest browsers and were able during dearths to reach even an inch above the others will often have been preserved. These will have left offspring inheriting the same bodily peculiarities, while the individuals less favoured in the same respects will have been the most liable to perish. By this process long continued, an ordinary hoofed quadruped might be converted into a giraffe.'

His observation is so seemingly obvious that it is probably one of the few evolutionary puzzles that has one universally accepted explanation. To challenge such a hallowed idea, one must be either be a little crazy or have a new tale to sell …

In 1996, Stephen Jay Gould described other reasons for the giraffe's long neck and made the point that the above story, which appears in every textbook on evolution, was never a main theme of Darwin's own writings. 'It is,' he wrote, '…a fairy story that Darwin was far too smart to tell, but that has entered our high-school texts as a classic nevertheless'.

I was firmly in the Darwinian camp until a few years ago, when I happened upon three young male giraffes standing together on a track in the Sabi Sand Game Reserve, bordering South Africa's Kruger National Park. Although I was studying eagles, these mammals aroused my curiosity. Unlike most giraffes, they were doing something other than watching tourists. All were standing flank to flank, legs apart, heads held high and sinuously rubbing their necks together, while pushing and gracefully straining against their opponents. 'Necking' had suddenly taken on a new meaning. But more was to follow.

One male moved away, and the interaction between the two more evenly matched animals intensified. The necking became rougher and the pushing more obvious, until eventually the animals were swinging their great necks in wide arcs and smashing the backs of their heads – and stubby horns – into the sides of their opponent. They were fighting and, unlike any other mammal on earth, they were using their necks and heads as clubs. And these were just youngsters. As I was to learn later, full-blown battles between large males are brief, often violent and on at least three written occasions, bone-crushingly fatal.

Clubbing using the neck and head is a fighting style unique to giraffes. Zebra, like many ungulates, bite or kick; kudu head wrestle, buffalo butt heads and rhino clash horns. In many cases, the fights don't progress beyond posturing and end when one opponent runs away. This is also true of giraffes

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– a mere skyward point of the head is usually sufficient to send potential competitors on their way. Imagine however, a 30-kilogram weight on a flexible two-metre carbon-fibre pole (itself weighing 100 kilograms), swung with maximum force by a one-tonne animal and you have some idea of how it would feel to be hit by a male giraffe.

Eyewitnesses to giraffe fights often report great thudding noises and this is no surprise, given the intensity of the battles. Giraffes reach an average of five metres and their necks comprise just under half of that. Of course, the longer the club and the bigger the head, the greater the force that can be used.

Some clue to the reason for the giraffe's long neck must surely lie in the past. Fossil evidence suggests that giraffids probably evolved in Asia and India and were shorter than the species we see today. One evolutionary line of giraffids – the Sivatheres – was physically massive, up to twice the weight of present-day giraffes. The Sivatheres were relatively short-necked browsers with weird antler-like horns, suggesting that these animals, like deer and moose, engaged in head wrestling and did not use their heads and necks as clubs. Fortunately for students of giraffid evolution, nature has left us with possibly the most handsome of all African ungulates – the velveteen okapi. Confined to the forests of the Congo, these shy animals are almost identical to the progenitor of the giraffe, a fast and agile animal that probably lived on the fringes of savanna and forest.

Some 12 million years ago, the first look-alike giraffe (*Giraffa jumae*) arose and was slightly larger than the extant giraffe with somewhat flattened horns. About one million years ago, there was a sudden radiation of giraffids, more gracile than today's species, but all sporting the elongated necks and short, stout horns that are used so effectively in clubbing. What factors moulded these animals and how did that controversial neck evolve? ▶

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My alternative to Darwin's tall story is that giraffes evolved long necks because males that have them can beat (and sometimes kill) those with slightly shorter necks

As Darwin argued a century ago, there are two main selective pressures shaping any organism – natural selection (the surviving) and sexual selection (the reproducing). The better you are at surviving and reproducing, the more likely you are to swamp future generations with your genes. My alternative to Darwin's tall story is that giraffes evolved long necks because males that have them can beat (and sometimes kill) those with slightly shorter necks. If they then gain access to oestrus females and father offspring, the process of sexual selection can operate. This is the sexual alternative to the universally accepted theory of natural selection, which suggests that giraffe are out-competing coexisting leaf-eaters by being able to reach food during times of famine.

When evolutionary biologists propose new twists on old chestnuts, they can either show that the old chestnut is hollow, or test their new hypothesis with existing or fresh data. I tried both. I first looked for evidence that giraffes use their great height to out-compete other browsers. However, all of the studies I consulted showed that giraffes spend an inordinate amount of time with their necks bent. In fact, females in both East and South Africa spend so much time in this position that it can be used to identify sexes at a distance. Furthermore, during the critical dry months, the 'dearths', when Darwin predicted that long necks would be most advantageous, leaves disappear from the tall trees and several studies have found the animals feeding from low bushes. Not much advantage there, then. Perhaps there are other feeding benefits that could explain the long necks?

A recent study by Elissa Cameron and Johan du Toit has found that knob-thorn acacias, a principal food type of giraffes, allocate more leaves per twig at two and four metres than they do at one-metre levels. Leaves from each level of the trees have similar quantities of leaf tannins, so giraffes are able to enjoy a meal beyond the reach of the smaller browsers, such as steenbok and impala. This is the first time that any feeding advantage has been found for browsing giraffe.

I also looked through fossil records of giraffid ancestors for evidence that past feeding habits may have favoured long necks. One problem here is that we have no idea how species such as the giant Samotherium actually fed. Studies of the wear on their fossilised teeth indicate that they were mainly browsers. Morphologically, they were about three-quarters of the leg length of present-day giraffes but, critically, did not have elongated necks. Their shorter necks do not suggest a feeding ▶

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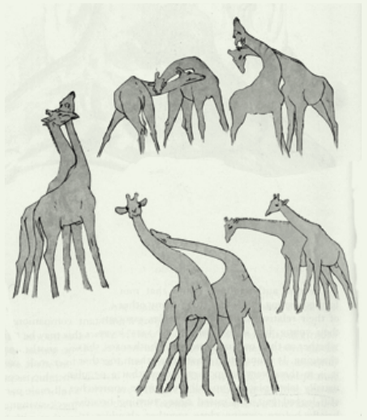
JEAN PATRICK SURAUD

The evolution of the giraffe?

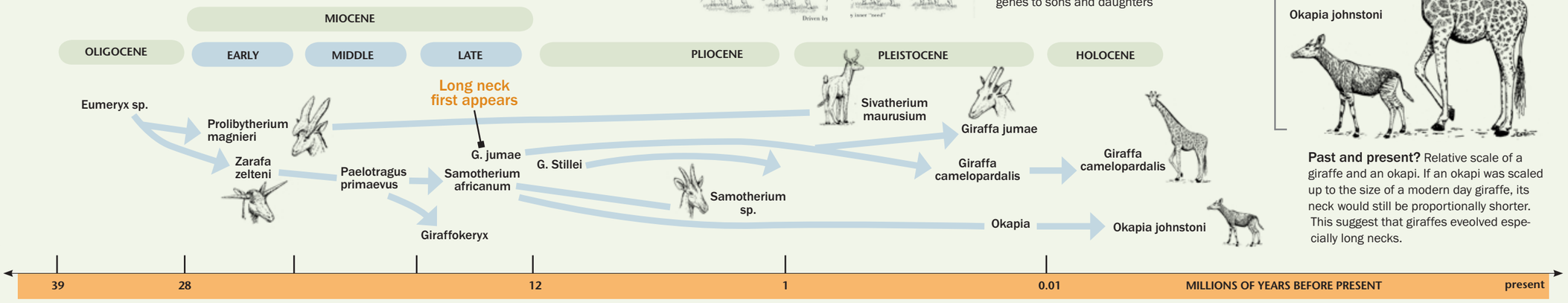
Fossil evidence from Africa and Asia indicates that the giraffid line began about 30 million years ago with an animal similar in size to the present-day okapi but with more elaborate horns. Separate lineages produced massive animals with short-necks, now extinct, and just two present day extremes – the forest-dwelling okapi and the savanna-dwelling giraffe.



Sexual advantages accrue to males with longer necks because they beat shorter-necked rivals and gain access to oestrus females.

Larmark {who is he?} postulated that the action of stretching reaching above the height of other browsers would be passed onto future generations. Darwin postulated that during times of dearth (fewer leaves on trees), giraffes that were able to reach above competitors would survive and pass on their long-necked genes to sons and daughters

Past and present? Relative scale of a giraffe and an okapi. If an okapi was scaled up to the size of a modern day giraffe, its neck would still be proportionally shorter. This suggest that giraffes eveolved especially long necks.



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advantage per se, but selective pressures may have favoured massive bodies over elongated ones. So, direct evidence for feeding competition is poor. Moreover, the morphology and antler-like horns of these ancient giraffids suggests that male-to-male combat took the form of head wrestling rather than clubbing.

It is useful to ask what sort of animal one would get if the giraffe's closest relatives were simply scaled up. One might argue, for example, that, with increased body size, the risk of predation might decrease and fortuitously giraffes could then feed off tall trees. However, contrary to popular – and even scientific – belief, giraffes are not immune to predation. Lions are not slow in tackling and bringing down one-tonne bulls and, indeed, males are almost twice as likely as females to fall victim to the big cats. In the Kruger, for example, researchers found that giraffes were the lions' third most-favoured meal. Size alone, it seems, is no protection against strong and savvy carnivores.

So, the predation theory is flawed, but let's follow the scaling-up idea nonetheless. Fortunately, as we have seen, the forest-dwelling okapi is morphologically very similar to the ancestral giraffid *Palaeotragus primaevus*. Simple scaling shows that an okapi with a leg the length of a modern giraffe would have a neck that is less than half that of its cousin. This suggests two things: that a giraffe is not simply a scaled-up version of its ancestors; and that there appears to have been specific selection regarding the neck.

So what of the sexual selection idea? It is clear that males fight with their necks and heads. But long-necked males must not only win battles, they must also father more offspring. Research in the Serengeti from 1985 showed that males with longer necks were dominant over shorter-necked ones, and were more often seen in the company of oestrus females. Intriguingly, the preference of some females for long-necked males was also apparent. These females allowed males with long necks to urine test them most often, while refusing shorter-necked males altogether. During such a test, the male passes a stream of urine over his Jacobson's organ (indicated by the curious flehmen behaviour) to determine whether the female is in oestrus or not. If a male is not allowed to determine a female's status, he has little chance of fathering any offspring.

A third clue that male necks are designed for fighting comes from some rather bizarre data collected by the late Lue Scheepers. He had the unenviable task of chain-sawing culled giraffe in Etosha National Park, Namibia, to measure the relative contribution of bodies and necks to the mass of each giraffe. By ageing both males and females through wear and tear on the teeth, he found that females stopped growing between eight and 10 years old. The necks and heads of males, however, continued growing at a rate of four kilograms and one kilogram per year respectively until they died. This increase was manifest in the sometimes grotesque bony growths at the top of the skull – exactly where one would expect protection during clubbing battles. Some male heads weighed in excess of 30 kilograms!

Of course, females don't fight and males do, so one expects size differences in heads and necks. However, even more exciting was the finding that large males grow disproportionately larger necks than smaller males. In other words, even when large old bulls are slowing down in body growth, the very instrument they need to out-neck a competing male continues to grow. The same phenomenon appears to take place with the tusks of older elephants. Both patterns are predicted by sexual selection. It is unlikely that the neck gets bigger simply to support a larger head since neck mass increases four times faster than head mass. And necks, are critical in the clubbing process.

Overturning a long-cherished idea, especially one formulated by Charles Darwin, is sure to stir the evolutionary pot. Many colleagues, for example, question the sexual selection idea because it doesn't easily explain the long necks of females. This is an interesting dilemma. As we've already discussed, females often feed with their necks bent, well within the zone used by other browsers, which suggests that they derive no competitive edge from this extra height.

Perhaps, then, they are not selected for anything? Many biologists are unhappy with such explanations because they are seen as poor substitutes for direct-benefit ideas. What we often fail to appreciate is that all organisms are the product of complex interactions

JAY COLLIER/CANON

Research in the Serengeti from 1985 showed that males with longer necks were dominant over shorter-necked ones

between constraints imposed by original body plans of ancestors, evolutionary brushes with predators, battles with conspecifics, food-finding abilities and surviving bottlenecks induced by climate and habitat change, all linked by genes over millions of years. The last ingredient is probably the key to explaining female size and neck length. I believe that female giraffes have been genetically 'dragged along' by the intense sexual selection on males. Arguments of this sort are used to explain other appendages that appear on both males and females, but are only used by one sex – nipples in male mammals, for example.

Experiments on fruit flies, mice and turkeys that have artificially selected for larger body size in one sex have also shown increases in the body sizes of the opposite sex, indicating that genetic links do exist. But, because these correlations are not exact, many females, as in the case of giraffes, have slightly smaller bodies than their male counterparts. Outside the lab, female ungulates often exhibit male-like horns that have no obvious function. This is the case in female giraffes, whose residual horns are so small that they would probably break if ever used in battle. It is possible that these too are the product of genetic correlations.

It remains for future ecologists, palaeontologists and geneticists to explore the ramifications of the two principal competing ideas on how the giraffe grew a long neck and to separate the truth from the tall stories. Perhaps, ultimately, there is no need, for as Darwin wrote: 'The preservation of each species can rarely be determined by any one advantage, but by the union of all, great and small'. ■

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