Cambridge University Press
978-1-107-03486-0 - Giraffe: Biology, Behaviour and Conservation
Anne Innis Dagg
Excerpt
More information

1 Time-line of giraffe

This chapter has four parts. First, a discussion of the contentious topic of why giraffe evolved to have a long neck. Was it for food? Was it for sex? Next is a short section on the ancestors of giraffe which moved into Africa from Asia millions of years ago and eventually died out there. Then a discussion of the DNA of *Giraffa camelopardalis* itself and what it tells us about the numbers (contested) of subspecies or races spread out over most parts of Africa, information expanded in Chapter 11 on conservation. The chapter ends with an extended description of the giraffe's place in European history.

Evolution – why are giraffe so tall?

Teachers often use giraffe as a tool to explain conflicting theories of evolution. Lamarck believed that the height of giraffe was caused by the acquired characteristics of its forebears; calves had longer necks because their parents and ancestors had acquired them by reaching up continually to obtain browse to eat. By contrast, zoologists today believe in the selection of natural traits. Changes such as longer necks began by chance mutations in individual giraffids. These individuals were more successful than their shorter-necked friends in that more of their progeny survived to breed themselves. Over millennia the necks of the ancestors of giraffe gradually elongated.

Now teachers use giraffe for a new evolutionary lesson. Did giraffe evolve long necks so that they could obtain more food? Or did they do so because females chose to mate with large males who had the longest necks? The obvious reason is that their long necks and legs enable them to browse at heights other large herbivores cannot reach. Elissa Cameron and Johan du Toit (2007) favour this explanation because they found that in Kruger National Park, giraffe did indeed feed on favoured tall trees such as *Acacia nigrescens*. They ingested more leaf mass per bite high in trees than they did when browsing on lower bushes (and in consequence left more food for other ungulates). (Or, conversely, they ate high leaves because the lower ones were already being consumed by these smaller animals.)

However, Robert Simmons and Lue Scheepers (1996) disagree with this idea. They noted that even in the dry season when feeding competition among all ungulates is most intense, giraffe generally fed on low shrubs rather than tall trees. Females spent most of their feeding time with their necks horizontal, in which position both sexes fed fastest. Indeed, browsing by giraffe on low plants rather than tall trees is common in many parts of Africa (Dagg and Foster, 1982). Simmons and Scheepers were the first to suggest that giraffe height did not evolve because of feeding competition, but because of sexual selection. Male giraffe fight over the chance to mate with females in oestrus by clubbing each other with their heads; these become a highly effective weapon when mounted on a long neck. The winning animal gets to pass his DNA on to the next generation.[1]

In response to this suggestion, Graham Mitchell and his colleagues (2009a and 2013) argue instead that from measurements of many dead giraffe bodies, they have found that the growth patterns of male and female heads and necks are similar, and 'that sexual dimorphism of the head and neck is minimal and can be attributed to secretion of sex steroids.'

Food or sex? Robert Simmons, elaborating on his earlier paper but this time with R. Altwegg (2010), examined these two main competing hypotheses. For the first hypothesis, as we have seen, early giraffids with longer necks than those of other species would be better able to survive food bottlenecks during dry seasons to pass on their genes to the next generation. However, giraffe often forage or browse at shoulder height during winter shortages. As well, giraffe are much taller than they need to be to outreach other animals, and have been for more than a million years. Why would they have evolved to a height beyond, say, 10 feet, which would be enough to out-compete all other ungulates? (Elephants and rhinoceros forage on the leaves of trees they knock down, but their behaviour would not compete with that of giraffe.) We must keep in mind, though, that the various species of giraffids evolved when large herbivorous animals such as deinotheres, mastodonts, sivatheres and baluchitheres, now extinct, were competitors for browse.

The second necks-for-sex hypothesis assumes that over time males evolved increasingly longer necks so they could more effectively combat other males for the right to mate with females in oestrus. Females don't fight, but two males do after positioning themselves side by side, whacking each other by swinging their necks to club their opponent's body with their heavy head and horns (ossicones). Rarely is a male killed in such a battle.

There is ample evidence to support this possibility:

(a) males with larger necks are more likely to win combats and to mate with females (Pratt and Anderson, 1982, 1985);
(b) females in oestrus prefer to mate with large-necked and older males – neck mass increases with age in males but not in females (Pratt and Anderson, 1985);
(c) males in dominance contests have a display walk during which they hold their heads high, indicating height is a measure of dominance (Innis, 1958);
(d) skulls of adult male giraffe weigh considerably more than those of adult females – about 10 kg vs. 3.5 kg (Dagg, 1965); and
(e) in theory, sexually selected features of males are often correlated with negative costs for them, which is true for giraffe (Kodric-Brown and Brown, 1984). For example, males are more often killed by lions than are females, which may be related to their often being

[1] This original concept of sexual selection was argued by P. Senter (2006) to apply to sauropod dinosaurs which also had a very long neck. However, as these animals are all extinct, there is no way to prove this.

alone while searching for females in oestrus (Owen-Smith, 2008). Their larger size and thus need of more rich browse may also disadvantage them if food sources dry up.

In early fossil giraffids without long necks such as *Giraffokeryx* sp., the horns were on the side of the head and backward-pointing (Churcher, 1978). Their positioning would indicate that males fought with sideways motions of the head, as okapi also seem to, perhaps standing side by side as do giraffe. During their evolution the necks of ancestral giraffids increased in length and mass while the horns became shorter and more compact. With such weaponry they would have fought using their heads as clubs (as opposed to forward-facing horns which imply head-butting (mountain sheep) and antlered heads which imply head wrestling (elk and moose)). Ludo Badlangana, Justin Adams and Paul Manger (2009) speculate how the long neck of giraffids may have evolved beginning about 14 to 12 million years ago.

The unique feature of the giraffe, its neck, is so spectacular that these same researchers also delved into how it differs anatomically from those of 10 other artiodactyls. Although the giraffe neck is of course much longer, comprising over half the length of the vertebral column, it is also composed of seven elongated cervical vertebrae each scaled appropriately for that particular vertebra. (Although an eighth vertebra has been suggested, it does not in fact exist (Solounias, 1999).) This scaling is also characteristic of the cervical vertebrae present in fossil giraffids. The related okapi does not have a significantly long neck, so its lineage separated from that of the giraffe before 12–10 million years ago; it was during the late-middle Miocene that the necks of some giraffids began elongating. The researchers hypothesize about how these changes in the neck lengths of giraffids may have occurred, which was different than how the necks of the camel and llama or the gerenuk lineages evolved.[2,3]

Fossil remains of African giraffids

Members of the giraffe family, Giraffidae, were and are medium to large ruminating artiodactyls, distinctive because almost all have ossicones on their heads which resemble horns, but which are covered by vascularized skin. (In this book I shall call these prominences of giraffe ‘horns’, as most authors do, despite their difference from true horns that are present in cattle.) Giraffids also had in common large sinuses below these horns, and lower canines that were bilobed and therefore wider and flatter than those in most species. Strangely, though, they did not have long necks like the giraffe; that was a relatively recent adaptation perfected in Africa. Early giraffids migrated from Eurasia into Africa by way of what is now Ethiopia. Nine genera of fossil giraffids and five species of *Giraffa* lived in Africa, but all of these are now extinct except for okapi and our hero (Churcher, 1978; Mitchell and Skinner, 2003).

One of the earliest giraffids from the early Miocene (about 18 mya) in Libya was *Zarafa zelteni*, a lightly built animal rather like an antelope with ossicones sticking out on either

[2] Birds and reptiles usually evolved long necks by increasing the number of their neck vertebrae.
[3] From a hypothetical point of view, the tallest organism in the world which could breathe and move about would be 3.6 m (Page, 2012).

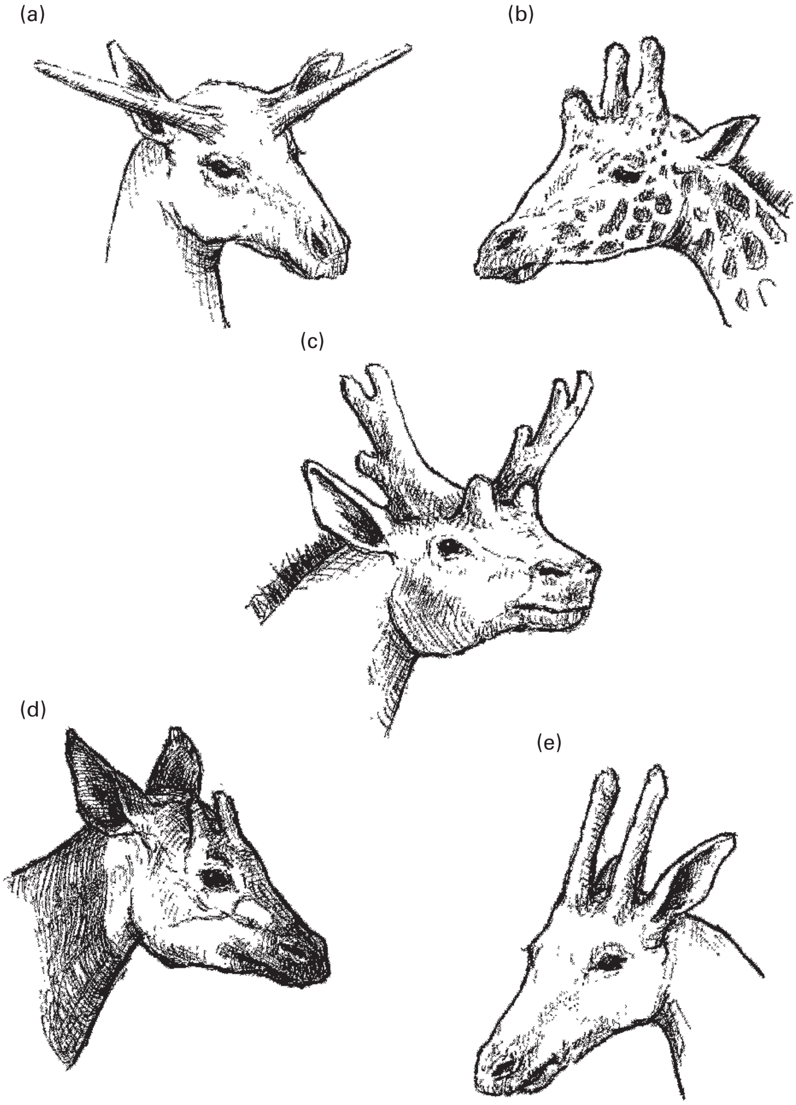

Figure 1.1 Giraffids from Africa: **a**, *Zarafa zelteni*; **b**, *Giraffa camelopardalis rothschildi*; **c**, *Sivatherium*; **d**, *Okapia johnstoni*; **e**, *Giraffa jumae*. After Churcher, Dagg and Foster, 1982; artist Jean Stevenson.

side of its head. Its line gave rise later to the okapi. By contrast, *Sivatherium maurusium* was the largest and most massive giraffid, as solid as an elephant and standing 2.2 m high. It was a more successful species because it lasted in Africa from the Pliocene to the late Pleistocene, about 8000 years ago; its fossil bones and teeth have been unearthed in South Africa, Uganda, Kenya, Ethiopia and Morocco, one cache spectacular because it involved 165 specimens (Franz-Odendaal *et al.*, 2004). This species had heavy spreading ossicones on its head, plus two smaller bumps in front of them, but it did not have a long neck (which would have been unable to support a weighty head) (Switek, 2009).

Giraffa jumae was apparently the earliest giraffe, existing from the Miocene to the mid Pleistocene, with fossils discovered in Tunisia, Ethiopia, Kenya, Tanzania and South Africa (Churcher, 1978). It was slightly larger than our present-day giraffe, with long legs but no median ossicone on the forehead. The earliest known bones of *Giraffa camelopardalis* are from the late Pliocene in Chad, from the early Pleistocene in Algeria and from the mid Pleistocene in Kenya and South Africa. Giraffe lived in Morocco until 600 AD, but then the drying of the Sahara made conditions impossible for it.

Formation of races

Recent research involving giraffe DNA tells the story of *Giraffa camelopardalis* as it spread out across the continent and evolved into different races (discussed in detail in Chapter 11). In their ground-breaking research, David Brown, Rick Brenneman and their colleagues (2007) of the International Giraffe Working Group analysed genetic material from 266 giraffe from 19 localities in Africa. This involved biopsy punches whereby a small amount of tissue was collected from each animal after it was darted in the flank or neck (Karesh, 2008). The researchers found that mitochondrial DNA sequences and microsatellite allele frequencies correlated with sharp geographic subdivisions. The divergence of these animals occurred in the mid to late Pleistocene when there was intense climate change in sub-Saharan Africa. Brown and his colleagues (2007) mention three specific climate-related factors that could have caused this diversification over time:

(a) in the late Pliocene conditions became cooler and drier which probably reduced connections between habitats frequented by giraffe;
(b) pronounced periodic oscillations (with a 21,000 year periodicity) of wet and dry conditions driven by changes in the intensity and location of maximal insolation may have facilitated habitat fragmentation and population isolation; and
(c) smaller-scale changes in habitat distribution perhaps promoted the isolation of specific populations, such as the expansion of a Mega Kalahari desert basin during dry periods of the late Pleistocene, which could have isolated the Angolan from the South African giraffe populations.

These climatic fluctuations, which presumably caused widespread changes in vegetation and habitat, leading to divergence, are evident in species other than giraffe, such as the hartebeest (*Alcelaphus* spp.).

For the past 50 years, no one doubted that giraffe all belonged to one species, *Giraffa camelopardalis*. Giraffe from specific regions of Africa often have similar spotting patterns (although never identical ones). As well, giraffe from all parts of Africa breed freely with each other in zoos. Giraffe have long legs that can carry them long distances; there seems to be no physical reason why, in the past, individuals from different parts of Kenya where there are now three races, for example, might not have interbred fairly often, given that there are no large rivers or mountains to prevent them from coming in contact.

Brown, Brenneman and the International Giraffe Working Group knocked this idea for a loop. From mitochondrial analysis, the team studied 381 individuals from 18 localities.

Figure 1.2 Rock-engraving of giraffe from Tuareg, Sahara. From Laufer (1928).

Only three of these animals were identified as hybrids between adjacent groups: one Masai/reticulated and two Rothschild's/reticulated animals. This emphasizes the low rate of interbreeding between subspecies/races. Indeed, even interbreeding among giraffe groups in the same ecosystem may be rare or non-existent judging from genetic material from members of four groups of Masai giraffe in the Serengeti that were only 60–130 km distant from each other. This has implications for research on the social behaviour of various races, as we shall see in Chapter 4.

The genetic data show that interbreeding among the current accepted subspecies of giraffe is almost unknown (0.8%). They rather are separately evolving lineages with

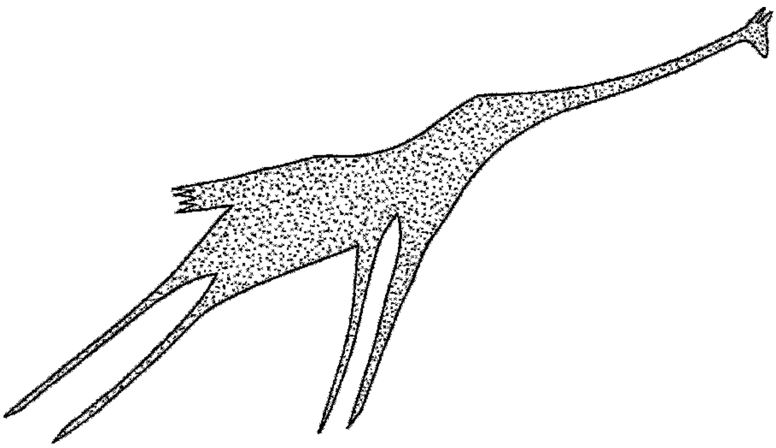

Figure 1.3 Rock-carving of running giraffe by Bushmen, South Africa. From Laufer (1928).

their own ranges. From mitochondrial-based coalescence analysis, it appears that these groups have been separated from one another from between 0.13 and 1.62 million years. Because of this, giraffe may be categorized in the future as being of more than one species rather than one single polytypic species. Indeed, the team suggests that the Masai giraffe might actually consist of two species, one on the east and one on the west side of the Rift Valley, and that some subspecies may have distinct population units within them. It is incredible to realize that this large mammal that spends its life constantly moving from one place to another while browsing actually covers a small area during its lifetime, and because of this has a taxonomy similar to that of a highly sedentary species.

Such a low rate of gene flow among different subspecies of giraffe living not that far apart is unprecedented for such a large, highly mobile African mammal. Why might this be? One suggestion from Brown and his colleagues is that reproductive cycles in giraffe (as in most large herbivores) are such that young are often born coincident with the growth of new browse rich in protein during the annual climate cycle. This occurs in July and August in the north, but in December–March in the south. The mortality rate of young giraffe is high (up to 67% a year: Leuthold and Leuthold, 1978a), so the faster they grow, the better. Should giraffe from north and south interbreed, young could be born with reduced fitness owing to environmental conditions. However, as we shall see in Chapter 9, giraffe can be born in any month; it may be that conception rather than birthing time tends to occur during the optimum growing season.

Another isolating factor may be the coat patterns of giraffe, remembering that communication among these animals is mainly visual. Calves who stay close to their mothers during their first few months may become imprinted on her spotting pattern and, of course, that of themselves. This could affect their choice of mating partners when they become adults. But again, the coat patterns of different races are often not that different.

Even food preferences might be important in separating giraffe populations. *Acacia tortilis* is a highly favoured food for Masai giraffe in the Serengeti (Pellew, 1983c), for example, whereas a population of *G. c. giraffa* browsed few of these trees in South Africa (Bond and Loffell, 2001). A map can be found in Chapter 11.

Such minimal interbreeding raises another interesting question. Until recently, many short-term studies of giraffe in the field have found that individual giraffe do not tend to hang around with other individuals to any extent. In his study of giraffe in Nairobi National Park, Bristol Foster documented that although giraffe were usually seen in groups, the members of these groups were constantly changing, which made him think that giraffe were not very sociable (Foster and Dagg, 1972). If two females were seen together in the Park more than a few times, these sightings were usually not successive, indicating that the two were far more often apart than together. One imagined them going off for days or weeks in different directions to browse, then wandering back to the Park as the spirit moved them. These new findings of minimal interbreeding between races, however, seem to indicate that giraffe are members of groups much larger than human researchers have been aware. It may be that giraffe breed within their very large groups rather than males, especially, going farther afield to find females in oestrus. This also implies that individuals recognize the scores or hundreds of other giraffe in their group, even though they do not see them particularly often. This indicates a fission/fusion system as is present in chimpanzees (Boesch, 2009), with extreme emphasis on fission rather than fusion.

Thinking of giraffe as belonging to many more species rather than one is far more important than just a matter of taxonomic interest. The number of total giraffe is decreasing each year because of pressure from expanding human populations and poaching, topics discussed in Chapter 11. Now we know that the decrease of some of these distinct populations is so great that they have become officially highly endangered – *peralta* with perhaps 300 members in Niger and Rothschild's population of about 700 animals (Brown, pers. comm., 2012). Every effort must be made to ensure they do not become extinct. It is no longer enough to think that there are many thousands of giraffe in national parks and reserves throughout Africa so what is the problem? Instead, we must ensure that all genetic populations remain viable.

Whereas nine subspecies have been accepted for many years (Lydekker, 1904; Dagg, 1962c; Dagg and Foster, 1982), now David Brown and his colleagues (2007) suggest the tentative number of possible species (but still considered subspecies at present) is six:

G. c. angolensis from southwest Africa;
G. c. giraffa from southeast Africa;
G. c. tippelskirchi, the Masai giraffe from southern Kenya and northern Tanzania;
G. c. rothschildi in Uganda and western Kenya;
G. c. reticulata, the reticulated giraffe from northeast Africa; and
G. c. peralta from Niger the northwest area of Africa.

Samples of their mitochondrial DNA sequences show that the first three southern subspecies and the last three more northern ones are more closely related to each other than to members of the other group. Giraffe of uncertain status include *G. c. antiquorum*, the central African form, animals from Zambia (*G. c. thornicrofti*) and those from Nubia and the Congo area.

Russell Seymour (2010), however, notes that the Masai giraffe, *tippelskirchi*, is actually more closely related genetically to the southern group despite its presence in Kenya and Tanzania. He also reports that the Zambian race, *thornicrofti*, is grouped within the southern clade but shares a mtDNA haplotype with giraffe from both north and south of Tanzania. Therefore, in the past, there must have been a migration of giraffe across the 'suboptimal habitat barrier'. Seymour also discusses tentatively the genetic relationships within the northern and southern groups.

The current status of and conservation measures for the races of giraffe are discussed in Chapter 11. Further information on recent genetic discoveries is reported by Liu *et al*. (1996), Vermeesch *et al*. (1996), Hassanin *et al*. (2007) and Huang *et al*. (2008).

Giraffe in European history

Giraffe were considered exotic and precious creatures to the early civilized nations of Egypt and Europe (Dagg and Foster, 1982; Mitchell, 2009). It was difficult to catch one in Nubia without hurting it to send down the Nile to Egypt, and demanding work to find it enough browse while in captivity to keep it healthy. Even so, individual giraffe were imported into Egypt as early as 2500 BC at a time where they no longer occurred there naturally. The two hieroglyphics representing the giraffe were translated as *ser* or *mimi*. The head of a giraffe on the body of a man was used in early times to represent Set, the god of evil who lived, like giraffe, in desert areas. That Set was always drawn with a long snout and square ears puzzled Egyptologists; what animal has square ears? It was finally decided that the ears were in fact horns, and therefore the animal must be a giraffe.

Queen Hatshepsut was given one for her zoological gardens in Alexandria by the region she conquered further south, and one was included in the Grand Procession (alias parade) in Alexandria about 270 BCE. Ostensibly it was given in honour of the god Dionysus by Ptolemy II, the Greek king who had recently taken over Egypt, but his real aim was to let his enemies know that this was a great and powerful new regime now that he was in command. It included 98 elephants marching four abreast, 48,000 foot soldiers, 23,000 cavalry, 2400 hounds led by slaves, 12 camels loaded with spice, 30 hartebeest, 24 oryx, 24 lion, 16 cheetahs and a single giraffe.

The first giraffe seen in Rome came from the zoo in Alexandria, given by Cleopatra to Julius Caesar in 46 BC. The animals were called 'cameleopards' in the advance publicity – they were as big as a camel but spotted like a leopard. Many Romans thought they would be as big as a camel but as fierce as a leopard, so they were disappointed in an age when the mass slaughter of gladiators and animals was valorized.

With the decline of the Roman empire, giraffe were forgotten in Europe. In 636 AD one scribe confused a cameleopard with a chameleon. Captive giraffe still existed in Egypt, but they were rare. When Egyptian forces defeated Nubians to the south, the annual tribute expected by Egypt was 360 human slaves and one giraffe.

Arab scholars wrote about this species, but few of them had ever seen a *xirapha*, the Arabic name of 'one who walks swiftly' for this creature. One Arabic pedant noted in 1022 that the father of a giraffe was a leopard and the mother a camel. He scorned those

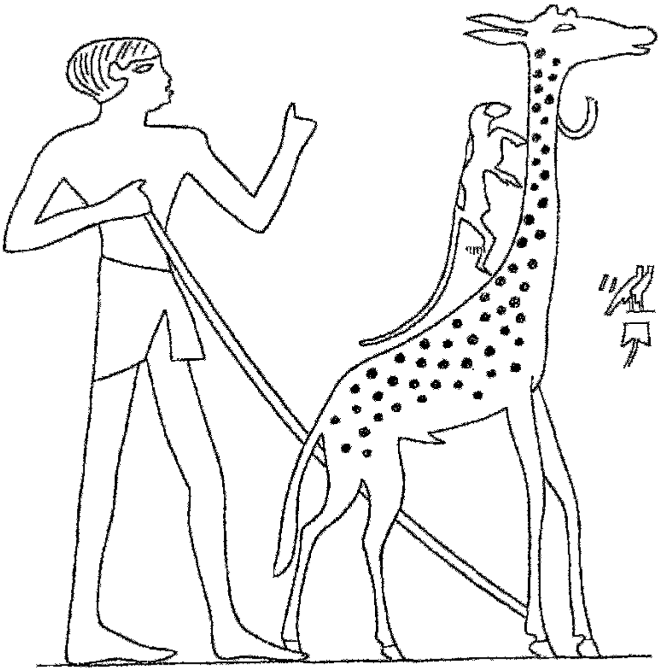

Figure 1.4 Giraffe depicted from an Egyptian tomb. From Laufer (1928).

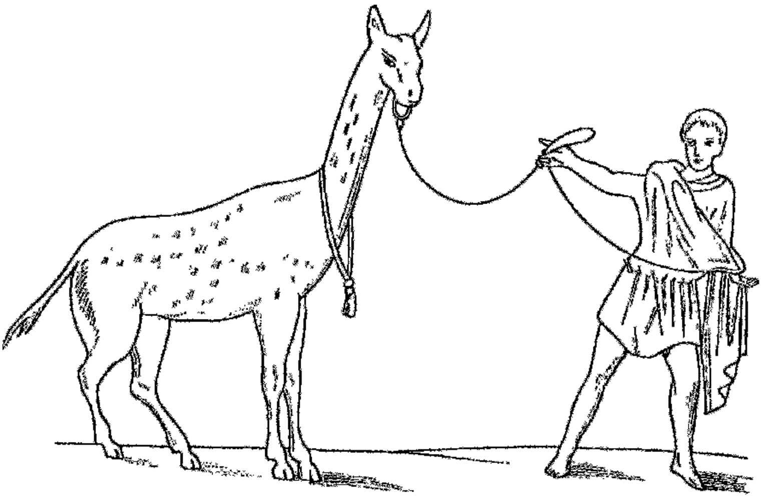

Figure 1.5 Giraffe with guide from Roman mural painting. From Laufer (1928).

who thought a horse could father a giraffe. ‘It is well known that horses do not mate with camels any more than camels mate with cows.’ Another Arab wrote that the offspring of a cross between a male hyena and a female camel had to be crossed in turn with a wild cow to produce a giraffe. It is clear that pedant Arabs had little to do with domestic stock.