Anatomy and Evolution of the Giraffe

Giraffe partes ignotae

"Giraffa" a Brunnich est appellata anno MDCCI (1771). Hic animal maioribus est notum ut camelopardalis. Habent vertebrae cervicales longae, scapula et metapodiales longissimas, latua descendit, vertebrae lumbales breves, membra longa graciliaque, et vertebrae caudales longae. Lingua est longa, et smaltum e Giraffe partes ignotae

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Parts Unknown

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To Alexander and Jason Solounias

Giraffe: partes ignotae

“*Giraffa*” a Brunnich est appellata anno MDCCI (1771). Hic animal maioribus est notum ut camelopardalis. Habent vertebrae cervicales longae, scapula et metapodiales longissimas, fatua descendit, vertebrae lumbales breves, membra longa graciliaque, et vertebrae caudales longae. Lingua est longa, et smaltum est crenulatum. Cornua sua sunt mira.

The giraffe: parts unknown

Giraffa was named by Brunnich in 1771. The animal was known to the ancients as camelopardalis. They have long cervical vertebrae, the longest scapula and metapodials, a down-turned snout, short lumbar vertebrae, long slender limbs and long caudal vertebrae. The tongue is long and the enamel is crenulated. Their horns are exceptional.

Giraffe: partibus ignotum

Describere per Brunnich anno 1771. Quod animalis, notum factum est ut veteres camelopardalis. Illi enim dum ceruicis vertebrae at scapulae atque longissimum. Etiam metapodials longae est. Conversus est eruerit rostro descendit,brevi vertebrae lumborum, longi graciles exureret artus, caudate vertebrae longae est. Lingua longa est et corium hyrcinum tabulae crenulated. Amplitudo cornuum est tutaretur.

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PREFACE

I have been fascinated and magnetised by bones and skeletons since I was four years old. At nursery school, I stood in front of an elementary display cabinet that contained a plastic anatomy torso for hours every day staring at the anatomy and the chart of a human skeleton. When I was seven, I searched for and found fossil bones on Samos. They were derived from the famous Miocene bone beds that have been excavated so many times since 1840. Our family is from Samos; all four grandparents were Samians. My grandmother Chrysoula Eleftheriadou Katsimatidis said to me "you like bones - why not go to the Samos elephant cemetery and find some". She said, "a long time ago there were elephants on Samos and their bones are still there". We stayed in Pythagorio in the summer. We travelled on a small black boat *The Kostakis* directly to Pythagorio from Piraeus. Grama's house was bombed during the war and there was no roof when I was young. We slept looking at the stars and the galaxies overhead and listening to the Aegean Sea. A farmer from the Mytilinii Village helped me find the fossil bones. He asked me "what are you looking for on the farms?" I replied "I am looking for the elephant cemetery." He took me on a donkey ride to the place. The first bone I found within minutes of prospecting was a *Samotheriuum* femur (a fossil giraffid). That was the most magic moment in my life. I still have it on my desk. We are never apart. I did not know what animal it belonged to when I found it, but I knew that it was a fossil. My fascination with bones remained strong. I would go to the window of the Museum of Paleontology in Athens and look in at the fossils as I was too embarrassed to go inside as a boy. You had to ring the bell and they would look at you strangely when going in; it was open to the public but it was a kind of unknown place. I always drew bones and had a few in my possession. One encounter with a real skeleton was at my paediatrician's office. I was six and when they opened the bone box, I was able to correctly assemble the entire skeleton on the floor. The doctor was amazed. We had an encyclopedia at home and every day I would open it to where the picture of the human skeleton was. I constantly admired that image and one of a Neanderthal for years.

My calling has materialised to study fossils, palaeontology, geology, biology and anatomy. In my life, I never changed or deviated from my plan and desire. Yes, there were many difficulties. So many difficulties. I grew up with little money and resources. We bought our first ice-box when I was six. We had to boil water on a wood fire so we could wash. We used cardboard paper from cigarettes to plug the holes in our shoes. Old shoes with holes were common. Now I am driving into Manhattan to the Natural History Museum with my own car and looking at the skyline of the city, I wonder how this happened? How did the boy from Samos end up being a professor and with keys to the palaeontology collections at one of the biggest museums of natural history? If I had stayed back, I would be selling postcards and little vases to the tourists on Samos. The path was full of obstacles. I had to leave my country in order to study animals. I came to the USA to study at the university. At Cornell, I worked in odd jobs to make ends meet. I stayed for free in the basement of a restaurant between the potatoes and the onions for a while. The obstacles continued as you can expect. Eventually, things materialised I got my PhD from the University of Colorado, in geology. After this, I looked for a job for 11 years. I was a postdoc trying to find something permanent. I finally got a job teaching anatomy and eventually became a professor. I started by studying whole faunas. I liked mammals and gravitated to hyenas and ruminants. I always thought the fossilised giraffes were fascinating. There was always a special space in my head for the giraffes. I travelled throughout Europe loving the fossils in the museums. I excavated in Tunisia and Kenya, and I run my own excavation on Samos. I went to Pakistan as part of the Harvard Siwalik expeditions. I also had an opportunity to see giraffid fossils in Beijing and in Gansu (the centre of China). Although I struggled with many fossils of the faunas, I always gravitated towards the fossils of giraffes. Eventually, after numerous adventures in science with faunas, hyenas, microwear and mesowear, I finally began to seriously investigate just ruminants; focusing on fossils and living giraffids. I have spent time with giraffe necks, limbs and the mysterious okapi.

I now have serious renal failure which makes life very difficult. I have many ideas about giraffids and I realised that I do not have the time to continue writing individual-specific papers on these topics. To do this, I will need thirty more years - time that I do not have. The future is unknown. A book is a more plausible answer to some of these problems. It is a way to publish new ideas and findings. Others will carry on and develop my ideas further. I am trying to summarise in this book some of what needs to be investigated more after me.

INTRODUCTION

The book explores giraffe anatomy and evolution. Most giraffe studies are focused on the behaviour of the animals. Dagg and Foster (1982), Dagg (2014) and Shorrocks' (2016) books are examples of the excellent coverage of what people have done. They are mostly a summary of behaviour and ecology. My book is different in two ways. First, it is a collection of mostly original and not previously published ideas. It is not a book summarising published works. The only exception to this is the neck chapter where I have already published some observations. Second, it is about anatomy and evolution. There is no other book like this for the giraffe and its close relatives. The giraffe anatomy cannot be studied in isolation. It is the comparisons of the giraffe to the other ruminants that enlighten us to the differences and the numerous similarities. The giraffe is a specialised, strange ruminant. Yet, we can learn from the giraffe about other ruminants because of it. Take the giraffe as an ambassador for the other ruminants. Among so many ruminants, the okapi, the deer and the water chevrotain are my basic comparative species. The same happened with humans and primates, which are studied disproportionally — what we know from humans can be extended to other species. The knowledge about humans is extended to other primates and more animals. Of course, the reverse has happened as well. I wish I could have had one more giraffe to dissect before completing the book. However, I have not been able to find a specimen. Thus, I go to build on what we know so far. In addition, the museums are closed because of the COVID virus. Therefore, it is impossible to even go to the collections to double-check many emerging issues. It is a strange time for everything.

There are so many people I wish to thank. Everyone who has helped me in my career has indirectly helped me learn about giraffes extinct and extant. Teaching in medical school is a problem for a researcher. Medical students want to be engaged in research but only have two months for that endeavor during the summer between the first and second years. There is really no time to actually research, complete and submit a paper in such a short time.

I have tried to publish with the medical students. Time is the only constraint. I feel sad that I cannot continue with them as they develop because their hospital work is brutal. I thank a bunch of these, now doctors, here as they helped me develop some of the anatomical observations. I did the artwork myself. So I was fortunate to be able to do that but unfortunate in not having my own laboratory and for being strongly dyslexic.

The book is organised into topics. In every topic, there are three parts (aspects). A general one sentence or two in summary (a), which is the easier part to read (b) a technical section and (c) a very short selection of references and acknowledgements relating to each topic. At the end, I acknowledge the doctors and colleagues who helped me with those topics of research years ago when they were students. The museums are referred to by the name of their city to make the reading simpler. You will find the official museum names in the back. I also provide a crude classification of taxa mentioned as an appendix for your reference.

The history of the giraffe comes first. This history is actually covered well in Wikipedia. Thus, I will not repeat much of this information. I do however have some surprises to offer from the Sahara petroglyphs and the *Histories* by Herodotus.

The skeleton comes next. Very few books cover the skeleton of a mammal in articulation. Descriptions of isolated bones can be found in many palaeontology studies but a whole skeleton is not presented anywhere. In Paris, the curators put up a ladder so I could photograph the articulated giraffe as a whole from mid-level. In Vienna University and the Palais Rumine of Lausanne, the skeletons were harder to study. There are also mounted skeletons in the Natural History Museum and the National Museum of Natural History. The giraffe as a whole has numerous peculiarities. These peculiarities become relevant when the giraffe skeleton is compared to other selected ruminants using stick figurines of them. One can even draw some evolutionary conclusions from these comparisons. It is possible to fairly accurately define what is a giraffid now.

Locomotion was actually researched recently by Basu *et al*. (2019). I did however find some new ideas considering the locking of the gelno-humeral joint and the knee. There are also new ideas about the lifting of the limbs as they walk.

The male fights are interesting. The males use the neck and the head in complex ways. Thoracic vertebra one is a pivot point for the flexible neck. Thoracic one takes the load of these combative movements. There is an asymmetry in the articular facets which opens up questions about the giraffe neck-siding. There may be left and right necked giraffes.

The long neck is so interesting. It is what everyone notices about the giraffe. I have tried to understand the neck specialisations. Several cervicals are homogenised in morphology. The neck fits very tightly and anteriorly on the pharynx. What secrets does the neck contain?

The head of the giraffe is full of unknowns. A giraffe has a droopy snout followed by a hard to find nasolacrimal duct. The head contains a spectacular frontal sinus which is a labyrinth of information.

Do giraffes make sounds? Can we find out how? And what is the story with the extra ocular muscles? Yes! They pull their eyeballs in upon impact of the head with an opponent. Dissecting the tongue surprised me. I had to go out to get some fresh air after what I saw. My students were not able to understand the significance of this. The tongue has two long cartilages inside. This is what chameleons have. Now we can comprehend better how they stick out their long tongue (see below).

The shoulder and the knee have locks. I think they lock these joints both when they are moving and in rest when they stand for hours. Motion with locked joints is very powerful for the distal limbs.

Little is known about this most interesting animal.

I wanted to dissect one or two more giraffe specimens before the completion of this book, but I was unable to find one. My kidneys are failing fast, and my active time is limited. My muscular dissection is very general and is based on Candy, a giraffe euthanised at Memphis Zoo, and also with specimens from the Sheyenne Mountain Zoo, the Columbus Ohio Zoo and

San Diego Zoo. I also thank Miami Zoo, Brookfield Zoo of Chicago, and the AMNH mammalogy database for specimens of giraffe and okapis.

Medical students come and go and often get involved in research. Sometimes their research gets published but other times the demands of medical school and the system make it very hard to complete a research paper. I acknowledge these now doctors for their help with the work and the ideas when they were medical students.

Terminology

Lower meaning closer to the ground - anterior meaning cranial and posterior meaning caudal

ANCIENT CONSIDERATIONS AND A NEW SPECIES OF GIRAFFE, *GIRAFFA SAHARA*

The history of the giraffe is interesting for its etymology and how the ancients saw it in the Sahara and elsewhere. It has been established that the Sahara was a rich woodland between 10,000 and 5000 years ago. As such it makes sense that people and central African mammals would occupy the region expanding their ranges. Actually, there are climatic cycles, and the Sahara was green multiple times. It was woodland numerous times during the Pleistocene. The oldest records of the giraffe are found in numerous petroglyphs in the Sahara (e.g. Fig.1). There are hundreds of drawings on rocks. Most are Neolithic or could be even older. It is well known that most ancient cave art and petroglyphs are really excellent representations of the animals in question. Details reveal the accuracy of the depictions. Dave Guthrie's book (1990) is full of examples (4.3, 4.11, 412, 5.13). The same is true for the giraffe petroglyphs. There are books covering these petroglyphs (e.g. Clottes, *et al.* 1999). I re-drew some of my favourites. To find the copyright for originals is difficult and so I made copies of the originals (Fig. 2). Google images display many petroglyphs should you be interested.

The majority of the rock art shows true and clear representations of giraffes and other species. However, I have made an interesting observation. Four of the petroglyphs show a giraffe with a spot pattern that has smaller and more densely packed patches of squares, actually circular spots. These are in Dabous, NE Niger and other places. The same is true for an ancient Egyptian mural in the Metropolitan Museum of Art in New York City where the giraffe has again numerous circular spots. These are unlike any of the modern giraffe varieties and subspecies. Carving on rock surfaces is labour intensive for the prehistoric artist. I infer that the close pattern of spots was true to an extinct unknown species of giraffe. Examination of the surface seems deliberate with details; like where the main terminates the limbs, the sex organs, the size of the ears, and the pelage patterns. The snout of this giraffe is also noticeably narrow. There is damage to the face and another area of the left scapula. Next to this natural size specimen, about eight meters high, is a second individual, perhaps a younger one drawn to fill a narrower section of the rock face. Both have small heads. The pelage of the larger one is more circular, which is even harder to carve. Nowadays giraffes have eight squares on the side of their neck (three rows of eight). This drawing has more than 200. The circles of the pelage of the neck are small and those of the rump are large which is logical compared to other modern animals. I believe this to be a true representation of an extinct species. Two more drawings are found on the rock with the same patterns. One is a group of seven giraffes facing the same direction. The other is four giraffes: one facing the other three. In addition, a final drawing shows a sitting giraffe. The posture of the leg position is very natural. This figure has 108 spots on its neck. Again, the rump spots are larger. In all these drawings, from different regions of Africa, the spots are more circular. Many species of animal have type specimens. This is common practice with registered specimens in museums. It is especially true for extinct species. A type is an individual on which the species is based. The type usually follows the original description of the species in a scientific journal. It is representative of that species. Often more representative (better preserved) individuals are found later on but the type remains as special and the date of the naming is locked. It is the proper tradition for describing new species. Many common animals, however, with older names from the nomenclature of Carolus Linnaeus and others, do not have type specimens. For example, this is true for elk, various deer, gazelles, oryx, lion, tiger, cat, foxes and wolves, the Nile crocodile, many common birds and common fishes. They do not have type specimens. None of the current giraffe species has a type specimen. I believe the giraffes should have type specimens for the four recently identified species (Fennessy et al. 2016). However, the logistics and the cost of selecting an individual and saving it in a museum is not possible at the present. This should be done some day and also the selection of types, for variety, can be added to museums. One may begin the process by selecting type specimens for the living populations at least. I propose to name the more famous petroglyph of this giraffe as a new species of bones which may be discovered someday in Holocene deposits. I think a good trivial name for this species would be Sahara. Sahara, but not because of the desert conditions there. Sahara is a huge geographic region that numerous times in the past was a savanna or even wooded with lakes and small rivers. The desert we see today is a rather recent outcome. *Giraffa sahara* rhymes well (two feminine names ending in an a) and is where this giraffe lived. If it is feasible, the holotype would be the now-famous petroglyph from Dabous, NE Niger. It is reasonable to do this and the term for such a species is an ichnospecies; a type not based on a fossil. This species is now extinct probably because of desertification. There are numerous lake deposits in the Sahara. Perhaps skeletons will be found there someday (Clottes et al. 1999).

Historic comments about the giraffe and the okapi

More recently, we have information about the giraffe from the ancients. The word *camelopardalis* means camel with spots in Greek. *Pardalos* is spotted and also can mean crazy or silly. Apparently, the ancient Greeks had seen the animal and named it that. Aristotle and others believed in the mixing of species. So it is plausible that they saw the giraffe as a mixture of a camel and a leopard. The name originally may also just mean a camel with spots. The other related names are leopard meaning lion with spots, and camel is *kamelos* from the Greek and is also of Semitic origin and used in the New Testament. The name *camelopardalis* was a genus until the researchers found the name *Giraffa* in the literature, which had been presented more officially (as they claim). The name is late 16th century: from the French *girafe*, Italian *giraffa*, or Spanish and Portuguese *girafa*, based on the Arabic *zarāfa*. Simpson (1945) and others have found the original scientific citation: *Giraffa* in Brisson 1756 and *camelopardalis* in *Schreber* (1784). Also *Giraffa* in Brunnich (1771), Simpson (1945) and Bell and McKenna and Bell (1997). Lamarck and even Darwin of course mentions the giraffe as many of us know in relation to the long neck and the evolution of that neck. The giraffe neck is an icon for evolution.

In Wikipedia, we learn that: the name 'giraffe' has its earliest known origins in the Arabic word *zarāfah* (زرافة), perhaps borrowed from the animal's Somali name *geri*. The Arab name is translated as 'fast-walker'. There were several Middle English spellings, such as *jarraf*, *ziraph* and *gerfauntz*. The Italian form *giraffa* arose in the 1590s. The modern English form developed around 1600 from the French *girafe*. Note that the root *gere* is interesting.

Note that *gerenuck* means the giraffe neck; the colloquial name of the gazelle *Litocranius walleri*.

Although the okapi was unknown to the western world until the 20th century, it may have been depicted since the early fifth century BCE on the façade of the Apadana at Persepolis, a gift from the Ethiopian procession to the Achaemenid Kingdom. For details see the Oriental Institute of the University of Chicago archives. The Oriental Institute identifies the carved relief as an okapi with a question mark. The animal was brought to prominent European attention by speculation on its existence found in press reports covering Henry Morton Stanley's journeys in 1887. In his travelogue of exploring the Congo, Stanley mentioned a kind of donkey that the natives called the *atti*, which scholars later identified as the okapi. Atti in Modern Greek means horse. Although Johnston did not see an okapi himself, he did manage to obtain pieces of striped skin from a ceremonial belt and eventually a skull. I have seen the holotype belt in the mammalogy collection of the Natural History Museum in London. The isolated skin resembles so much that of a zebra that originally it was inferred to be a new species of zebra. From this skull, the okapi was correctly classified as a relative of the giraffe; in 1901, the species was formally recognised as *Okapia johnstoni*. Lankester, Fraipont and Forsyth Major were pivotal in the early studies of the okapi. In 1901, Sclater presented a painting of the okapi to the Zoological Society of London that depicted its physical features with some clarity. Much confusion arose regarding the taxonomical status of this newly discovered animal. Sir Harry Johnston himself called it a *Helladotherium;* one extinct giraffids species from Pikermi. Based on the description of the okapi by Pygmies, who referred to it as a "horse", Sclater named the species *Equus johnstoni*. Subsequently, zoologist Ray Lankester identified the okapi as a new genus.

Johnston identified the okapi and named it *Equus johnstoni* in honour of the finder. Ray Lankester named the okapi correctly in a new genus *Okapia,* but the holotype specimen is the ceremonial belt which I was fortunate enough to see and touch that the Natural History Museum in London. It contains the typical rear-end okapi stripes (Lankester 1901, 1902, 1907).

This is an interesting story that may relate to the okapi as an inhabitant of the old wooded Sahara; prior to it being a desert. Could the ancients have seen okapis and thought they were zebras? Herodotus describes the fauna of Libya west of the Triton River (Si Dewald and Marincola eds., 2006). In Herodotus Book Four, Paragraph 191 he writes:

> ….has more wildlife and many more trees than the rest of Libya as a whole – has far more wildlife and many more trees than the rest of Libya. I mean the eastern part of Libya, where the nomads live, is flat and sandy; but then the land of the farmers west of the river Triton is very hilly and thickly wooded and teems with wildlife. There are enormous snakes there, and also lions, elephants, bears, asps, donkeys with horns, dog-headed creatures, headless creatures with eyes on their chests (at least this is what the Libyans say, wild men and wild women and a large number of other creatures whose existence is not merely the stuff of fables…

Paragraph 192…These species are unknown in the territory occupied by the nomads, but there are others there:

> white romped impalas, gazelles, elands, donkeys [not the horned but a non-drinking variety, because they never drink], antelopes which are the size of oxen and whose horns are used to make the sides of lyres, foxes, hyenas, porcupines, wild sheep, fennecs, jackals, panthers, addaxes, three were cubit long land crocodiles which look very like lizards, ostriches and tiny one-horned snakes. These animals are peculiar to this part of Libya …

Here we have the text that says “donkeys with horns.” Remember that the locals from Zaire also called it an *atti*; a donkey. Could that be an okapi in Libya? There is no way to prove this hypothesis but note also that the okapi was mistaken for a zebra by the first observers who discovered it. The original label in the Natural History Museum reads *Equus johnstoni*, the name of a horse. Maybe the Libyans thought it was a donkey-zebra of sorts with horns. Consider now the big antelope with lyre horns of Herodotus? Could that be a *Sivatherium*? There are rumours that *Sivatherium* made it to the present day (Colbert 1936). Notice before we end, that the ancients had the concept of species established well enough. I have found two petroglyphs where an antelope could be interpreted as *Sivatherium*. In these petroglyphs, the front limbs are characteristically short (bottom of Fig. 1). This is a feature of *Sivatherium*.

Today the trivial name of one of the four giraffe species is *camelopardalis*. The four species are *Giraffa giraffa*, *Giraffa tippelskirchi*, *Giraffa reticulata* and *Giraffa camelopardalis* (Fennessy et al. 2016). Other scientists believe there are more species (Groves and Grubb 2011; Bercovich et al. 2017; Winter et al. 2018).

THE GIRAFFE SKELETON

I will now provide a whole skeleton evaluation and description of the giraffe and other close relatives. Whole skeleton caparisons are rare. They are however common in humans and apes and *Australopithecus* but for other taxa, they are hard to find. Most researchers compare individual bones but the entire skeleton reveals different types of information. I try to summarise some of this information here. There are skeletons of mounted giraffes in the natural history museums in Oxford, London and Lausanne, three in Paris, Lausanne at Palais Rumine, the University of Vienna, Harvard and in the Smithsonian. A view from below standing on the museum floor hinders the true proportions. I was offered a ladder in Paris and at Harvard and I climbed close to the midline of the displayed specimens. In addition, taking photos from the mid-level give better proportions for such a large animal. I have seen these specimens and have used photographs for the following drawing. The museum mounts are not perfect and there were some corrections as one can expect. The Smithsonian okapi is a great skeleton assembled artistically. There are also two okapi skeletons figured in Fraipont 1907. Articulated bones reveal spaces and angles of orientation and relations which are not obvious from isolated bones in a box. Photos of live animals were also used in my studies. The skeletons of the giraffe and the okapi are original. I did refer to Goldfinger (2004) and Fraipont (1907) also in my reconstructions. Many of the fossils were drawn from publications. *Palaeotragus* and *Schasitherium* were from real skeletal mounts in Tianjin and Hezheng museums. Certain vertebrae were sometimes in question in these two mounts, and I was not permitted to get close. Fraipont (1907) and Goldfindger (2004) provide skeletons of the okapi and the giraffe respectively. Figures 3, 4 and 5 illustrate the skeletons of *Giraffa* and *Okapia*.

Observations on the articulated skeleton

1. The head of the giraffe is small in relation to the body but more correct if it is compared to the length of the thorax.

2. The giraffe displays a tight throat. In ruminants, the top of the neck articulating with the head is looser. The surface skin of the ventral neck meets the jaw at the level of the mandibular angle. In the giraffe, the neck meets the jaw more posterior to the mandibular angle. This suggests a tight area for the larynx and pharynx. This was verified by my dissections. A different way of saying this is that the space anterior to the atlas between it and the jaw is very tight when compared to other taxa. These observations suggest that the oropharynx occupies a restricted space.

3. C1, the atlas, is very long in lateral view. In most ruminants, the atlas is short compared to a side view where the jaw is lower. In the giraffe, the atlas is longer than the jaw in an articulated specimen. Thus, the atlas reflects the elongation of the neck. In camels and the horse, the atlas is short in that lateral view although their neck is long overall.

4. The cervical vertebrae are clearly long in the giraffe. The C3, C4, C5, C6 and C7 are similar in morphology and are similarly long. The C5 is very similar in morphology to C6 and C7 which is another unique characteristic of the giraffe. It can be called homocervical. In a typical ruminant, this occurs with C3, 4 and C5 only. In the giraffe, C6 and C7 are added to the homocervical segment. Basically, the typical ruminant morphology of C6 possesses a broad ventral lamina for longus capitis and the longus thoracis. In the giraffe, this morphology has been lost. The same is true for the morphology of C7. C7 is totally different from a typical C7. A typical C7 has no ventral tubercle and has short vertebra. In the giraffe, C7 possesses a ventral tubercle, and it is long. The C7 resembles the C6 and C5. T1 is very strange too. It resembles a C7 and T2 resembles a T1. T1 is cervicalised. The bottom line is that there is a shift in morphology, a frame shift. This frame shift makes the C3-C7 similar and enables the giraffe to have a longer neck unit there; somewhat homogenous of five vertebrae (C3-C7), for male combat.

5. In a typical ruminant there are interspinous muscles. They span the distance between the spinous processes. The caudal thoracics and the lumbar vertebrae possess spinous processes which are approximated. The interspinous space is narrow in the giraffe and the interspinous muscles are reduced. These are compressed in a giraffe.

6. In lateral view, the distal thoracics and the lumbars form a concave outline – like a waist. The lumbar region is short (four vertebrae). In typical ruminants, there is no concave area there.

7. The thorax is deep. The ribs are long but individually appear normal. The thoracic inlet is very narrow and small.

8. Ruminants have lost their clavicles. They are a-clavicular. The same is true for the giraffe. The first rib is slightly mobile and different from the other ribs. It acts a little like a clavicle. This is important and it relates to the cervicalised T1. Thus, the anterior thorax is somewhat different from other ruminants. The distal ribs are approximated which is also a reflection of the compressed lumbar area (5).

9. The scapula is long and parallel to the deep thorax. The distal scapula is situated normally at the level of the manubrium. The anterior supraspinous fossa is rather narrow. The spine of the scapula is distally reduced.

7. The front limb is positioned rather anteriorly. That is, the shoulder protrudes outside the thorax. Thus, the glenohumeral joint is forward characteristically. This is actually a more ancient design than that we see in cervids. The limb there is situated rather deep in the thorax.

8. The pelvis is tilted down in lateral view. In most ruminants, the pelvis is more horizontal to the ground.

9. The knee is not exactly at the same level as the elbow. The elbow is slightly higher in lateral view. This is a reflection of the anterior body elongation of the giraffe. In most ruminants, these two joints are about the same level.

10. The olecranon is small. They may move their triceps less strongly because the entire locomotion is specialised (see below).

11. The humerus possesses three tubercles like in perissodactyls. The median tubercle is to lock the shoulder mechanism. The biceps locks there.

12. The distal femur has an enlarged median crest. This is similar to perissodactyls, and it may be a lock mechanism for the knee.

13. The elbow is slightly more extended at rest. The knee joint is more extended at rest. This gives the giraffe additional height and makes the limbs different from a typical ruminant. They are more vertical.

15. The ankle is at the same level as the wrist (carpals and tarsals) and thus the metapodials are subequal in length and rusticity. The slenderness of the shaft of the metacarpal is characteristic, in that it is parallel to the metatarsal. The distal phalanx is slightly larger in the anterior limb. The distal sesamoid is large.

16. The caudal vertebrae of the giraffe are really long. This is not typical in ruminants. It is an interesting detail that may relate somehow to the elongation of the cervical vertebrae. Caudals are far from the neck in embryos and adults. I wonder what the deeper ontogenetic meaning of this may be?

The following figure summarises some comparisons to other related ruminants.

		lumbar vertebrae long	intermediate	lumbar vertebrae short
		pelvis relatively horizontal to the ground		pelvis tilted down
Scapula type B	foot elongated	*Cervus*		*Schansitherium* *Samotherium*
Scapula type A	foot elongated	*Gazella* *Cephalophus* *Antilocapra* *Tragulus*	*Micromeryx* *Leptomeryx*	*Giraffa* *Palaeotragus* *Bramatherium* *Decennatherium* *Okapia* *Helladotherium* *Palaeomeryx* *Sivatherium*
Scapula type A	Foot short	*Archaeomeryx* *Hypertragulus* *Blastomeryx* *Machairomeryx*	*Hyemoschus*	*Lagomeryx*

SKELETAL COMPARISONS OF RELATIVES AND COUSINS

Comparisons are how one begins to understand issues of morphology. The giraffe in isolation would not be very informative by itself. Given the limited recourses, I drew stick figures of a selection of comparative species. These are accurate although very small. Spaces are left blank where the carpals and tarsals are located. The femur-tibia contact is always rotated creating a difficult setting to make a cartoon; it was left blank. The vertebrae are drawn as tubes. They include the vertebral bodies and the spinous processes in the thick tube-like outlines. Photos of live animals were also used in the construction of these figures.

A true evolutionary story is not available. There are numerous opinions in the literature like Simpson's classification (1945), Janis and Scot (1987) and Rios Ibanez and Sánchez (2017). There are numerous ruminants that when examined can give an approximate evolutionary morphological sequence leading up to the giraffids and the giraffe. These evolutionary sequences are not the true exact ancestors, but the pattern simulates a realistic story well enough. Key observations can be made on this simulation. It is not useful enough to describe the observed changes leading to Giraffidae in isolation. Other families need to also be considered to develop a deeper understanding of these groups.

The first stage can be represented with the condylarth *Phenacodus* (Fig. 7). We can begin with *Phenacodus* which is a basal ungulate, and most people agree with that. The skeleton of *Phenacodus* is long. The thorax is long and the lumbar region is also very long. The anterior scapular fossa is very large. The limbs are composed of broad stalky elements which are situated in a primitive position. Forward locomotion was possible but some lateral abductions in the limbs could take place. The ulna is large and full suggesting some supination. The pelvis is positioned almost horizontally in relation to the ground. The manus is supporting weight through the bones of the metacarpals and proximal phalanges. In addition, the manus gains strength by the flexor tendons which act as a supporting bow. Thus, the manus has both tendinous and bone columnar support. The pes is more vertical (less contact of the metatarsals with the ground) and therefore the pes increases the bone columnar support but with substantial tendinous support. The pes and the manus are short and pentadactyl. The forelimb and hind limb are bent forming strong zigzags. These limb orientations act like springs. The scapula and the humerus create a wide angle and it is extended at rest. The humerus and the radius form a closed angle and represent flexing at rest. The femur and the tibia also form a strong flexing angle. These limbs clearly rely on muscular controls for support as the joints are flexed. They can be extended like springs. This is in contrast to an elephant where it is well known that the weight passes through the columnar arrangement of the bones; minimal zigzag. In *Phenacodus*, the overall spine is slightly arched like a bow. This bow is mostly in the distal thoracic and lumbar areas. This arching also works like a spring during locomotion.

Scapulae of ruminants are of two types. Type A has a straight anterior edge. The anterior fossa is small. Type B has a concave anterior edge. This scapula is narrow by the glenohumeral joint but broad close to the spinous processes.

The next stage is represented by *Archaeomeryx*, *Hypertraguls*, *Machairomeryx* and *Blastomeryx* (text figure). The word *meryx* is common in ruminant nomenclature as it means ruminant in Greek (myrikastiko). The majority of the skeletal features are similar to those of *Phenacodus*. There are, however, some critical differences. They are: The anterior scapular fossa is very small (type A). The limbs are composed of more slender elements. Locomotion appears to be more restricted going forward. The lateral excursions are restricted. The ulna is reduced rendering supination impossible. The zigzagging of the long limb elements still acts like complex springs during locomotion. The weight is mainly supported by the muscles. The manus is supporting weight partially through the bones of the phalanges. The flexor tendons act like bowstrings reinforcing the support. The metacarpals are orientated more vertically for columnar support. Thus, contact with the ground is more restricted on the distal phalanges. There is more similarity in the structure of the pes and the manus. The strength of the manus phalanges relies primarily on the flexor tendons. Columnar support is small in the manus phalanges. The pes is like the manus but more vertical. The pes is longer than the manus. The metacarpals and metatarsals are more vertical, elongated and slender overall and become more columnar in weight support. They become like additional proximal limb elements rather than a primitive raccoon-like manus or a pes. They elongate. Many people confuse the ankle joint as if it were the knee. They think the knees bend backwards in these animals because they are looking at the ankles of the animals instead of the knees. This simple popular mistake explains the trend of elongation.

There is a scientific misconception of digit loss. The manus and the pes are rather like tulip flowers that never open. The pes and the manus of the adults experience the apparent compression of five digits where two digits (three and four) dominate. Hence, the term artiodactyl means even-toed (Owen, 1847). Digits three and four are dominant and large. The other digits however can be present near the proximal end by the carpals and tarsals and perhaps distally in the hooves. Digits two and five can be fused onto three and four and appear as ventral ridges. Digit one is proximally a very small bump. Therefore, the species are in general still pentadactyl but with an emphasis on three and four (Yohe and Solounias, 2020).

The forelimb and hind limb are bent forming zigzags. These limbs clearly rely on active muscular controls for support as the joints are flexed. In these taxa, the overall spine is strongly arched like a bow. This bow is in the thoracic and lumbar areas. This arching also works like a spring during locomotion.

Hyemoschus has more primitive pes and manus than *Archaeomeryx*, *Hypertraguls*, *Machairomeryx* and *Blastomeryx*. The digits are short, and the elements are less fused. The metacarpals are more primitive than in the previous group. This is also true for the metatarsals. *Tragulus* is more specialised in the elongation of the metatarsals and the reduction of digits two and five. The scapula is a type A in these.

The next stage is represented by *Micromeryx* and *Leptomeryx* (Fig. 7). *Gelosus* which is supposed to be the best plausible ancestor of the Giraffidae