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An osteological comparison between bontebok Damaliscus pygargus pygargus and blesbok, Damaliscus pygargus phillipsi and its bearing on the evolution of bontebok

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1. **CHAPTER ONE: INTRODUCTION**

This research forms part of a larger study on the Late Pleistocene evolution of African bovids, following studies by Brink (2005), who found that black wildebeest from coastal localities show a distinct reduction in body size when compared to contemporary inland populations, a result confirmed by Rossouw (2001) for springbok. Here I focus on the genus and species *Damaliscus pygargus* (formerly *dorcas*), comprising two subspecies blesbok and bontebok and their osteology in the context of their recent evolutionary history. Aspects of their taxonomy, biogeography and climate change in southern Africa are also considered.

1.1 Family Bovidae

The mammal family Bovidae comprises all artiodactyl ungulates with non-deciduous horn cores and sheaths, including antelopes, cattle, sheep and goats (Gatesy *et al.*, 1992). Their body mass ranges from an adult 2 kg royal antelope (*Neotragus moschatus*) to an African buffalo (*Syncerus caffer*) weighing about 900 kg (Nowak, 1991).

This family is known from the Miocene (23-5.5 Mya) in African and Eurasian fossil records, and also from North America from the late Neogene between 23-1.81 Mya (Vrba & Schaller, 2000). Evolution within the family Bovidae is characterized by different factors such as global immigrations, adaptive radiations, and mass extinctions which gave rise to the forty-nine extant genera and more than one hundred and forty species known today (Matthee & Davis, 2001). The complex evolution of the bovids was moulded by

different mechanisms such as temperature adaptation, feeding ecology, vegetation physiognomy (the physical appearance of a landscape), rifting, and climatic fluctuations (Kingdon, 1989).

1.1.1 Taxonomy

Because the evolution of bovids is complex, some scientists refer to them as one of the most troublesome groups of mammals to classify (Simpson, 1945). Bovid tribes are of uncertain phylogenetic affinity; however, a conservative classification could be set as follows: at least six monophyletic subfamilies, and about twelve currently recognized tribes (Matthee & Davis, 2001). These subfamilies are (1) Bovinae: Bovini (cattle-like bovids), Boselaphini (nilgai and four-horned antelope), and Tragelaphini (spiral-horned antelopes); (2) Cephalophinae: Cephalophinai (duikers); (3) Hippotraginae: Hippotragini (horse-like antelopes) and Reduncini (waterbuck group); (4) Alcelaphinae: Alcelaphini (hartebeest and allies) (5) Antilopinae: Antilopini (gazelles) and Neotragini (dwarf antelopes); and (6) Caprinae: Caprini (goats, sheep, and relatives), Ovibovini (muskox and takin) and Rupicaprini (chamois-like caprines). The taxonomic status of the four genera *Aepyceros* (impala), *Pantholops* (chiru), *Pelea* (vaal rhebok), and *Saiga* (saiga) remains unclear, and they are often placed in the three isolated tribes Aepycerotini, Peleini, and Saigini (saiga and chiru) (Hassanin & Douzery, 1999).

In addition to the problem of taxonomic classification based on skeletal elements, bovids have varying dietary preferences, with some specializing on fresh grass, leaves or fruits, whilst others have a more generalized mixed diet (Gagnon & Chew, 2000). Originally, bovids and other herbivores were classified as either grazers or browsers; however, some

scientists argue that these terms are too simplistic, hence different categories have been proposed (Gagnon & Chew, 2000). Hofmann and Stewart (1972) described a commonly used system based on bovid stomach structure: three main dietary categories, bulk and roughage eaters (grazers), selectors of juicy, concentrated herbage (browsers) and intermediate feeders. Langer (1988) proposed a dietary rating scheme consisting of six categories, four of which are roughly the same as those of Hofmann and Stewart. Bodmer (1990) proposed that fruits are an important component of bovid diets and he suggested that dietary categories be arranged along a continuum from frugivory to grazing, with browsing as an intermediate.

1.1.2 Biogeography

The diversity and abundance of extant African bovids is reflected in the geological past, and more than one hundred species are known from the fossil record of the past 16 million years (Gagnon & Chew, 2000). This diversity resulted from bouts of prolific speciation since they first appeared in the early Miocene, coupled with lower extinction rates recorded among African mammals, compared to mammals on other continents, during the Plio-Pleistocene (Georgiadis, Kat, Pat & Patton, 1990). Fossil bovids are commonly used in palaeo-environmental studies because they favour, and thus signal specific surroundings. Their frequent association with the remains of early hominids has made them an integral part of the literature pertaining to the ecological context of early hominid evolution (Vrba, 1995) in South and East Africa. In East Africa, increased tectonic uplift due to the formation of the East African Rift System resulted in the production of dynamic landscapes conducive to the preservation of fossils in open air

sites (Brink, 2005), providing long stratigraphic sequences that record evolutionary changes in a number of different animals, including bovids. In South Africa, fossils of the same age are found in open air sites and Plio-Pleistocene limestone cave deposits. Interbedded volcanic tuffs at East African sites are radiometrically dated, providing ages for the stratified fossil beds they bracket. This enables the relative dating of similar forms from South Africa, and the study of faunal evolution in the two regions.

The biogeographical distribution of extant bovids (Gentry, 1992) shows that groups are restricted to Eurasia (e.g. caprines), or Africa (e.g. duikers), or may span Eurasia and Africa (e.g. gazelles), but are poorly represented in the Americas.

Here I focus on modern southern African bovids, found in different habitats, ranging from tropical rain forest to woodland, grassland and desert (Gagnon & Chew, 2000). Two main physiographic zones occur in southern Africa: an uplifted central plateau and a coastal zone. The central plateau comprises essentially the Karoo geographical region and the Highveld, and is bound to the south by the Cape Fold Mountain ranges (Brink, 2005). Botanically, the central plateau encompasses the Nama Karoo and the Grassland Biomes. The Cape coastal zone includes the Succulent Karoo Biome in the west, favoured by bovids like the steenbok and duikers, the Fynbos Biome in the south and southwest, home to most of our endemic plants in South Africa, the Thicket Biome in the southeast home to most insects, and Savanna Biome outliers to the northeast, where mammals such as the lion, elephant, giraffe and cheetah are found (Brink, 2005). The Nama Karoo Biome is on the western half of the central plateau and it is elevated between 1000 and 14000 m above sea level (Low & Rebelo, 1996). It is mainly a summer rainfall area with precipitation

varying between 100 and 520 mm per year. The Nama Karoo grades into the drier Succulent Karoo to the west as winter rainfall becomes more predominant (Low & Rebelo, 1996). The Nama Karoo is adjoined by the Grassland Biome to the northeast on the central plateau at elevations of between 1350 and 2150 m above sea level. Rainfall is predominant in summer and it equates approximately with the term “Highveld” (Low& Rebelo, 1996). These biomes accommodate similar large mammal fauna, which are characterised by springbok, blesbok, black wildebeest and plains zebra or Cape quagga (Skead, 1980).This suggests that the distinction of the two biomes based on botanical considerations, does not affect the distribution patterns of large mammal populations (Brink, 2005).

1.2 Tribe Alcelaphini

This project has chosen to focus on the genera *Damaliscus*, which falls under the subfamily Alcelaphinae, and the tribe Alcelaphini (Gentry, 1992). Members of this tribe are confined to Africa. They are usually of medium to large size, are adapted to open environments and are specialized grazers (Gentry, 1978). Some of the main osteological features of this tribe include a long skull, horns in both sexes, horn cores often of irregular course and commonly with transverse ridges, generally no keels, extensive internal sinuses of frontal and horn pedicels; short braincase angled strongly on the face axis, anteriorly deepened zygomatic bars under the orbits, a central longitudinal groove on the basioccipital, cheek teeth strongly hypsodont, without basal pillars, complicated central cavities, rounded lingual lobes of upper molars, and buccal lobes of lowers,

widely outbowed ribs of upper molars, and short premolar rows with P_2 reduced or absent (Gentry, 1978).

The most completely known early alcelaphines are *Damalacra neanica* and *D. acalla* from Langebaanweg (Gentry, 1980). These early alcelaphines are blesbok-sized and have narrow similar to extant genera *Damaliscus* and *Alcelaphus*, but unlike *Connochaetes.* They had less hypsodont teeth, small basal pillars, poor rib development on upper molars with prominent mesostyles, molar lobes were pointed rather than rounded, and the P_4 is less reduced posteriorly and with paraconid not usually fused with metaconid (Gentry, 1990). *D. neanica* is more advanced than *D. acalla* in that the former has horn cores that are less backward and more outward in curvature, their insertions are further behind the orbits, and their brain roof is more inclined than in *D. acalla* (Gentry, 1990).

There are three extant genera in the tribe Alcelaphini, and they are *Damaliscus, Alcelaphus,* and *Connochaetes* (Gentry, 1992). The genus *Damaliscus* has two species which are *D. pygargus* comprising blesbok and bontebok, and *D. lunatus* (tsessebe, korrigum, topi, tiang) (Lynch, 1974).

Older literature refers to bontebok and blesbok as *Damaliscus dorcas,* while new literature refers to these animals as *Damaliscus pygargus,* and it is an example of taxonomic revision based on the principle of priority (Bronner, *et al,* 2003). Rookmaaker (1991) states that the name change occurred because Pallas (1766) who first discovered bontebok called it *Antilope dorcas* not realizing that the name was already assigned to another animal. When he realized that the name was assigned to another species, he then changed the name to *pygargus* (Pallas, 1767). Because the name change occurred before

1966, the second name which is *Damaliscus pygargus* is now used, and the first one, *Damaliscus dorcas* is redundant (Rookmaaker, 1991).

1.3 Pleistocene climate change in southern Africa

The Pleistocene geological epoch was characterized by dramatic glacial advances and retreats (Richerson, Boyd & Bettinger, 2001). These dramatic glacial advances set the Pleistocene apart from the earlier epochs of the Cenozoic, and it is, therefore, logical to define the beginning of the Pleistocene as the onset of the first continental glaciation (Ericson, Ewing & Wollin, 1963). The geographical distribution of fossil plants and animals yields evidence of a gradually decreasing temperature during the late Pliocene. One can visualize under such a climatic regime, a succession of mountain glaciers, each a bit larger than the preceding one, followed by restricted continental glaciations that gradually expanded into the great continental glaciations of the later Pleistocene (Ericson, Ewing & Wollin, 1963).

The development of glaciers on land is due to the dropping of local seasonal temperatures below freezing-point, so that the rate of accumulation of snow exceeds that of wastage by melting and evaporation (Cornwall, 1970). Low temperatures alone are not sufficient, for without accompanying high precipitation in the form of snow, accumulation cannot take place.

The formation of land-ice begins in mountainous areas, and even in such high snowfields, daily and seasonal ambient temperatures may fluctuate about the freezing point of water. In time, alternate softening and re-freezing of freshly fallen, loose snow will result in

gradual compaction under its own weight and expulsion of air trapped among the original ice crystals (Cornwall, 1970). This process will continue with the added weight above it of later snow-falls until the still relatively porous “ice” is finally converted into solid, almost glassy-clear glaciers.

The growth of ice-sheets on land has drastic effects on ocean sea levels as water becomes locked up in ice. The subsequent lowering of sea-level due to widespread maximum glaciation would have laid bare the submarine continental shelves over the whole world (Cornwall, 1970). As a consequence, shallow seas disappeared and continental islands were joined for a while to their mainlands, and even in much deeper seas like the Mediterranean, the fringing shelves were more or less exposed, so that on-shore winds could drive sand-dunes inland from new coasts (Cornwall, 1970).

Data from latest Pleistocene palaeo-climate records demonstrate that African fauna and vegetation responded swiftly to abrupt changes in high-latitude temperatures (deMenocal, 1995). Climatic fluctuation during the Pleistocene are also recorded in the sea in alternations of “cold” and “warm” fossil marine faunas, and by alternations of organics deposits and layers of sediment believed to have been deposited from abundant floating ice (Flint, 1948).

Valley glaciers are found in Africa only on very high mountains (Nilsson, 1983). The Pleistocene glaciations are recorded from the Atlas Mountains in the north and from the high mountain peaks further south around the equator, including Kilimanjaro, Mt. Kenya, Ruwenzori, and Mt. Elgon in East Africa (Nilsson, 1983).

In tropical and subtropical areas of Africa, dry, arid areas are widespread today, and their geological developments shows climatically controlled alternations, between moist, pluvial and dry-interpluvial (nonpluvial) episodes (Nilsson, 1983). North Africa is now characterized by lakes without outlet, desiccated basins, and dry river valleys, so called "wadis" (Nilsson, 1983). During interpluvial times, conditions were more or less the same. However, during the pluvials, the river valleys were filled with more water; and most closed basins were transformed into lakes. The water level was raised to past threshold in many basins, and a spillway to the sea formed (Nilsson, 1983).

From sites that have a glacial fossil record, such as Swartklip (False Bay coast), Sea Harvest (Saldanha), Elandsfontein Bone Circle (Saldanha), Nelson Bay Cave (Plettenberg Bay) and Boomplaas Cave (Oudtshoorn) a pronounced grazing component in the fauna is evident (Klein 1983, 1984). This has been interpreted as a response to an increase in grassland habitat during glacials in the Cape coastal zone, which today has mainly Fynbos vegetation (Deacon *et al.* 1984; Klein 1983, 1984), and is supported by other palaeo-environmental indicators (Deacon *et al.* 1984), including fossils found in the area. Therefore, it appears that during glacials, plains game, which originated in the central interior of southern Africa, occupied the coastal plains of the eustatically (a worldwide change in seal level due to the melting of glaciers or earth movements) exposed continental margin (Brink 1993, 2005). These dispersals included almost the full range of extant and extinct Florisian grazers, referring to bovids (dating these bovids is a bit tricky since the ESR dating of the Florisbad Spring material dates between 100 000

and 400 000 years BP). Glacial black wildebeest from these coastal localities show a distinct reduction in body size when compared to contemporary inland populations (Brink 1993, 2005). This is also evident to some degree in coastal springbok (Rossouw, 2001). See the section on modes of speciation below for an explanation of the allopatric mode of speciation thought by these authors to have arisen from the barrier to breeding presented by mountains following dispersal of populations during glacials.

The species *Damaliscus pygargus* is present in almost all the glacial deposits on the Cape coastal zone. However, towards the end of the Late Pleistocene, with the return of high sea levels, virtually all the plains-living forms became extinct when the coastal plains habitat was reduced to the narrow strip that it is today. In addition, towards the end of the Late Pleistocene Fynbos seems to have expanded in the southern Cape area at the cost of grassland habitat (Deacon *et al.* 1984). The only plains living form that occurs today in the Cape coastal zone is the bontebok (*D. pygargus pygargus*), which is very closely related to the blesbok (*D. pygargus phillipsi*) of the interior.

1.4 *Damaliscus pygargus phillipsi*

This subspecies is slightly bigger than *D. pygargus pygargus* in that it stands about 95 cm at the shoulder. It is similar to *D. pygargus pygargus* in terms of colour in that they are also dark brown with a white blaze, underpants, and the lower legs, while the adult males are distinguishable by a dark colour and white scrotum (Estes, 1991). The only difference between these two subspecies is that *D. pygargus phillipsi* lacks the rump patch, and the

blaze is bisected by a band unlike in *D. pygargus pygargus.* The newborns are tan with a dark blaze and there are no white markings (Estes, 1991).

Both sexes have horns but these horns are heavily ridged for most of their length, and they curve backwards from the top of the head, then swing outwards, the points curving evenly forward (Smithers, 1983).

Distribution

These antelopes are one of the four grazers that once thronged the South African Highveld in many thousands (Estes, 1991). Their present distribution is to a large extent artificial and they now occur only in protected areas (Smithers, 1983).

Habits and Food

They are similar to their counterparts in that they are also diurnal, gregarious grazers, but the difference is that they prefer sprouting grasses which appear after a burn (Smithers, 1983). They are territorial and their social organization is similar to that of *D. pygargus pygargus* in that they consist of territorial males, female herds and bachelor groups. This subspecies is a seasonal breeder.

D. pygargus phillipsi occur only within the limits of the subregion, and their present distribution is to a large extent artificial as they are now occur only in protected herds on fenced farms and reserves (Smithers, 1983).

These animals were first seen in the treks northeast from the Cape on the open grassland of the Middelberg/Richmond areas, and they were common in parts of the eastern

Province of the Cape Province, in the Free State and northwestwards to near the Molopo River (Smithers, 1983).

1.5 *Damaliscus pygargus pygargus*

These antelopes are smaller of the two subspecies, standing about 90 cm at the shoulders, and their horns are s-shaped (about 35-37 cm). Their coloration is dark brown with white blaze, underparts, and lower legs, and the adult males are distinguishable by the dark colour and a white scrotum (Estes, 1991). The above mentioned colours are glossier with purple-black blotches on upper limbs and sides, with a small white rump patch, and a facial blaze usually not completely bisected by a brown blaze.

Both sexes have ridged horns rising from the top of the head, curving backwards and outwards and then slightly forwards towards the unridged tips (Smithers, 1983). The recognition of the sexes is a bit difficult in the field, but one character that might make it easier is that the females have more slender horns than the males, and these horns hardly thicken up at the base (Smithers, 1983).

Another characteristic outline is their long face and sloping hind-quarters, and these are reminiscent of that of their close relatives, the wildebeest and the hartebeest (Smithers, 1983).

Distribution

D. pygargus pygargus had a local distribution in the 17th century when it was first spotted by colonizers at the southern-most tip of the Cape (Estes, 1991). This subspecies is now

confined to a restricted area in the southwestern Cape Province, lying between Bredasdorp and Cape Agulhas (Smithers, 1983).

Habits and Food

They are diurnal, gregarious, grazing species with a preference for feeding on short grass. Their social organization consists of territorial males, female herds and bachelor groups (Smithers, 1983). They are seasonal breeders, and their gestation period is between 238 and 254 days, and their lambs are born in the spring (Smithers, 1983).

Table 1 Summary of the morphological differences and habits of the two subspecies

Damaliscus pygargus pygargus	*Damaliscus pygargus phillipsi*
90 cm at shoulders	95 cm at shoulders
S-shaped, ridged horns rising from the top of the head	Heavy ridged horns rising from the top of the head (Smithers, 1983)
Dark-brown blaze	Dark-brown blaze but bisected by a band in blesbok
Diurnal, grazing species	Diurnal, grazing species
Presence of rump patch	Absence of rump patch

The table above shows what was mentioned before that these two subspecies (bontebok and blesbok) show small, but yet significant differences in their exterior morphology.

1.6 Speciation

Speciation, the process through which new species come into being, is one of the central topics of evolutionary biology (Howard & Berlocher, 1998). It links the great fields of micro- and macro-evolutionary biology and intersects a wide variety of related biological disciplines, including behavioral biology, ecology, genetics, morphology, palaeontology, physiology, reproductive biology, and systematics (Howard & Berlocher, 1998).

Speciation is ultimately an adaptive process that involves establishment of intrinsic barriers to gene flow between closely related populations by development of reproductive isolating mechanisms (Bush, 1975).

Over the last half century, biologists have established a minor industry devoted to the production of new definitions for the term *species.* In order to try and understand what a species is, scientists have come up with different species concepts, a topic of much debate among population geneticists, ecologists, philosophers, and the systematics community (Luckow, 1995).

1.7 Modes of speciation

Most biologists agree that in order for organisms to speciate, gene flow between diverging populations must be reduced to a level where “foreign” genes entering the population as a result of hybridization can be eliminated by natural selection (Bush, 1975). Scientists recognize a number of species concepts, all used in an attempt to explain what a species is and why there are different types. Below I outline five main species concepts accepted today.

1.7.1 *Biological Species Concept*

This species concept refers to organisms that interbreed but are reproductively isolated from other such groups (Coyne & Orr, 2004). Dobzhansky (1937) proposed that "a species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of hybrids, or both)".

This species concept falls into the category of Mechanistic Species Concepts, and these concepts begin with a theory of how evolution (speciation) works and base species recognition on what is considered to be the most important causal factor/factors leading to speciation (Luckow, 1995).

1.7.2 *Isolation Species Concept*

There are two theories trying to explain the origin and development of reproductive isolation between populations. One theory considers isolation as an accidental-by-product of genetic divergence, meaning populations that become genetically more and more different may eventually be unable to interbreed because their gene pools cannot connect (Ayala, 1982).

The other theory regards isolation as a product of natural selection, whereby if offsprings of hybrids are less fit than their hybrid parents, then natural selection will favour the development of reproductive isolation as gene variants interfering with hybridization have greater fitness than those favoring hybridization (Ayala, 1982).

1.7.3 *Recognition Species Concept*

Species definitions associated with the "recognition concept" emphasize the unification of species rather than their separation from one another (Howard & Berlocher, 1998). More specifically, they emphasize the common fertilization and specific mate recognition system shared by conspecific organisms, rather than the reproductive isolation between heterospecific organisms.

1.7.4 *Evolutionary Species Concept*

This term has been used for definitions pointing the extension of species through time and attempting to accommodate both the observation that some populations appear to maintain their distinctness despite interbreeding with other populations and the idea that asexual organisms form species (Howard & Berlocher, 1998).

1.7.5 *Ecological Species Concept*

Van Valen (1976) proposed this concept for his modification of Simpson's (1961) definition. It emphasizes the importance of ecologically based natural selection in maintaining species: "a species is a closely related set of lineages which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range" (Van Valen, 1976). This concept also falls into the category of Mechanistic Species Concepts like the Biological Species Concept (Luckow, 1995).

Now that different species concepts have been outlined, four modes of speciation will be discussed. Different modes of speciation have traditionally been named with reference to biogeographic criteria (Cracraft, 1984).

1.7.6 *Allopatric Speciation*

Without a doubt, allopatric speciation is very common in almost all groups of sexually reproducing animals. This kind of speciation, regarded by many evolutionary biologists as the major means of generating new species in sexually reproducing animals, can occur in two different ways (vicariance and founder effect). In terms of vicariance, a barrier to dispersal can be created somewhere within the range of an ancestral species by some environmental change, isolating previously connected and interbreeding populations (Lomolino, Riddle & Brown, 2006). The founder events (also known as jump dispersal) involve populations or individuals that may disperse across an existing barrier to colonize a previously uninhabited region (Lomolino, Riddle & Brown, 2006). The phenotypic differences in coastal black wildebeest and springbok are interpreted as examples of vicariance in isolated daughter populations after dispersals from the central interior (Brink 2005). In this scenario the Cape Fold Mountains would have acted as a biogeographic barrier.

There are two stages involved in allopatric speciation. The first stage begins as a result of geographic separation between populations, and as a result of natural selection, these geographically separate populations become adapted to local conditions, and thus become genetically differentiated (Ayala, 1982). If geographic separation continues for some

time, then incipient reproductive isolation may appear, especially in the form of post-zygotic mechanisms.

The second stage of speciation begins when these previously separated populations come into geographic contact again (Ayala, 1982). Once these isolates come together again, they may either not interbreed because they have developed prezygotic isolating mechanisms, or they may fail to produce fertile offspring if they do interbreed (Lomolino, *et al.* 2006). They may also interbreed and produce fertile hybrids that will eventually backcross to parental populations to the extent that the barriers will disappear and these isolates will merge genetically. If they don't do the above mentioned, the two populations may not have developed prezygotic isolating mechanisms and do mate producing hybrids, but these hybrids may be/are less fit than the offspring of within-population matings (Lomolino, *et al.* 2006).

In terms of *D. pygargus pygargus* and *D. pygargus phillipsi,* it is thought that the former is the survivor of the last glacial period (15-70 kya), and it is during this time that there was a separation, hence the two subspecies. The bontebok (*D. pygargus pygargus*) may be the last surviving remnant of dispersals of open grassland ungulates from the interior onto exposed continental platforms during glacials, when sea levels were lower (Brink 1993, 2005).

After the glacial period, a barrier (possibly the Cape Fold Mountains) formed between the parent population and the daughter population (isolates that moved to a different location), and the gene pools became different. The significance of this project is that it provides an example of allopatric speciation in the early phase. It is a means of testing whether we can identify distinct morphologies due to incipient reproductive isolation

caused by biogeographical factors and the distance of the daughter population from the ancestral population. Given time, one can predict that bontebok will show increased differences from blesbok.

1.7.7 *Peripatric Speciation*

The only difference between vicariant and peripatric speciation is that in the latter case, one population is very small, and two very crucial consequences follow from this distinction (Coyne & Orr, 2004). Firstly, peripatric speciation may often involve the invasion of novel habitats that exert strong selection, and secondly, genetic drift becomes important in small populations and could play a role in speciation. The forces causing this kind of speciation are thought to be identical to that causing vicariant speciation (Coyne & Orr, 2004). However, colonization events have special features that may lead to especially rapid speciation.

1.7.8 *Parapatric Speciation*

Parapatric speciation is usually defined as the process of species formation in the presence of some gene flow between diverging populations (Gavrilets, 2000). In population-genetic terms, such speciation occurs when the fraction of genes initially exchanged between taxa lies between 0 (Allopatric speciation) and 0.5 (sympatric speciation).

Unlike allopatric speciation, parapatric speciation does not require impermeable geographic barriers, but merely restricted gene flow and environmental differences between populations (Coyne & Orr, 2004).

The geographical structure of most species, which are usually composed of many local populations experiencing little genetic contact for long periods of time, fits the one implied in the parapatric speciation scenario (Gavrilets, 2000).

Traditionally, studies of this kind of speciation have emphasized the importance of strong selection for local adaptation in overcoming the homogenizing effects of migration, but it has also been theoretically proven that rapid parapatric speciation is possible even without selection for local adaptation if there are many loci affecting reproductive isolation and mutation is not too small relative to migration (Gavrilets, 2000).

1.7.9 *Sympatric Speciation*

This kind of speciation involves the evolution of reproductive isolation within the average dispersal distance ("cruising range") of a single individual, sympatric speciation thus differs from parapatric speciation, in which interbreeding is initially restricted by distance, as mentioned before (Coyne & Orr, 2004).

There appears to be a fuzzy line between parapatric and sympatric speciation speciation, strong pre- and post mating reproductive isolation develops as the population penetrates a new niche. In sympatric speciation, on the other hand, premating reproductive isolation arises before a population shifts to a new niche (Bush, 1975). Sympatric speciation appears to be limited to special kinds of animals, namely phytophagous and zoophagous parasites and parasitoids (Bush, 1975). Futuyma and Mayer (1980) propose that sympatric speciation is also unique because the initial restriction of gene flow is caused not by geography or distance, but by biological features of organisms.

1.8 Aims

The aim of this study is to test if there are consistent morphological differences between osteological samples of modern blesbok and bontebok, as has been demonstrated for inland and coastal wildebeest (Brink 2000), and to a lesser degree, springbok (Rossouw 2001). These authors propose that dispersals of inland plains-living fauna into the Cape coastal zone during glacials, account for the speciation events. An additional osteological case study that differentiates a third genus in the tribe Alcelaphinae would lend support to this hypothesis.

Damaliscus pygargus has been chosen for this purpose as it was once widely distributed, but is now recognised as subspecies *D. pygargus phillipsi* on the upland zone, and *D. pygargus pygargus* in the Fynbos zone of the southern Cape.

1.9 Hypotheses

1. The osteology will reflect whether there are differences between the two subspecies that exhibit only a few distinct external features.
2. If there are osteological differences, then they may be the outcome of speciation, caused by geographical barriers during Late Pleistocene glaciations (15-70 kya).

Besides evaluating the taxonomic status of bontebok and blesbok, this study will trace the recent evolution of the taxon, considering the effects of climate and environmental change in southern Africa. Distinguishing them osteologically may also be of use in their conservation, as known hybridization has been taking place in the Free State since the introduction of *D. pygargus pygargus* in the 1960s.

2. CHAPTER TWO: MATERIALS AND METHODS

Materials

Training

Training was undertaken at Florisbad in Bloemfontein in April 2006 with Dr. J. Brink from the National Museum. Training included taking measurements of different bones from different parts of the body, and this was done following von den Driesch (1976). These measurements were also used in the write-up. Material from the South African Museum in Cape Town was also used to check the morphological characters and expand the metrical database.

Twelve specimens were measured from the Iziko Museum, and seven specimens were measured from Florisbad.

The relatively small sample size may have an effect on the reliability of the results.

Measurements were taken from the cranium and the limb bones, especially ankle bones; since these two animals are found in different environments, and might, therefore, have different shapes of horns, and their ankle bones might be different in measurements. Only the first phalanx was used because it was thought that most differences will be found there in terms of the shape of this particular bone.

Below are guidelines of how these measurements were taken following von den Driesch (1976).

When I was in Florisbad, I looked for differences between the two subspecies in their osteology; I then noted those differences in a notebook. I then used those differences in the notebook when I was looking at the specimens at the Iziko Museum, Cape Town, just to see if the differences noted in Bloemfontein were consistent among all members of these subspecies.

2.2 Methods

The work involved basic morphological and morphometric comparison. The instrument used was a vernier calliper.

2.2.1 Cranial measurements

2.2.1.1 *Measurements of the cranium*

1) Profile length = Akrokranion-Prosthion. Due to the length and shape of the skulls a long box will be used to take the measurements. The skull will be placed in box and then the box adjusted to fit the length of the skull. The measurement will be taken from the edge of the box which is touching the Prosthion to the Akrokranion.
2) Condylobasal length: Aboral border of the occipital condyles-Prosthion.
3) Basal length: Basion-Prosthion.
4) Short skull length: Basion-premolar
5) Premolare-Prosthion

6) Neurocranium length: Basion-Nasion
7) Viscerocranium length: Nasion-Prosthion
8) Median frontal length: Adrokranion-Nasion
9) Akrokranion-Bregma
10) Frontal length: Bregma-Nasion
11) Greatest length of the lacrimal: most lateral point of the lacrimal-the most oral point of the lacrimo-maxillary suture
12) Greatest length of the nasals: Nasion-Rhinion
13) Short lateral facial length: Entorbitale-Prosthion
14) From the aboral border of one occipital condyle to the Infraorbitale of the same side
15) Dental length: Postdentale-Prosthion
16) Oral palatal length: Palatinoorale-Prosthion
17) Lateral length of the premaxilla: Nasointermaxillare-Prosthion
18) Length of the cheektooth row (measured along the alveoli)
19) Length of the molar row (measured along the alveoli on the buccal side)
20) Length of the premolar row (measured along the alveoli on the buccal side)
21) Greatest inner length of the orbit: Ectorbitale-Entorbitale
22) Greatest inner height of the orbit.
23) Greatest mastoid breadth: Otion-Otion
24) Greatest breadth of the occipital condyles
25) Greatest breadth at the bases of the paraoccipital processes
26) Greatest breadth of the foramen magnum

27) Height of the foramen magnum: Basion-Opisthion

28) Least breath of parietal=least breadth between the temporal lines

29) Greatest breadth between the lateral borders of the horncore bases

30) Greatest breadth across the orbits=greatest frontal breadth=greatest breadth of skull: Ectorbitale-Ectorbitale

31) Least breadth between the orbits: Entorbitale-Entorbitale

32) Facial breadth: breadth across the facial tuberosities

33) Greatest breadth across the nasals

34) Greatest breadth across the premaxillae

35) Greatest palatal breadth: measured across the outer borders of the alveoli

36) Greatest (oro-aboral)diameter of the horncore base

37) Least (latero-medial)diameter of the horncore base

38) Length of the horncore on the front margin (tape measure).

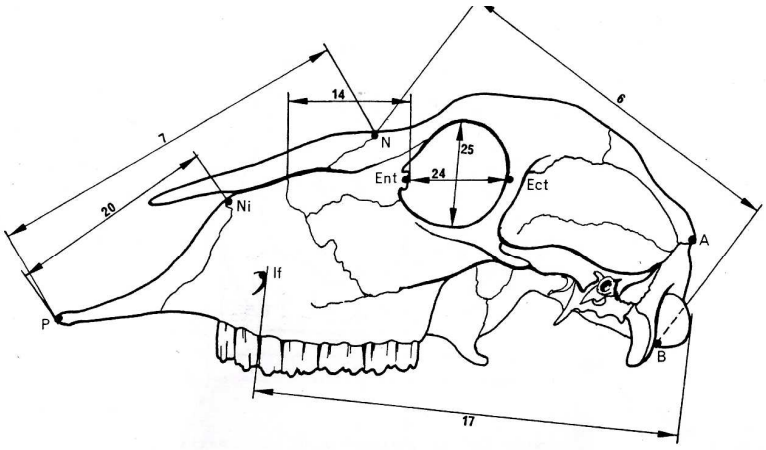


Figure 1: Left side view of the cranium (after Von den Driesch, 1976)

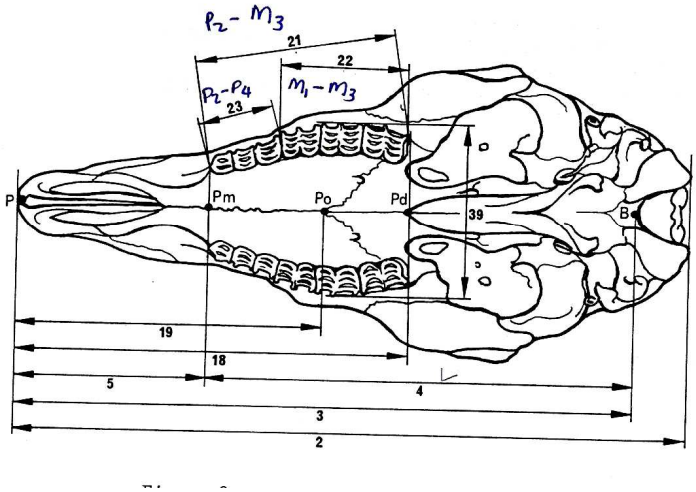


Figure 2: Basal view of the cranium (after Von den Driesch, 1976)

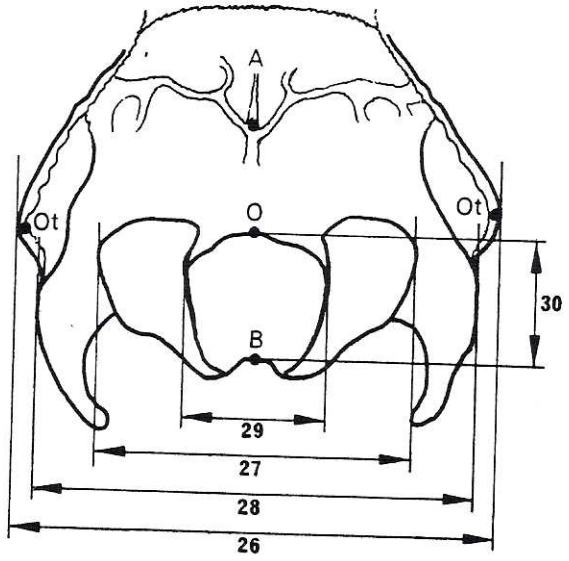


Figure 3: Nuchal view of the cranium (after Von den Driesch, 1976)

2.2.1.2 *Measurements of the mandible*

1) Length from the angle: Gonion caudale-Infradentale
2) Length from the condyle: aboral border of the condyle process-Infradentale
3) Length: Gonion caudale-aboral border of the alveolus of M_3
4) Length of the horizontal ramus: aboral border of the alveolus of M_3-Infradentale
5) Length: Gonion caudale-oral border of the alveolus of P_2
6) Length: Gonion caudale-the most aboral indentation of the mental foramen
7) Length of the cheektooth row, measured along the alveoli on the buccal side
8) Length of the molar row, measured along the alveoli on the buccal side
9) Length of the premolar row, measured along the alveoli on the buccal side
10) Length and breadth of M_3, measured near the biting surface
11) Length of the diastema: oral border of the alveolus of P_2-aboral border of the alveolus of I_4
12) Aboral height of the vertical ramus: Gonion ventrale-highest point of the condyle process
13) Middle height of the vertical ramus: Gonion ventrale-deepest point of the mandibular notch
14) Oral height of the vertical ramus: Gonion ventrale-Coronion
15) a. Height of the mandible behind M_3 from the most aboral point of the alveolus on the buccal side

15) b. Height of the mandible in front of M_1

15) c. Height of the mandible in front of P_2

2.2.2 Post-cranial measurements

2.2.2.1 *Measurements of the atlas*

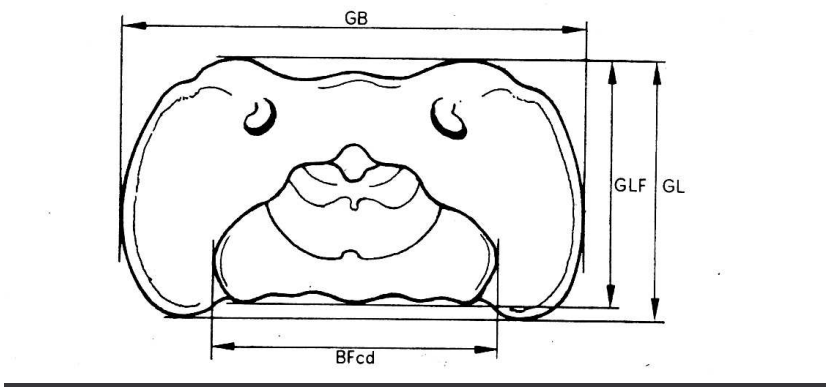


Figure 4: Caudodorsal view of the atlas (after Von den Driesch, 1976).

GB- Greatest breadth over the wings

GL- Greatest length

BFcr- (Greatest) breadth of the Facies articularis cranialis (= cranial articular surface)

BFcd- (Greatest) breadth of the Facies articularis caudalis (= caudal articular surface)

GLF- Greatest length from the Facies articularis cranialis to the Facies articularis caudalis

H- Height. Measured in a measuring box in such a way, that one lays the atlas with its cranial side on the bottom of the box and closes the blocks over the dorsal and ventral archs

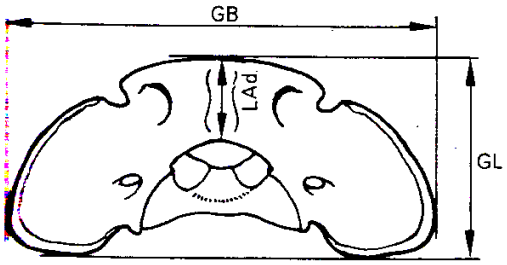


Figure 5: Dorsal view of the atlas (after Von den Driesch, 1976).

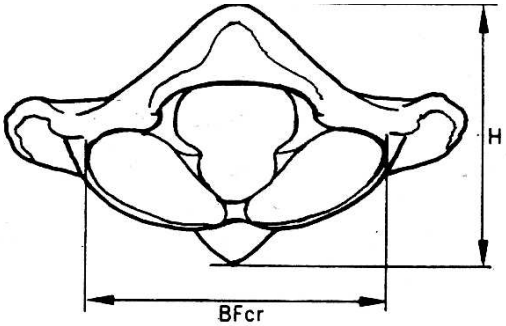


Figure 6: Cranial view of the atlas (after Von den Driesch, 1976)

2.2.2.2 *Measurements of the axis*

LCDe- (Greatest) length in the region of the corpus (= body) including the dens. If the caudal epiphysal plate has not yet fused, one measures without the caudal articular surface adding a note to that effect.

LAPa- (Greatest) length of the arch including the Processus articulares caudales

BFcr- (Greatest) breadth of the Facies articularis cranialis (= cranial articular surface)

BPacd- (Greatest) breadth across the Processus articulares caudales

BPtr- (Greatest) breadth across the Processus transverse

SBV- Smallest breadth of the vertebra

BFcd- (Greatest) breadth of the Facies terminalis caudalis (= caudal articular surface)

H- (Greatest) height. Measured in a measuring box. One lays the two basal prominent points of the body of the vertebra on the fixed block of the instrument and closes the other block over the highest point of the spinous process

Lad- Only measured in carnivores

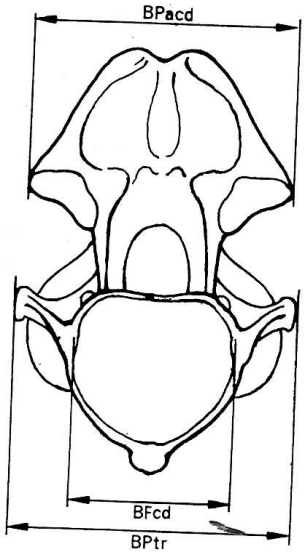


Figure 7: Caudal view of the axis (after Von den Driesch, 1976).

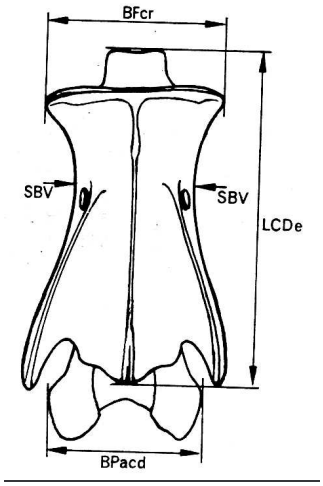


Figure 8: Ventral view of the axis (after Von den Driesch, 1976).

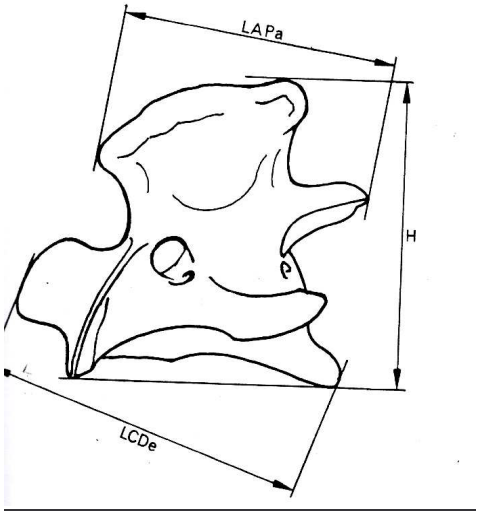


Figure 9: Left side view of the axis (after Von den Driesch, 1976).

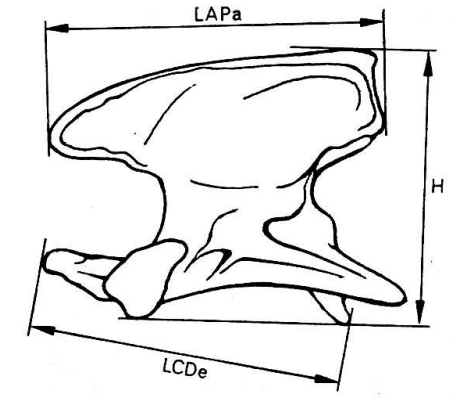


Figure 10: Left side view of the axis (after Von den Driesch, 1976)

2.2.2.3 *Measurements of the sacrum*

GL- Greatest length on the ventral side: from the cranial borders of the wings to the caudoventral border of the body of the last vertebra

PL- Physiological length, measured between the centers of the bodies of the most cranial and the most caudal vertebrae

GB- Greatest breadth (across the wings)

BFcr- (Greatest) breadth of the Facies terminalis cranialis (= cranial articular surface)

HFcr- (Greatest) height of the Facies terminalis cranialis

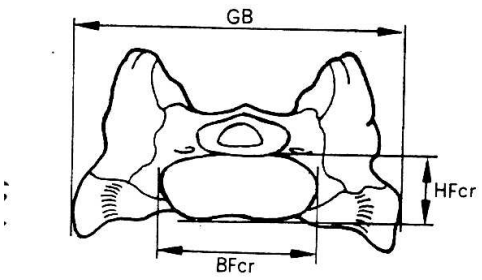


Figure 11: Cranial view of the sacrum (after Von den Driesch, 1976)

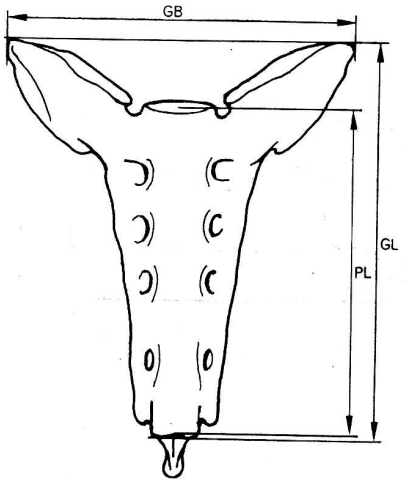


Figure 12: Ventral view of the sacrum (after Von den Driesch, 1976)

2.2.2.4 *Measurements of the scapula*

HS- Height along the spine

DHA- Diagonal height: from the most distal point of the scapula to the thoracic angle.

Ld- (Greatest) dorsal length.

SLC- Smallest length of the Collum scapulae (neck of the scapula).

GLP- Greatest length of the Processus articularis (glenoid Process)

LG- Length of the glenoid cavity

BG- Breadth of the glenoid cavity-Greatest breadth of the glenoid angle

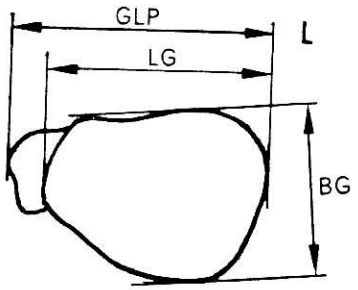


Figure 13: Distal view of the scapula (after Von den Driesch, 1976)

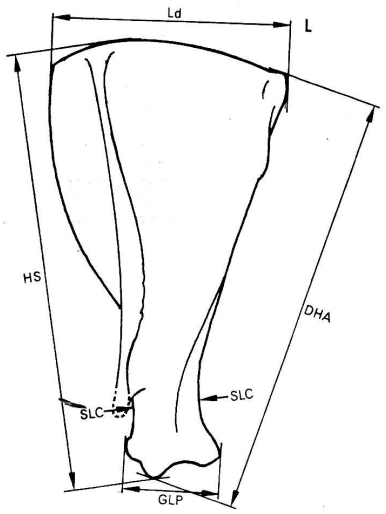


Figure 14: Lateral view of the scapula (after Von den Driesch, 1976)

2.2.2.5 *Measurements of the Humerus*

GL- Greatest length

GLC- Greatest length from caput (head)

Bp- (Greatest) breadth of the proximal end

SD- Smallest breadth of diaphysis

Bd- (Greatest) breadth of the distal end

BT- (Greatest) breadth of the trochlea

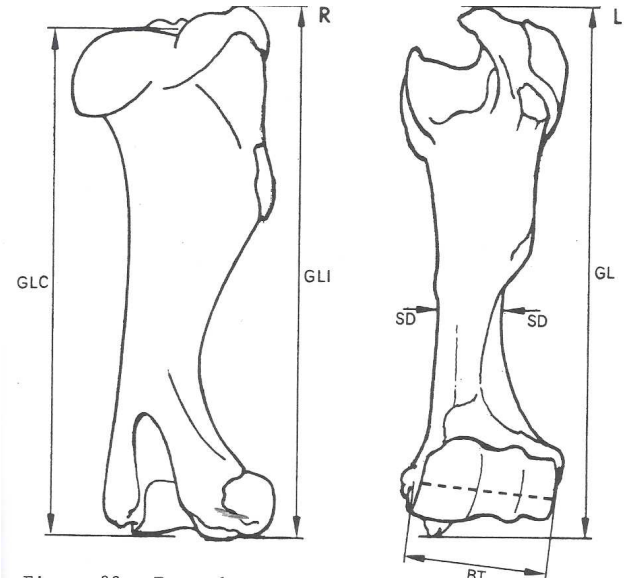


Figure 15 and 16: caudolateral view (on the left) and cranial view (on the right) of the humerus (after Von den Driesch, 1976)

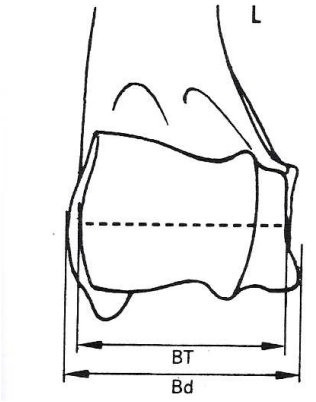


Figure 17: cranial view of the distal end of the humerus (after Von den Driesch, 1976)

2.2.2.6 *Measurements of the ulna*

GL- Greatest length

LO- Length of the olecranon

DPA- Depth across the Processus anconaeus. One measures the shortest distance from the Processus anconaeus to the caudal border of the ulna

SDO- Smallest depth of the olecranon

BPC- (Greatest) breadth across the coronoid process= greatest breadth of the proximal articular surface

2.2.2.7 *Measurements of the radius*

GL- Greatest length

PL- Physiological length

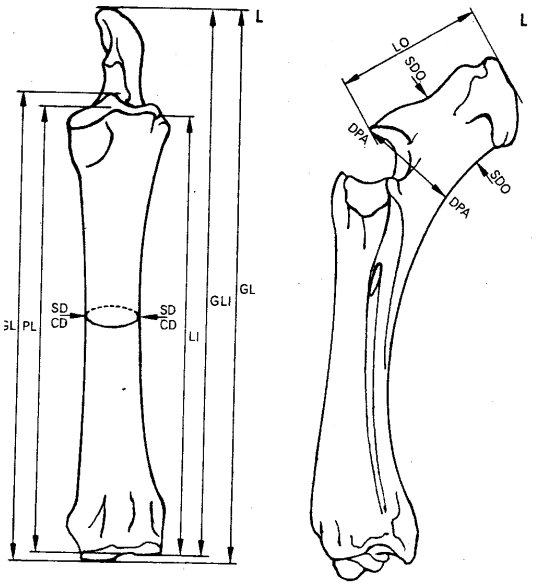
BP- (Greatest) breadth of the proximal end

BFp- (Greatest) breadth of the Facies articularis proximalis (humeral articular surface)

SD- Smallest breadth of diaphysis

Bd- (Greatest) breadth of the distal end

BFd- (Greatest) breadth of the Facies articularis distalis



Figures 18 & 19: dorsal view of the radius and ulna (on the left) and the lateral view of the radius and ulna (on the right) after Von Den Driesch, 1976

2.2.2.8 *Measurements of the pelvis*

GL- Greatest length of one half

SB- Smallest breadth of the shaft of ilium

GBTc- Greatest breadth across the Tubera coxarum-greatest breadth across the lateral angle

GBA- Greatest breadth across the acetabula

GBTi- Greatest breadth across the Tubera ischiadica

SBI- Smallest breadth across the bodies of the ischia

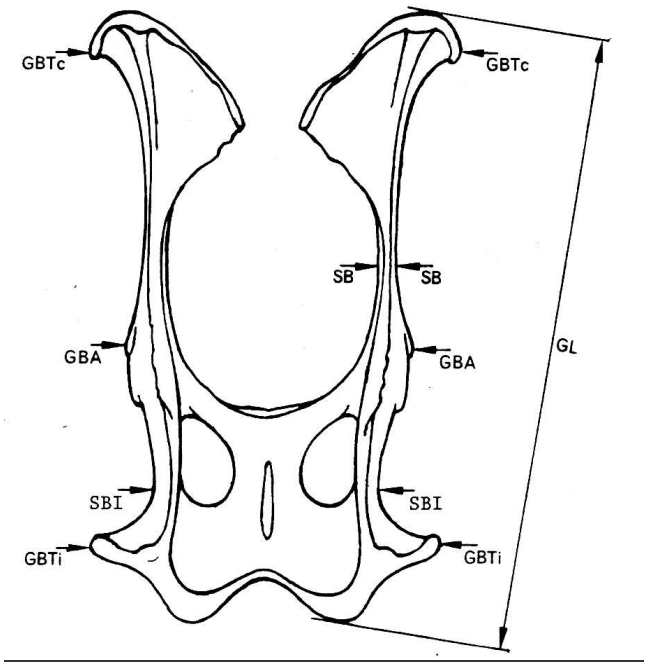


Figure 20: Dorsal view of the pelvis (after Von den Driesch, 1976)

2.2.2.9 *Measurements of the femur*

GL- Greatest length

GLC- Greatest length from caput femoris (head)

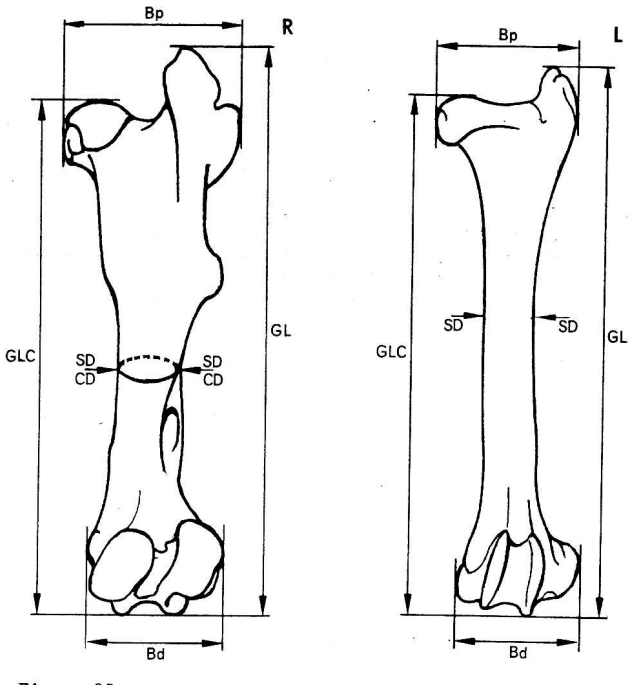
Bp- (Greatest) breadth of the proximal end

DC- (Greatest) depth of the Caput femoris

SD- Smallest breadth of diaphysis

CD- (Smallest) circumference of diaphysis

Bd- (Greatest) breadth of the distal end



Figures 21 & 22: Caudal view (on the left) and the cranial view (on the right) of the femur (after Von den Driesch, 1976)

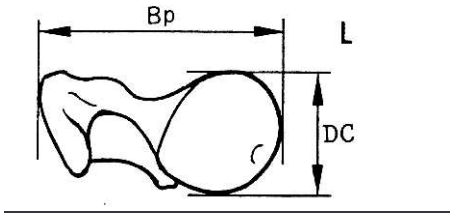


Figure 23: Proximal view of the femur (after Von den Driesch, 1976)

2.2.2.10 *Measurements of the patella*

GL- Greatest length

GB- Greatest breadth

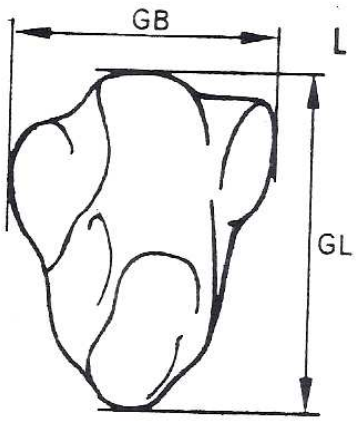


Figure 24: Proximal view of the patella (after Von den Driesch, 1976)

2.2.2.11 *Measurements of the tibia*

GL-Greatest length

Bp-(Greatest) breadth of the proximal end

SD-Smallest breadth of the diaphysis

CD-(Smallest) circumference of the diaphysis

Bd-(Greatest) breadth of the distal end

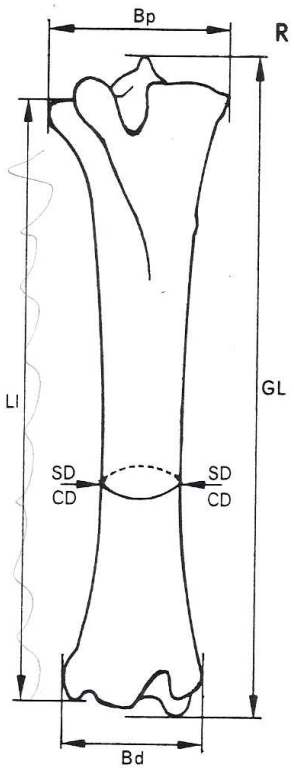


Figure 25: Dorsal view of the tibia (after Von den Driesch, 1976)

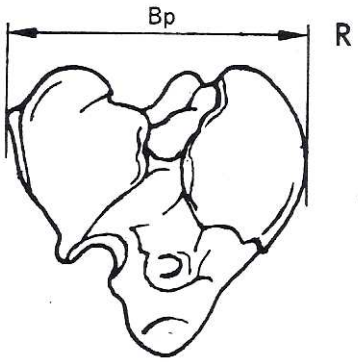


Figure 26: Proximal view of the tibia (after Von den Driesch, 1976)

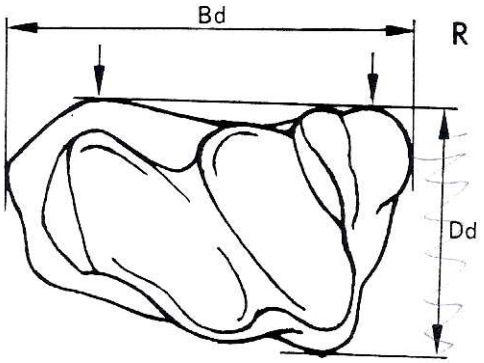


Figure 27: Distal view of the tibia (after Von den Driesch, 1976)

2.2.2.12 *Measurements of the talus (astragalus)*

GLI- Greatest length of the lateral half

GLm- Greatest length of the medial half

DI- (Greatest) depth of the lateral half

Dm- (Greatest) depth of the medial half

Bd- (Greatest) breadth of the distal end

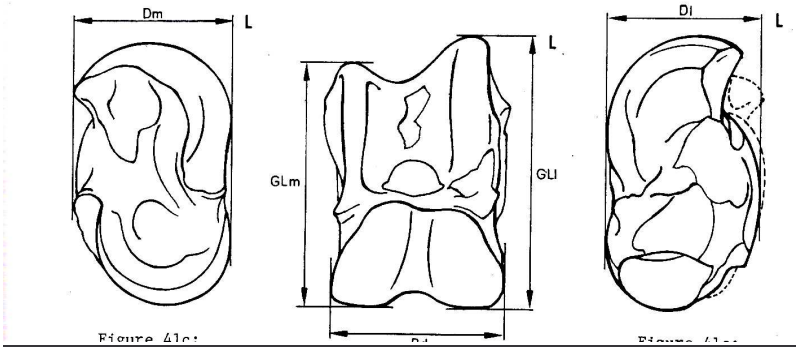


Figure 28: Medial, dorsal and lateral view of the talus (after Von den Driesch, 1976)

2.2.2.13 *Measurements of metapodials*

GL- Greatest length

Bp- (Greatest) breadth of the proximal end

Dp- (Greatest) depth of the proximal end

SD- Smallest breadth of the diaphysis

CD- (Smallest) circumference of the diaphysis

DD- (Smallest) depth of the diaphysis

Bd- (Greatest) breadth of the distal end

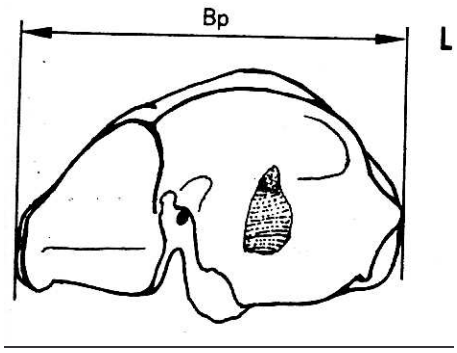


Figure 29: Proximal view of the metacarpus (after Von den Driesch, 1976)

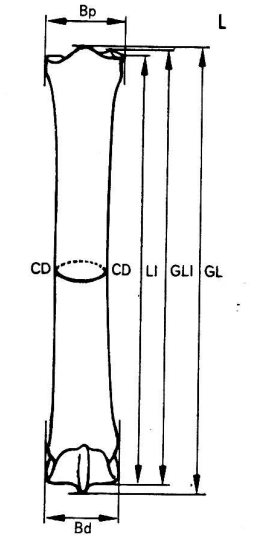


Figure 30: Dorsal view of the metatarsal (after Von den Driesch, 1976)

2.2.2.14 *Measurements of the calcaneus*

GL- Greatest length

GB- Greatest breadth. Measured in a measuring box or with a slide gauge with broad callipers

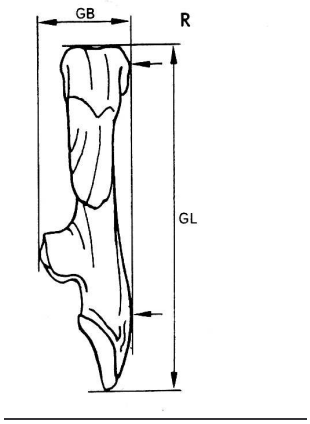


Figure 31: Plantar view of the calcaneus (after Von den Driesch, 1976).

2.2.2.15 *Measurements of phalanx I*

GLpe- Greatest length of the peripheral (abaxial) half

Bp- (Greatest) breadth of the proximal end

SD- Smallest breadth of the diaphysis

Bd- (Greatest) breadth of the distal end

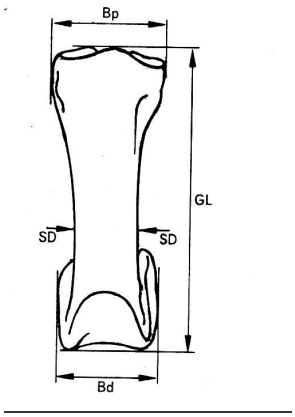


Figure 32: Dorsal view of phalanx 1 (after Von den Driesch, 1976)

Upon acquiring these measurements, a statistical T-test was used to evaluate if there are any significant differences in the means of these two groups. Statistical analysis of the measurements was made using the STATVIEW program.

3. CHAPTER THREE: RESULTS

Morphology and statistical analyses

3.1.1 *Crania*

In this instance, a scale bar of 5 cm was used. In all the illustrations bontebok is on the left and blesbok is on the right. The specimens used were male (both of them).



Figure 33: Photo showing the bontebok and blesbok.

When one looks at these specimens, it is clear that the bontebok is larger or longer than the blesbok. Another difference is that the cranium of the bontebok is broader whilst that of the blesbok is narrower and more elongated.

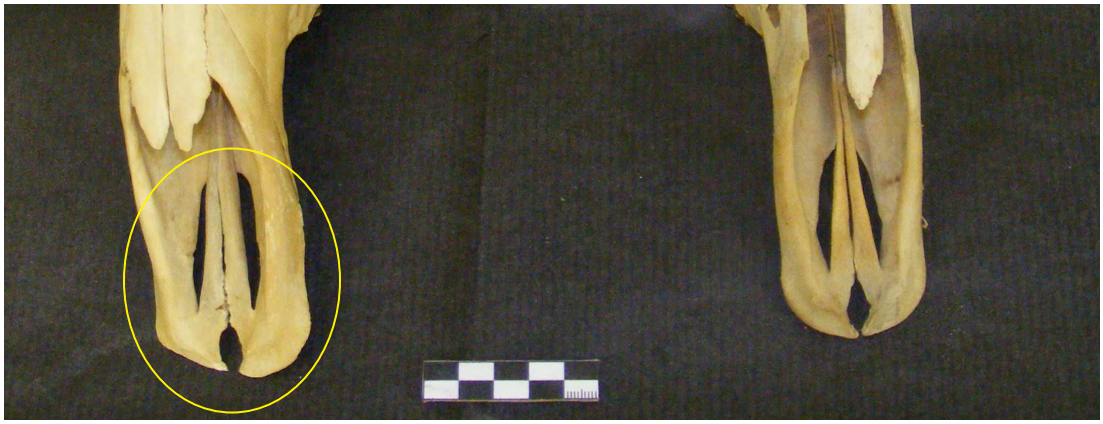


Figure 34: Photo showing the premaxillae of bontebok and blesbok.

When looking at the premaxillae, they are both curved, but that of bontebok is more curved than that of blesbok. It is also shorter (blesbok) when comparing their heights.



Figure 35: Photo of the frontal of the bontebok and the blesbok

The frontal of blesbok is wider near the horns whilst that of bontebok is narrower. The orbitals are also different in that those of bontebok are bigger and wider than those of blesbok.



Figure 36: Photo showing the basal view bontebok and the blesbok

The blesbok specimen is longer when looking at these basal views of the specimens. The curvature of the base of the premaxillae is also clearer in bontebok.



Figure 37: Photo showing the auditory bullae of the bontebok and the blesbok

When one looks closely at the auditory bullae of the two specimens, it is clear that the auditory bullae of the blesbok are inflated and its occipital condyles are bigger than those of the bontebok. What can also be seen in the above photo is the foramen magnum of blesbok is bigger or wider than that of bontebok.

Metric statistical analysis

The statistical analysis of the crania shows that there are some differences in the cranial morphology of the two subspecies. In three of the graphs (Figs. 38, 39, 43) *D. pygargus phillipsi* is above the regression line. In another two (Figs. 41, 44) they are mostly below the line, and in Figs. 42 and 45 they are roughly equally above and below the line. This means that *D. pygargus phillipsi* is larger than *D. pygargus pygargus*.

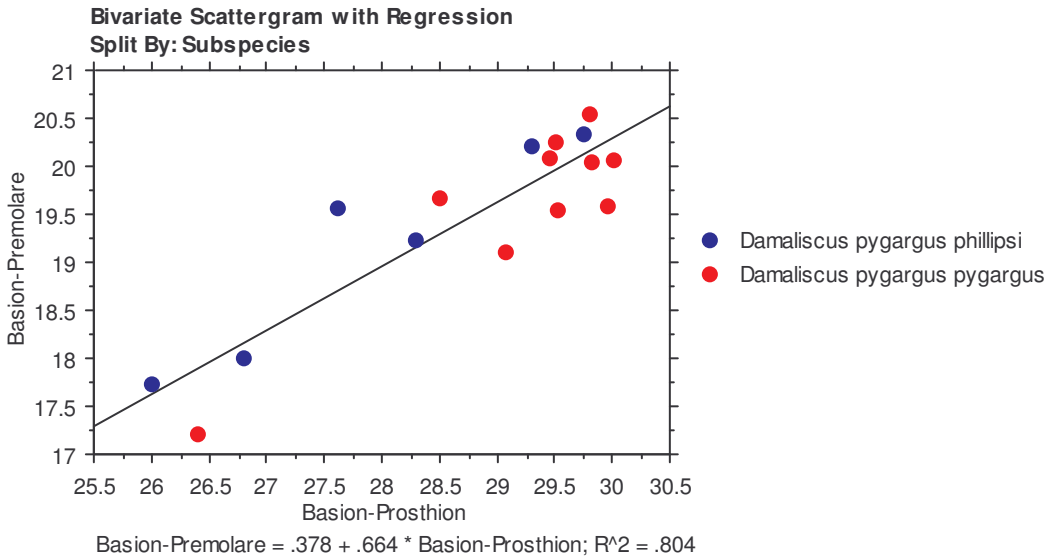


Figure 38: Bivariate plot of the cranium from the basion to the prosthion versus from the basion to the premolare showing the regression line of both bontebok and blesbok.

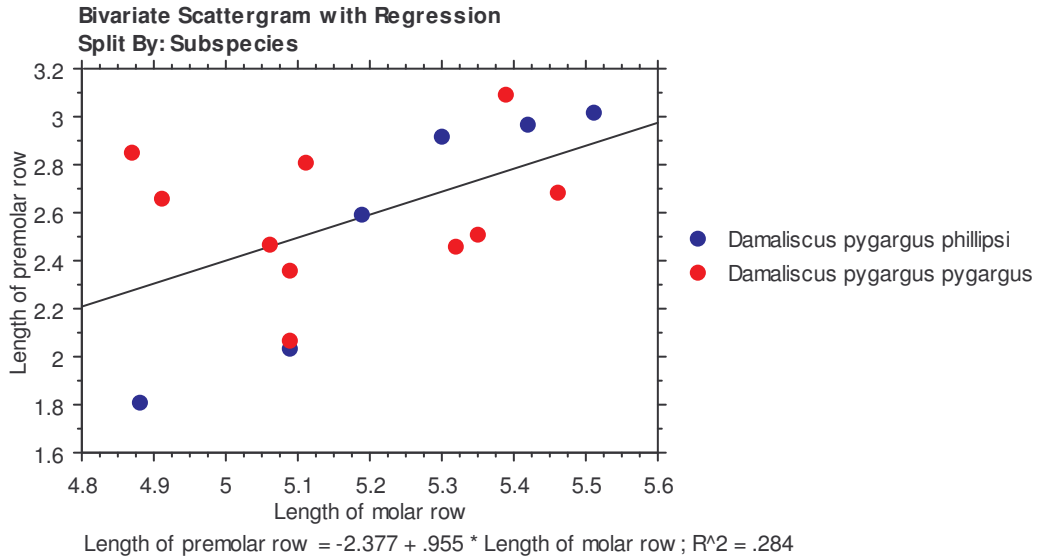


Figure 39: Bivariate plot of the length of the molar row versus the length of the premolar row showing regression of both groups.

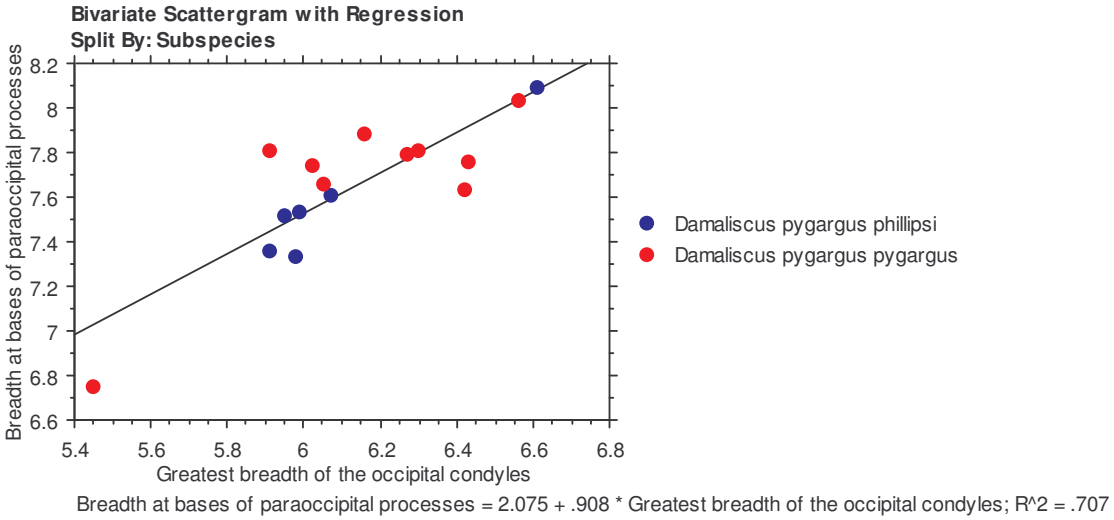


Figure 40: Bivariate plot of the greatest breadth of the occipital condyles versus the breadth at the bases of paraoccipital processes showing regression of both groups.

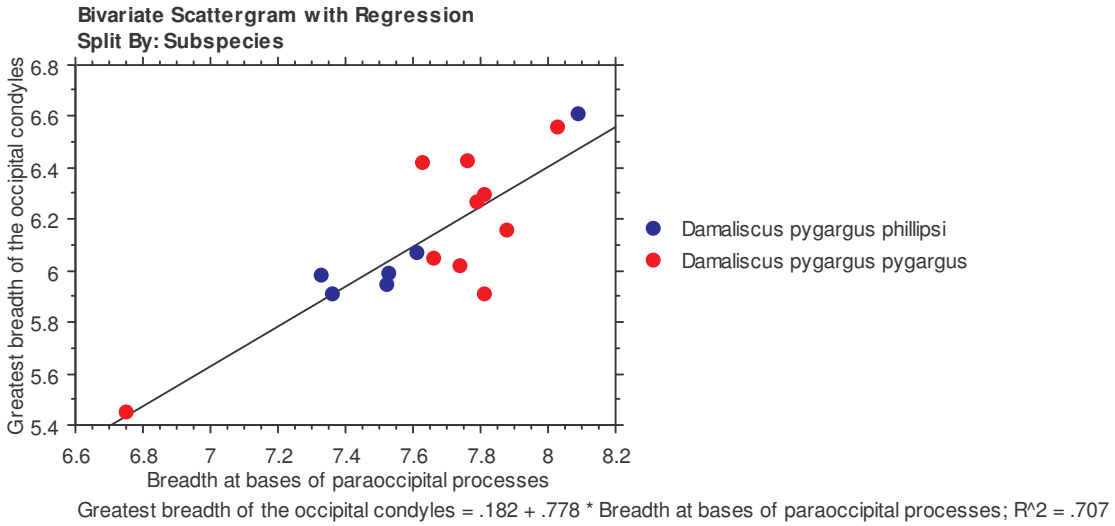


Figure 41: Bivariate plot of the breadth at bases of paraoccipital processes versus the greatest breadth of the occipital condyles showing regression of both groups.

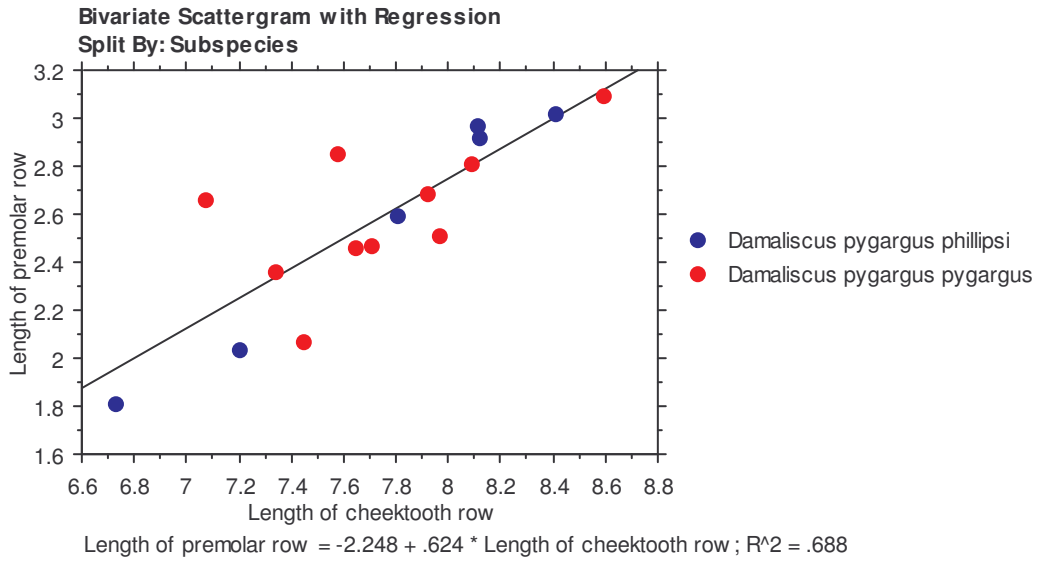


Figure 42: Bivariate plot of the length of the cheektooth row versus the length of the premolar row showing 95% regression of both groups.

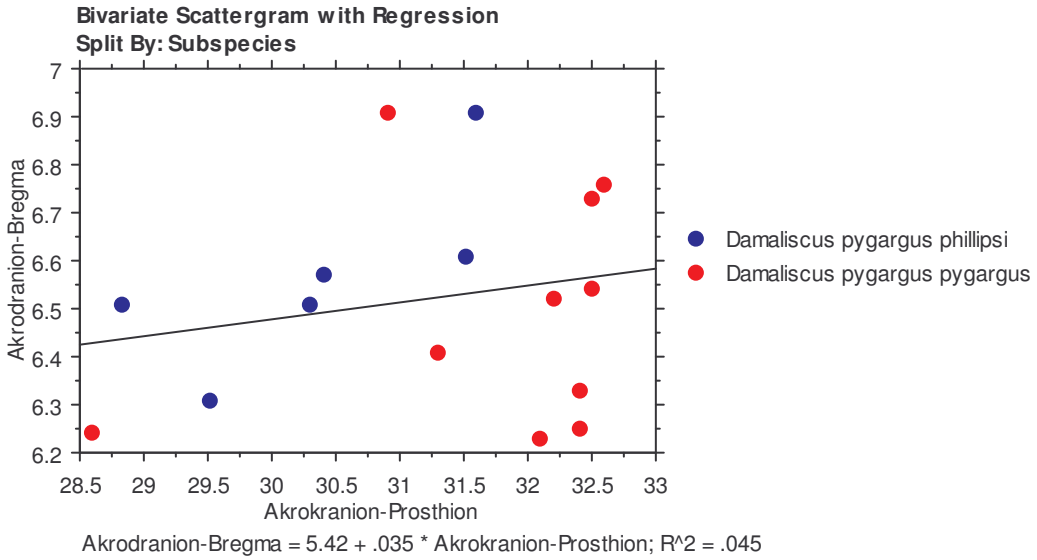


Figure 43: Bivariate plot of the akrokranion to the prosthion versus the akrokranion to the bregma showing regression of both groups.

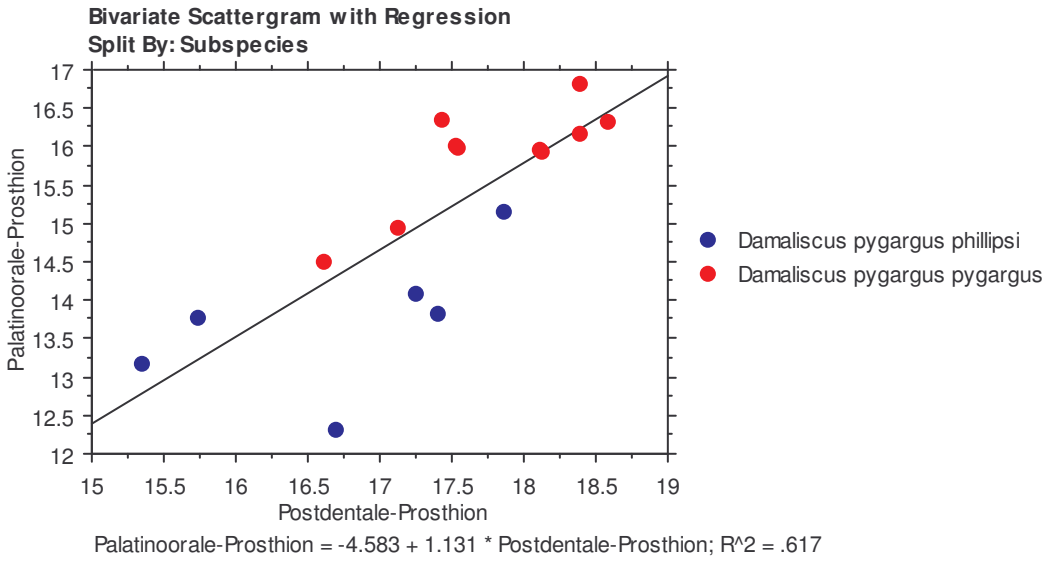


Figure 44: Bivariate plot of the Postdentale to the prosthion versus from the palatinoorale to the prosthion showing regression of both groups.

Figure 44 shows an overlap between the two subspecies. It shows blesbok further down the regression line, whilst bontebok above the regression line. This could be interpreted by saying that there is a clear distinction between the two subspecies when looking at some parts of the skull.

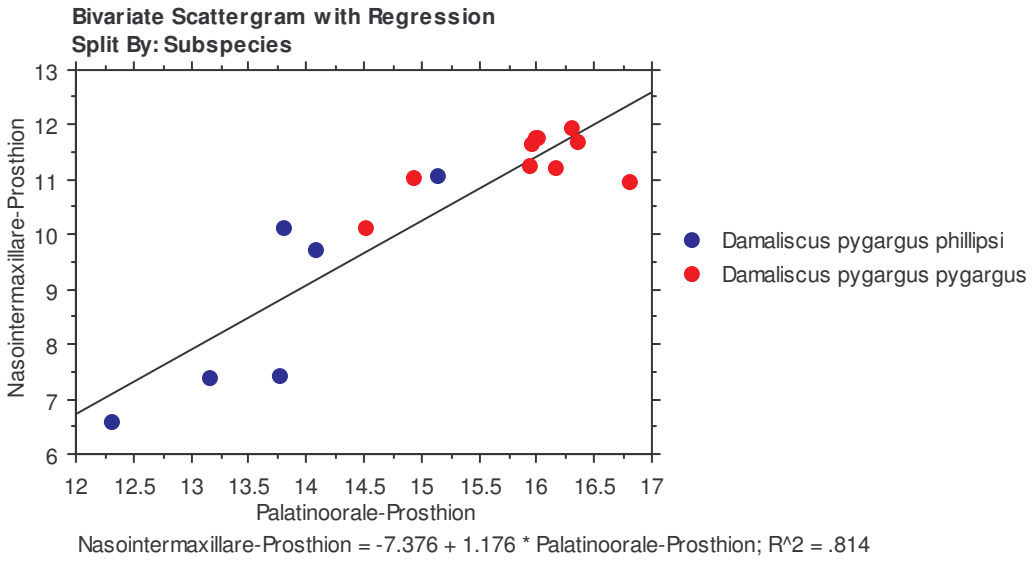


Figure 45: Bivariate plot of the palatinoorale to the prosthion versus nasointermaxillare to the prosthion showing 95% regression of both groups.

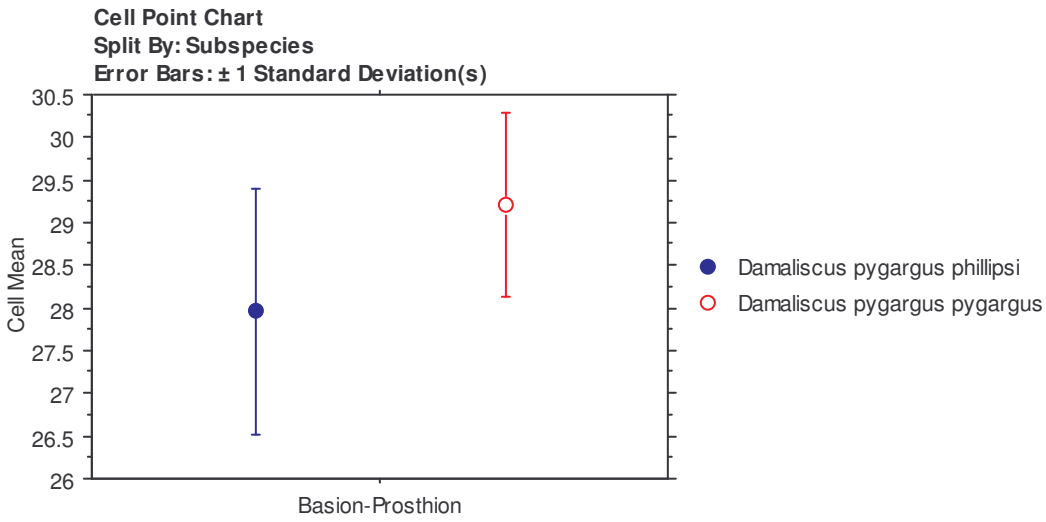


Figure 46: Standard error cell plot of the skull from the basion to the prosthion (error bars: ±1 STD deviation).

Figure 46 shows that there are differences between the two subspecies when looking at the distance from the basion to the prosthion of the skull. Even though there is an overlap between the two, this still shows that there are differences.

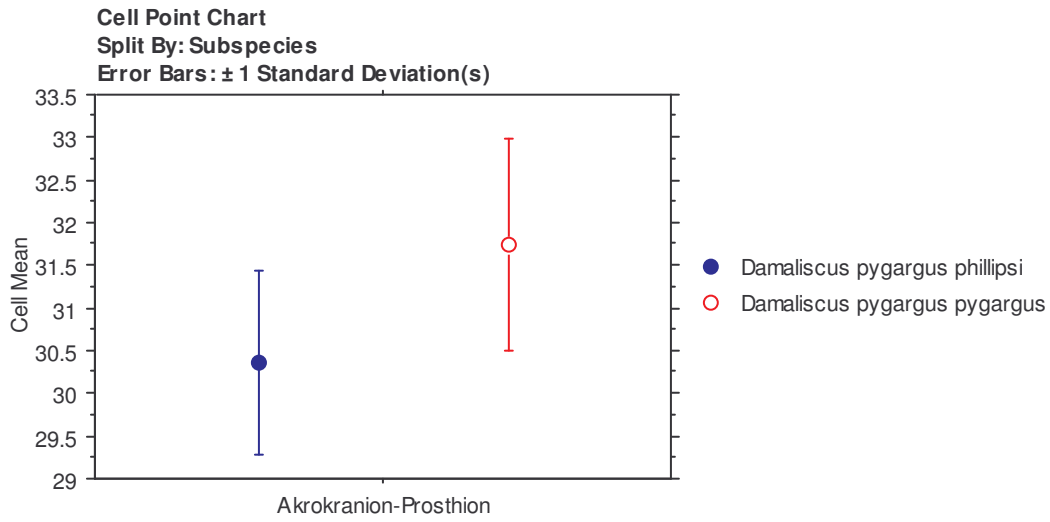


Figure 47: Standard error cell plot for the length of the skull from the akrokranion to the prosthion (error bars: ±1 STD deviation).

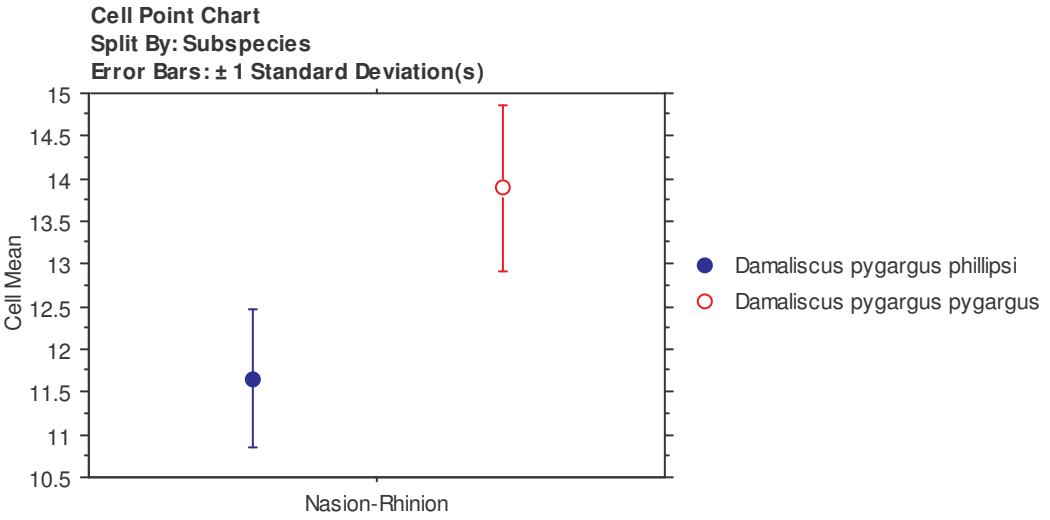


Figure 48: Standard error cell plot of the skull from the nasion to the rhinion (error bars: ±1 STD deviation)

3.1.2 *Mandibular Morphology*

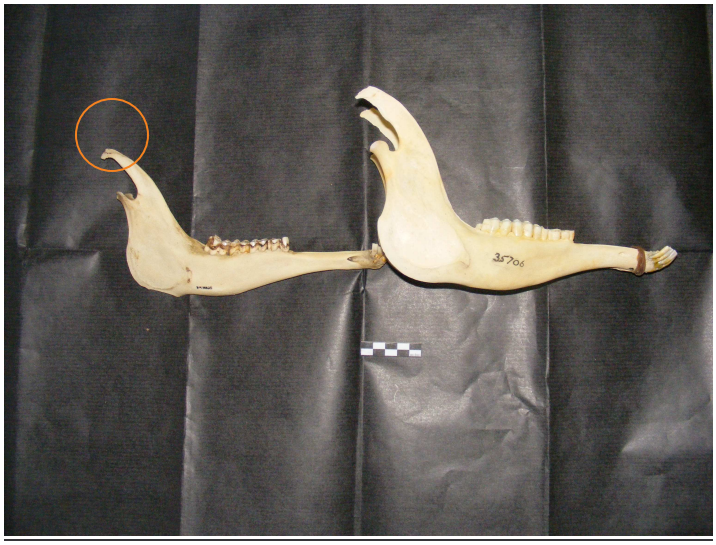


Figure 49: Photo showing the mandibles of bontebok and blesbok.

The above photo shows size difference between the two specimens. Bontebok is smaller than blesbok although both specimens are adults. The gonion caudale of bontebok is a bit sharper at the bottom whilst that of blesbok is a bit rounded. The coronion (the highest point of the coronoid process) of bontebok is sharper and narrower than that of blesbok (circled above).

3.1.3 Post-crania

3.1.3.1 *Atlas*

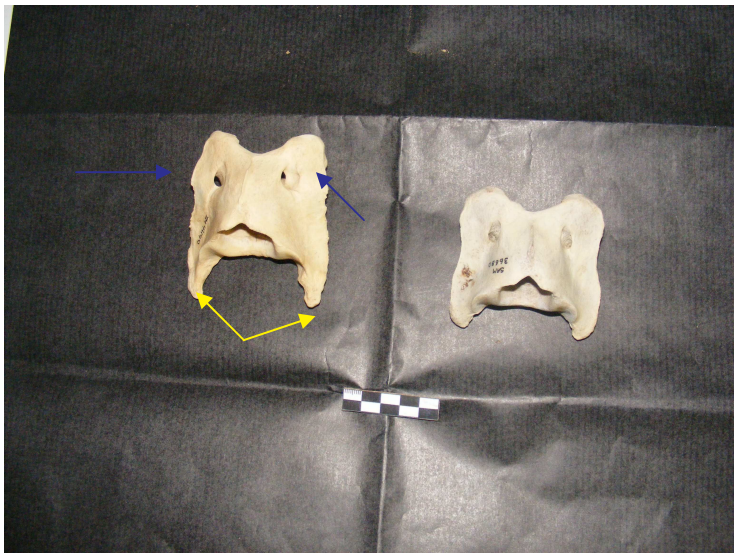


Figure 50: Photo showing the proximal view of the atlas of bontebok and blesbok.

Figure 50 shows the difference between the two in terms of height, whereby bontebok has a bigger atlas than blesbok. Another difference (yellow arrows) is that the wings (*alae*) of bontebok project caudally.

When looking at the two above, it can be seen that blesbok is broader than bontebok. Another difference is that the *alae* (blue arrows) of the bontebok extend more caudally than those of the blesbok.



Figure 51: Photo showing the dorsal view of the atlas of bontebok and blesbok.

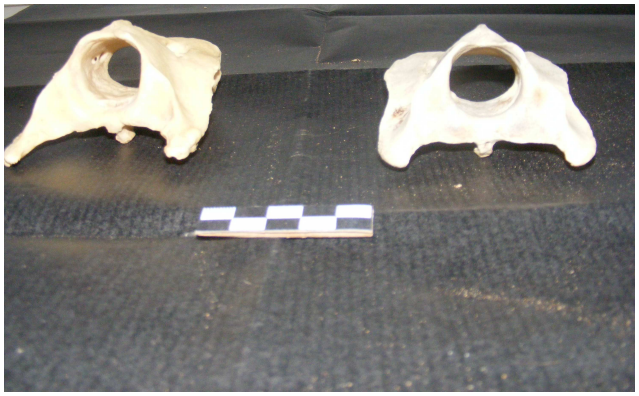


Figure 52: Photo showing the caudodorsal view of the atlas of bontebok and blesbok.

Figure 52 shows that the Facies articularis caudalis of bontebok is larger than that of blesbok.

Metric statistical analysis

The vertebral bones don't show much differences within these two groups even though they are found in different habitats\terrains as mentioned above.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GLF	3.052	.214	.068	10	2.710	3.350	1
H	4.625	.305	.092	11	4.150	5.080	0

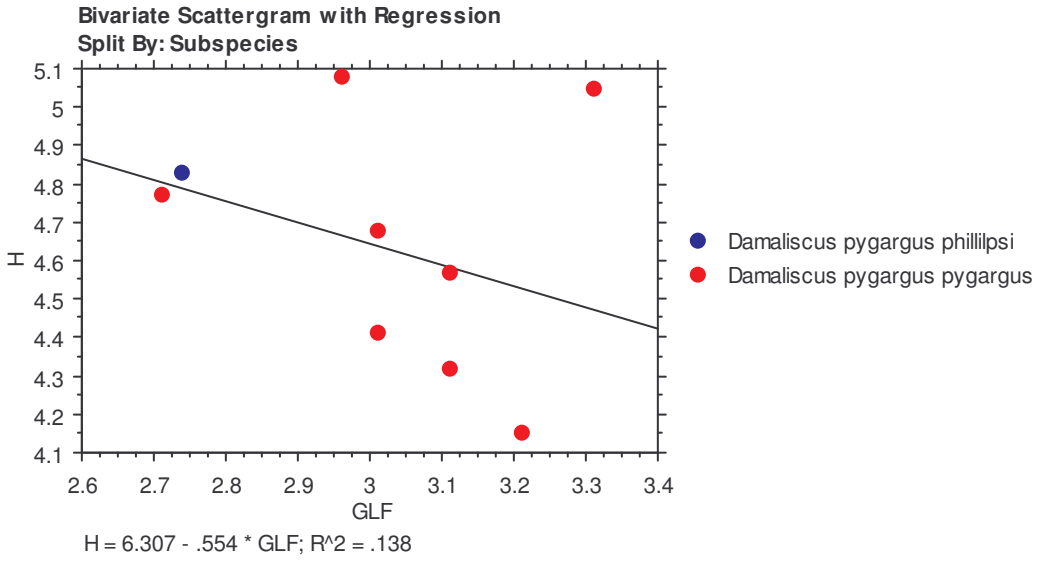


Figure 53: Bivariate plot of the greatest length from the Facies articularis cranialis to the Facies articularis caudalis versus the height of the atlas showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
BFcr	5.649	.206	.062	11	5.310	6.010	0
BFcd	3.255	.124	.037	11	3.110	3.450	0

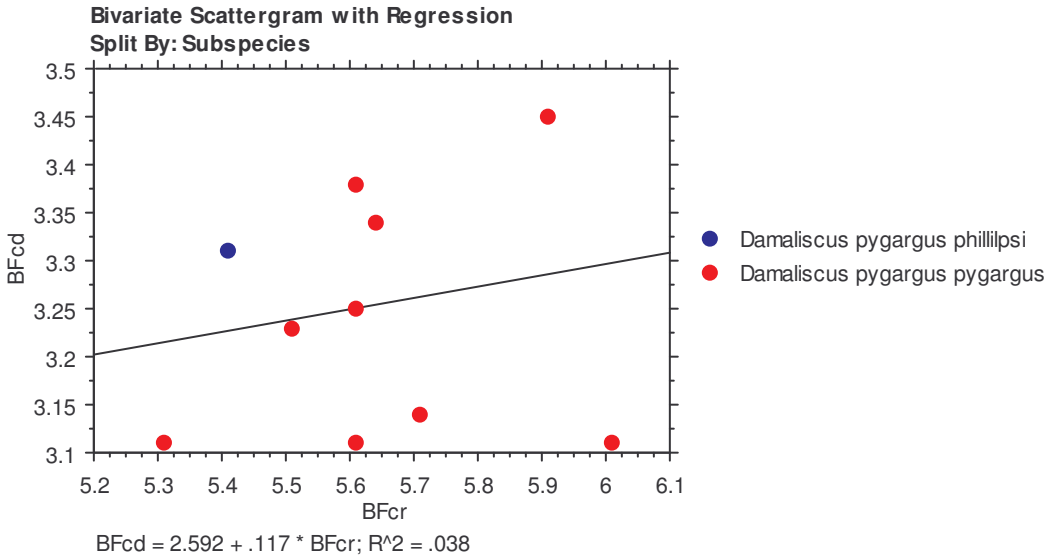


Figure 54: Bivariate plot of the breadth of the Facies articularis cranialis versus the breadth of the Facies articularis caudalis of the atlas showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GL	3.057	.189	.060	10	2.740	3.320	1
GB	6.487	.345	.104	11	5.990	6.930	0

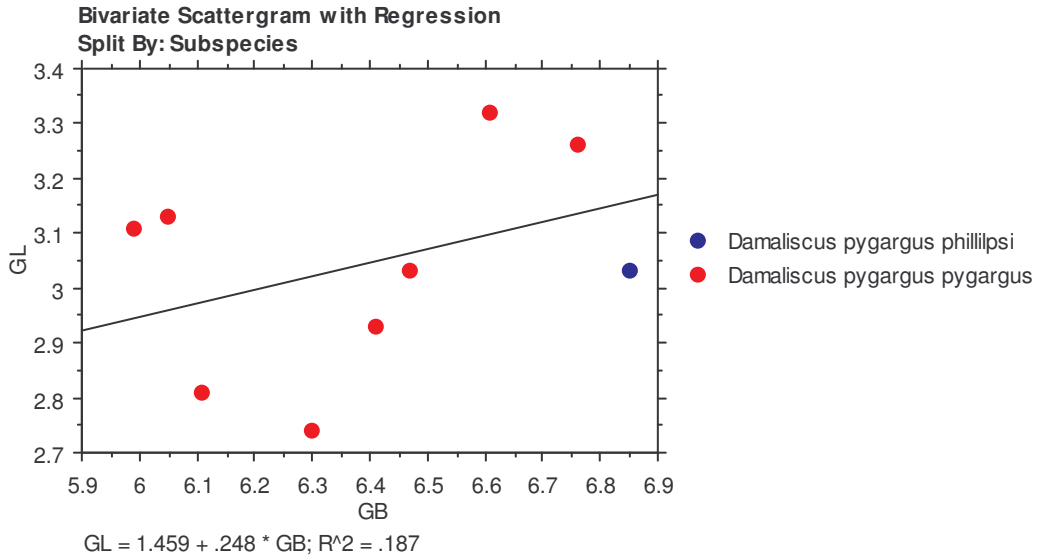


Figure 55: Bivariate plot of the greatest breadth over the wings versus the greatest length of the atlas showing regression of both groups.

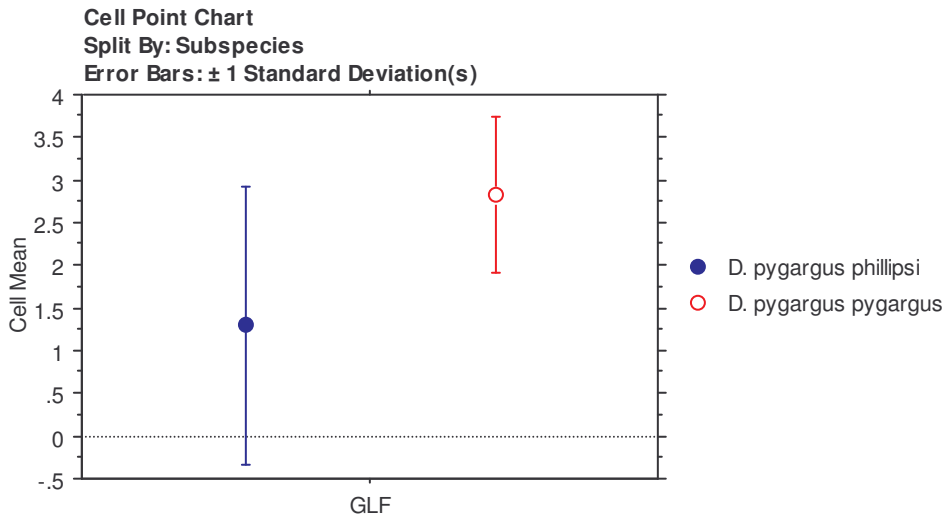


Figure 56: Standard error cell plot of the greatest length from the Facies articularis cranialis to the Facies articularis caudalis (error bars: ±1 STD deviation).

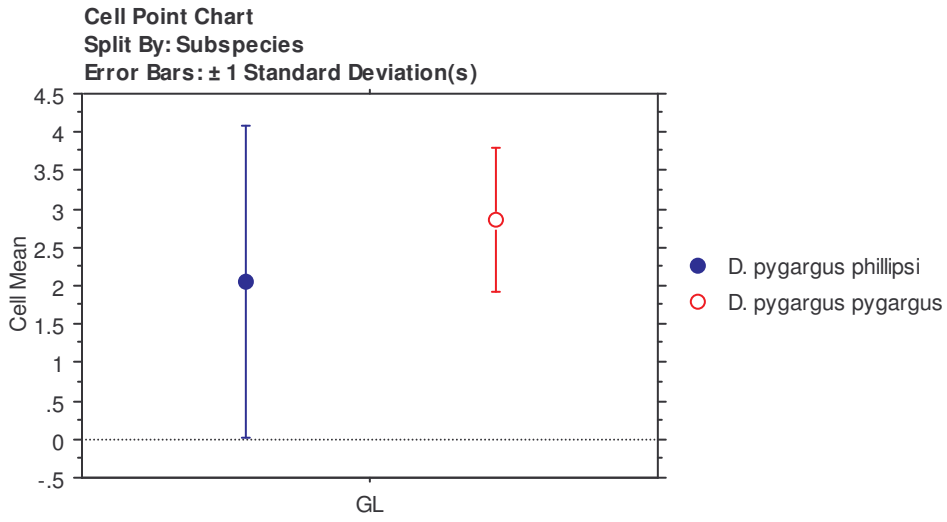


Figure 57: Standard error cell plot of the greatest length of the atlas (error bars: ±1 STD deviation).

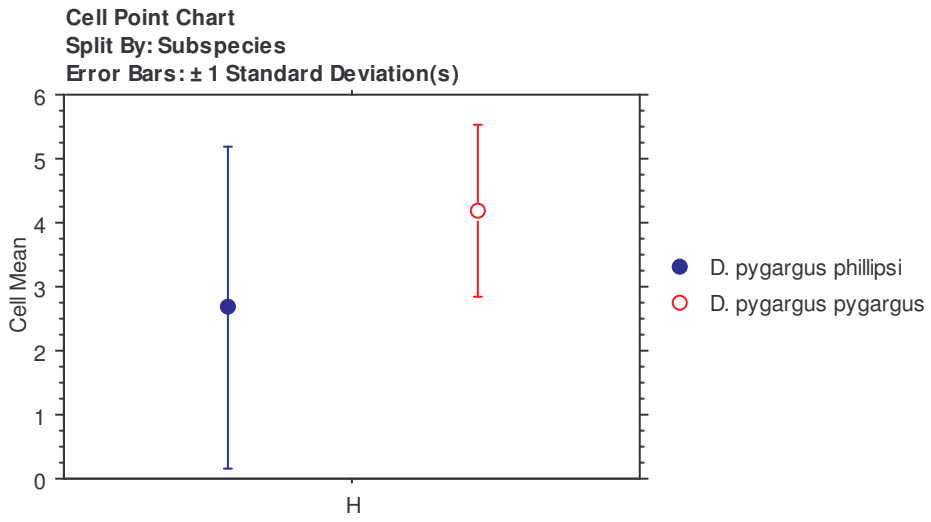


Figure 58: Standard error cell plot of the height of the atlas (error bars: ±1 STD deviation).

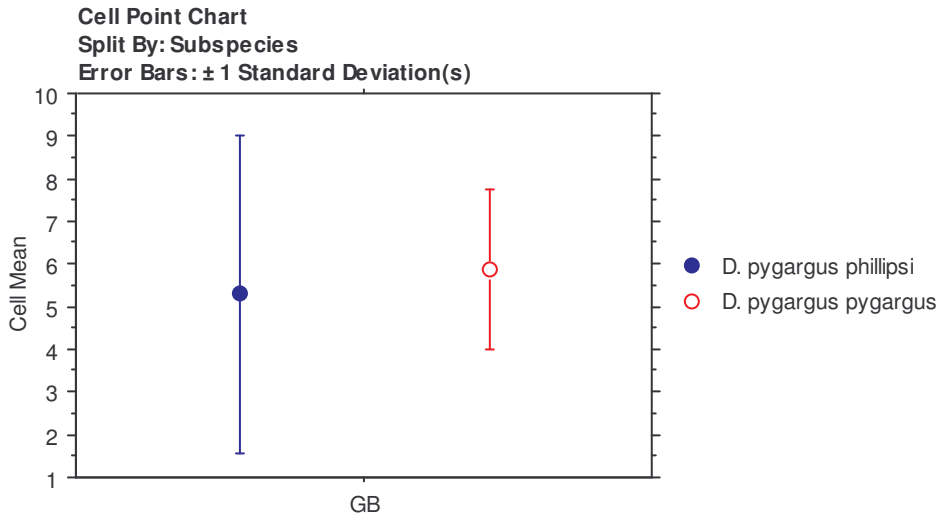


Figure 59: Standard error cell plot of the greatest breadth over the wings of the atlas (error bars: ±1 STD deviation).

Descriptive Statistics

	BFcr
Mean	5.649
Std. Dev.	.206
Std. Error	.062
Count	11
Minimum	5.310
Maximum	6.010
# Missing	0

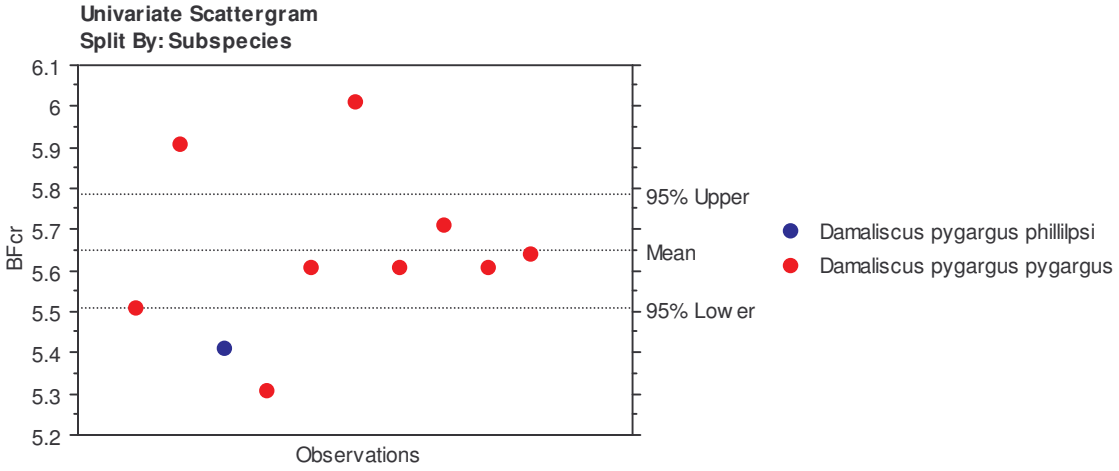


Figure 60: Univariate analysis of the breadth of the Facies articularis cranialis of the atlas.

Descriptive Statistics

	BFcd
Mean	3.255
Std. Dev.	.124
Std. Error	.037
Count	11
Minimum	3.110
Maximum	3.450
# Missing	0

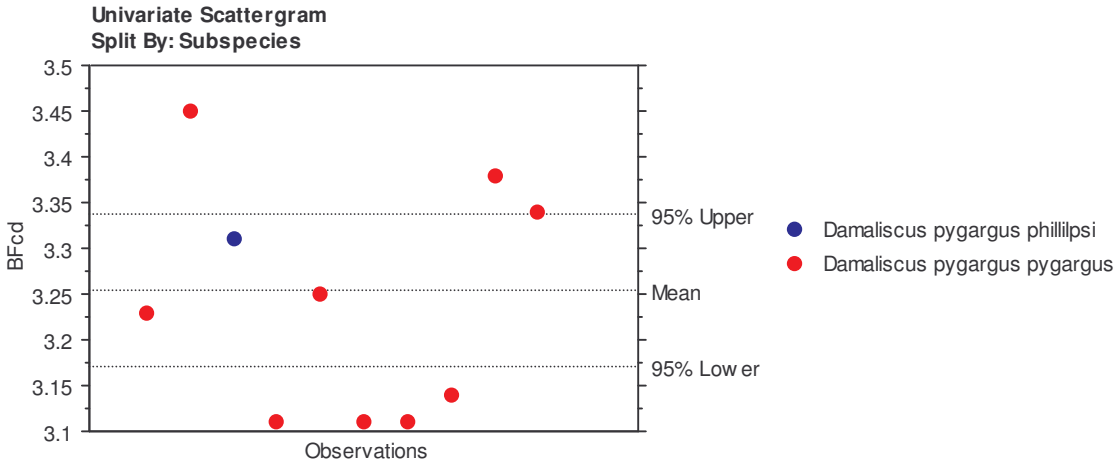


Figure 61: Univariate analysis of the breadth of the Facies articularis caudalis of the atlas with outliers.

3.1.3.2 *Axis*



Figure 62: Photo showing the left side view of the axis of bontebok and blesbok.

Figure 62 shows that there is no significant difference between the two in terms of height. But there is one visible difference between the two (pointed above); blesbok has a curved arch, whilst bontebok has a rounded arch.



Figure 63: Photo showing the arch of the axis of bontebok and blesbok.

Figure 63 shows some height differences between the two subspecies; bontebok is bigger than blesbok.

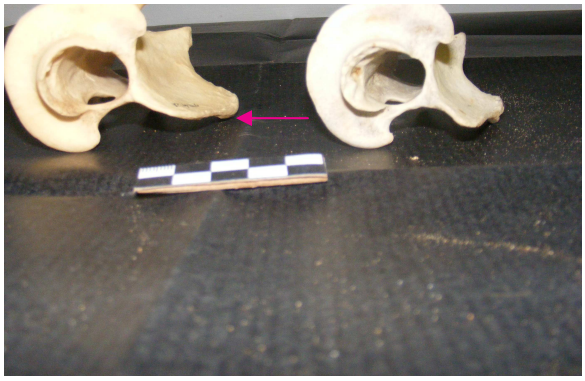


Figure 64: Photo showing the Facies articularis cranialis of the axis of bontebok and blesbok.

Figure 64 show that the Facies articularis cranialis of both subspecies is almost the same. Figure 64 also shows the thickness of bontebok (shown above in red, indicating the caudal end of the *proc. spinosus*) than blesbok.

Metric statistical analysis

The results don't show many differences as in other results above.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
LCDe	7.911	.333	.092	13	7.450	8.540	2
LAPa	6.381	.371	.103	13	5.610	6.870	2

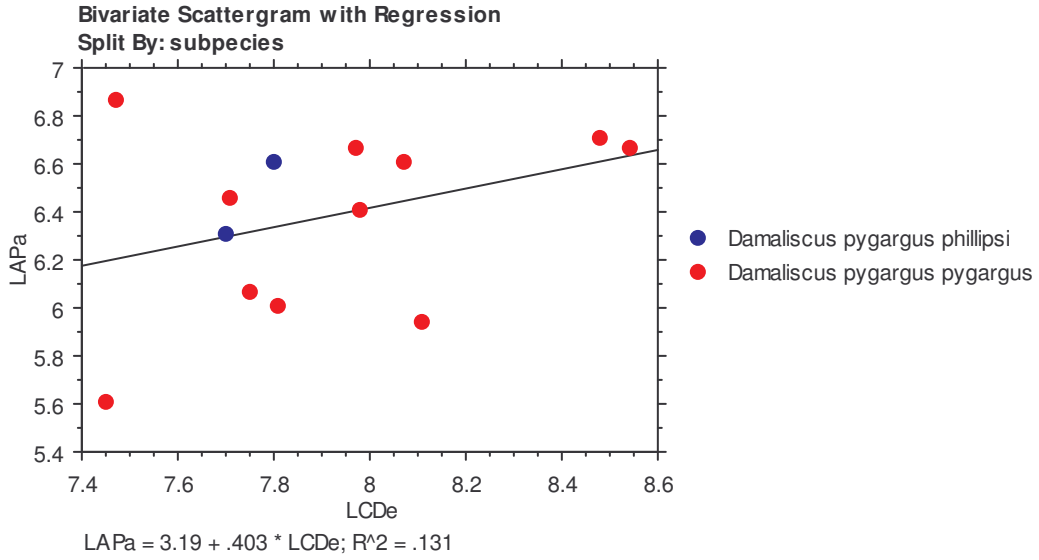


Figure 65: Bivariate plot of the length of the axis in the region of the corpus including the dens versus the length of the arch including the Processus articularis caudalis showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
BFcr	5.649	.206	.062	11	5.310	6.010	0
BFcd	3.255	.124	.037	11	3.110	3.450	0

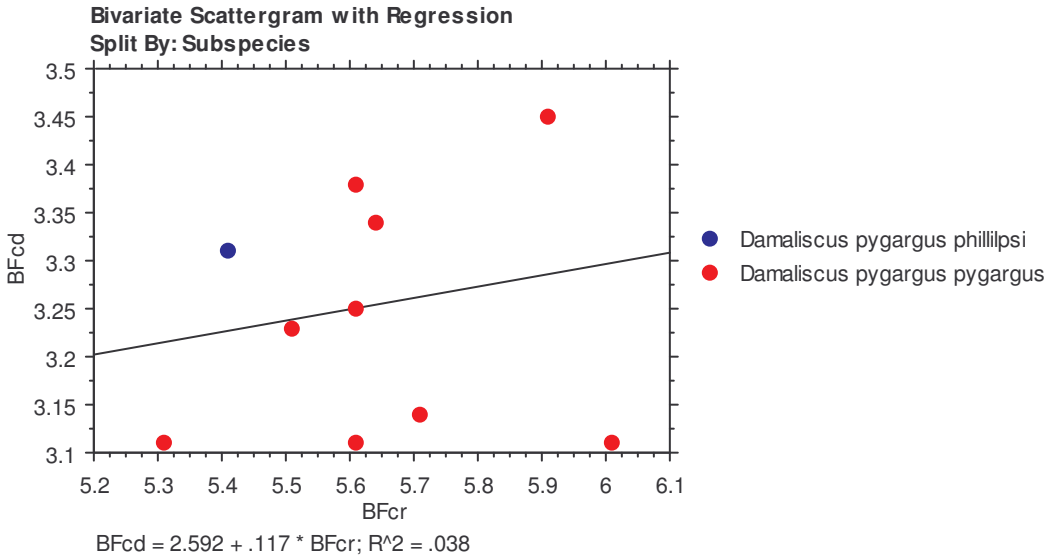


Figure 66: Bivariate plot of the breadth of the Facies articularis cranialis versus the breadth of the Facies terminalis caudalis of the axis showing regression of both groups.

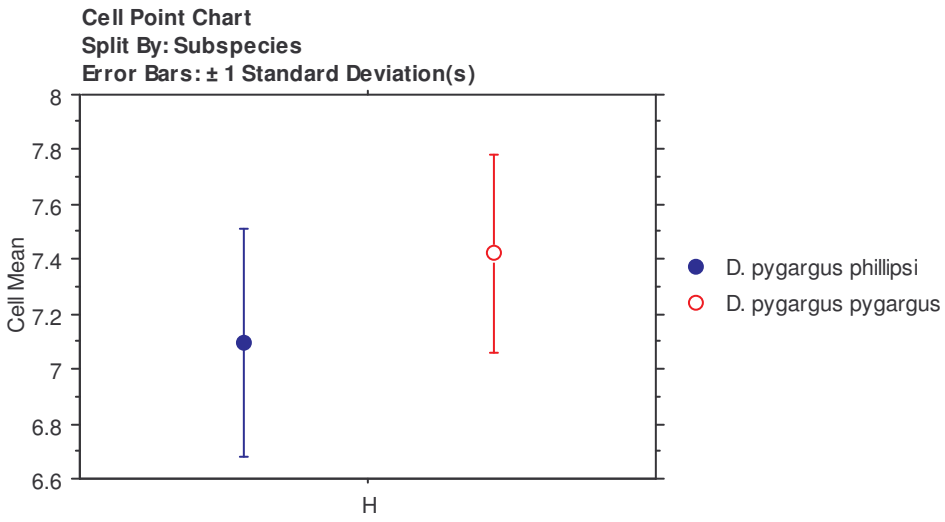


Figure 67: Standard error cell plot of the height of the axis (error bars: ±1 STD deviation).

Figure 67 shows a clear distinction in the height of both subspecies (even though they overlap). It shows that the axis of bontebok is bigger in terms of height than that of blesbok. This could be linked to the different terrains these animals are found in and the different stresses they encounter.

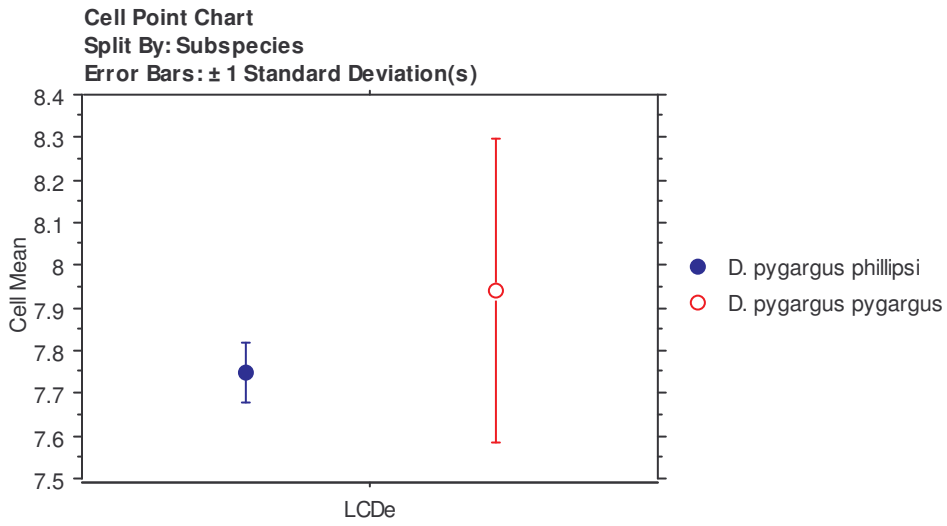


Figure 68: Standard error cell plot of axis of the length in the region of the corpus (error bars: ±1 STD deviation).

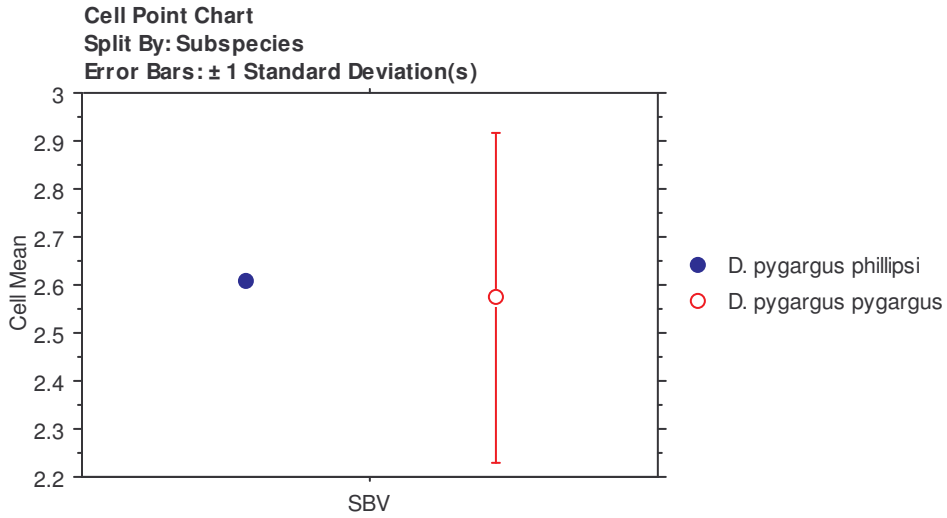


Figure 69: Standard error cell plot of the smallest breadth of the vertebra of the axis (error bars: ±1 STD deviation).

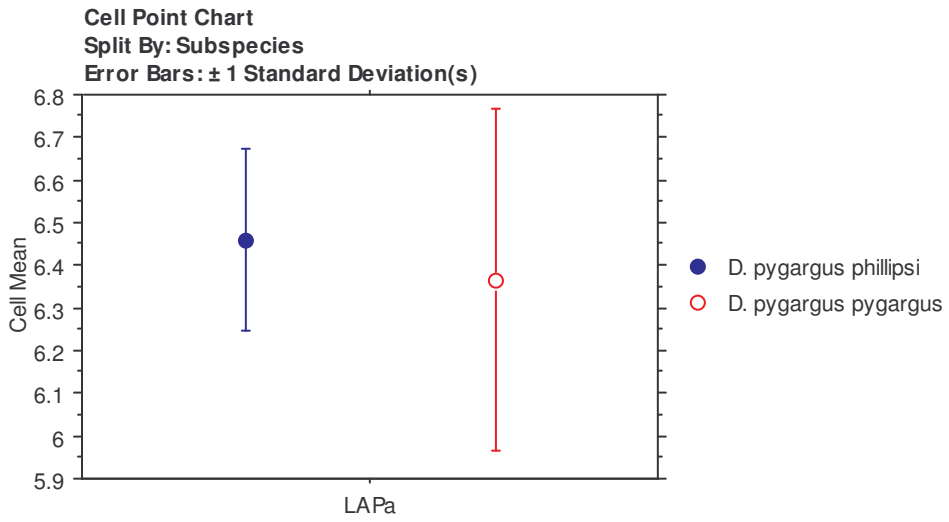


Figure 70: Standard error cell plot of the length of the arch including the Processus articularis caudalis of the axis (error bars: ±1 STD deviation).

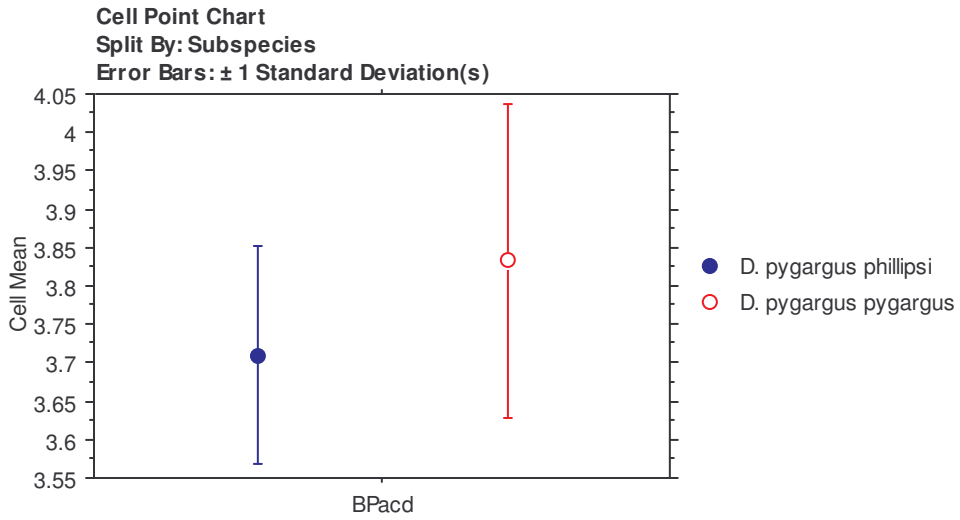


Figure 71: Standard error cell plot of the breadth across the Processus articularis caudalis of the axis (error bars: ±1 STD deviation).

Figures 68, 69, 70 and 71 also show bontebok's axis to be bigger than that of blesbok. This again was unexpected since older literature show bontebok to be smaller than blesbok (Smithers, 1983).

Front Limb

3.1.3.3 *Scapula*



Figure 72: Photo showing the scapulae of bontebok and blesbok

When looking at the photo above, it again, shows size difference. The scapula of bontebok is bigger than that of blesbok. When looking at the blades, that one of blesbok is flatter and broader than that of bontebok.



Figure 73: Photo showing the thickness of the scapulae of bontebok (top) and blesbok (bottom).

The broadness of the blades can also be seen; blesbok is flatter and broader especially in the middle. This clearly shows that the scapula of the bontebok is bigger (larger) than that of the blesbok.

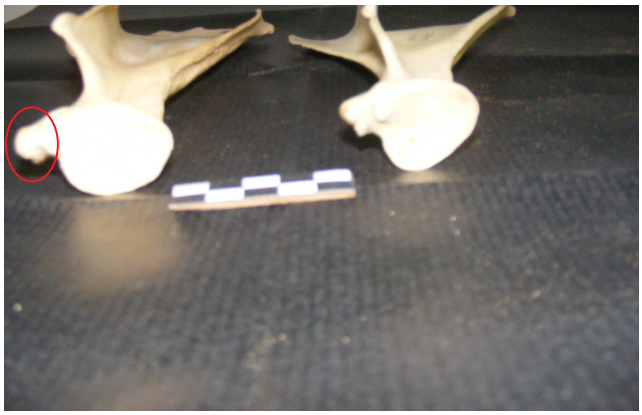


Figure 74: Photo showing the distal view of the scapulae (the glenoid cavity) of bontebok and blesbok

The glenoid cavity of bontebok is rounder than that of blesbok. It is also bigger in size. When looking at the tubular scapulae of both specimens; that of bontebok protrudes more outward than that of blesbok.

Metric statistical analysis

In the instance of the scapula, both groups show that these animals are not distinct; they are similar as it can be seen in figure 75 whereby both these subspecies are above and below the regression line. This could mean that even though they experience different stresses, that does not affect their osteology that much (see figure 75).

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
HS	23.039	.946	.273	12	20.860	24.220	0
DHA	23.143	1.219	.352	12	21.110	24.530	0

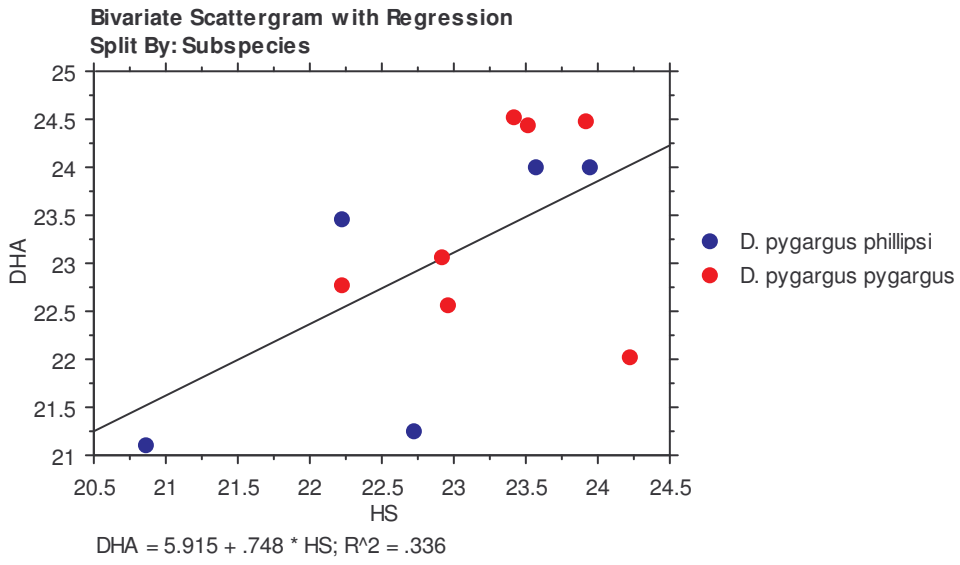


Figure 75: Bivariate plot of the height along the spine versus the diagonal height of the scapula showing regression of both groups.

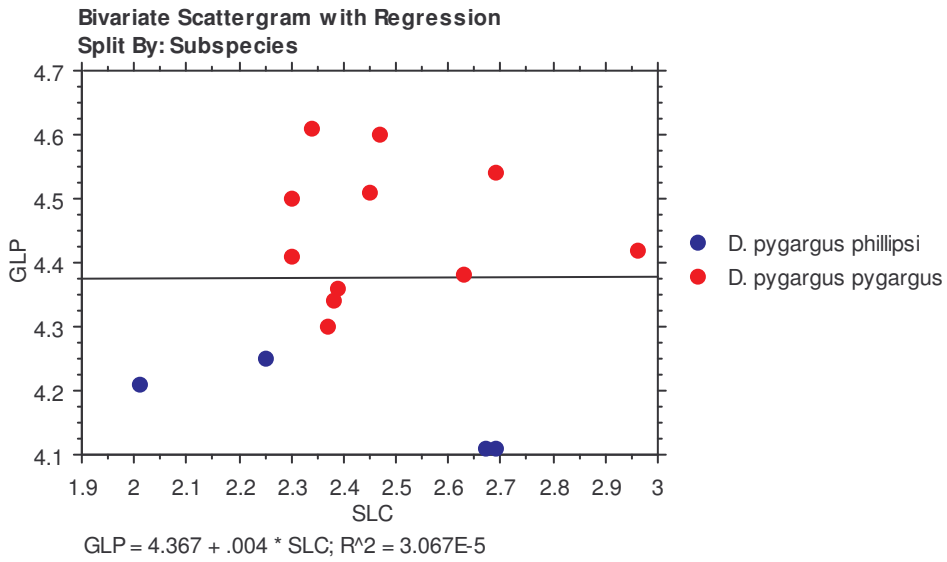


Figure 76: Bivariate plot of the smallest length of the Collum scapulae versus the greatest length of the Processus articularis of the scapula showing regression of both groups.

Figure 76 shows a clear distinction between the two subspecies, whereby blesbok is below the regression line whilst bontebok is above the regression line. This clearly shows that the scapula of the bontebok is bigger (larger) than that of the blesbok.

Descriptive Statistics

	DHA
Mean	23.143
Std. Dev.	1.219
Std. Error	.352
Count	12
Minimum	21.110
Maximum	24.530
# Missing	0

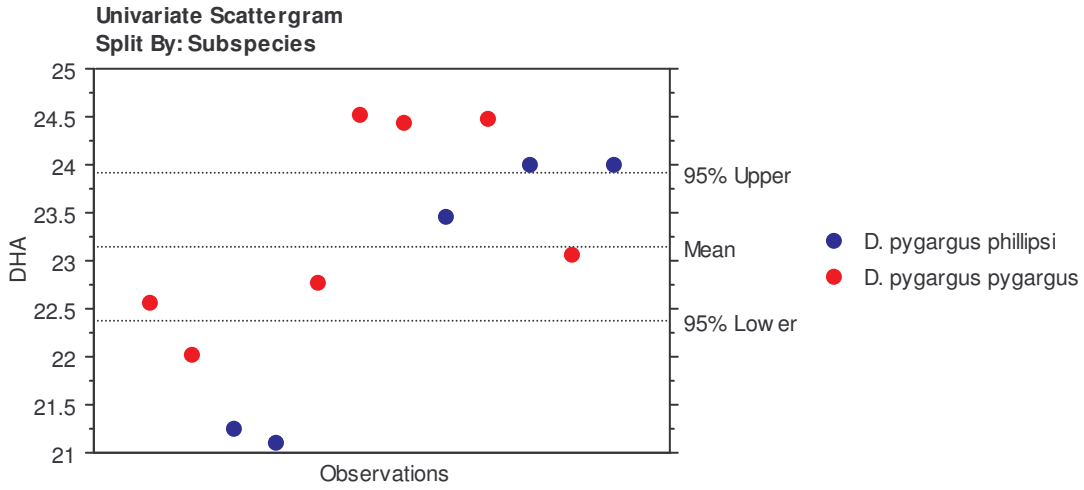


Figure 77: Univariate plot of the diagonal height of the scapula showing the mean at 95% confidence interval of both groups.

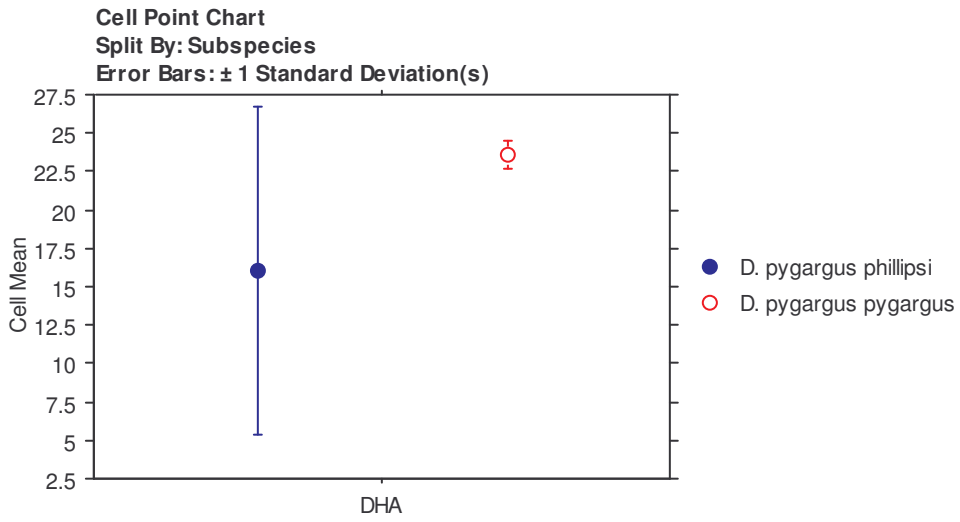


Figure 78: Standard error cell plot of the diagonal height of the scapula (error bars: ±1 STD deviation).

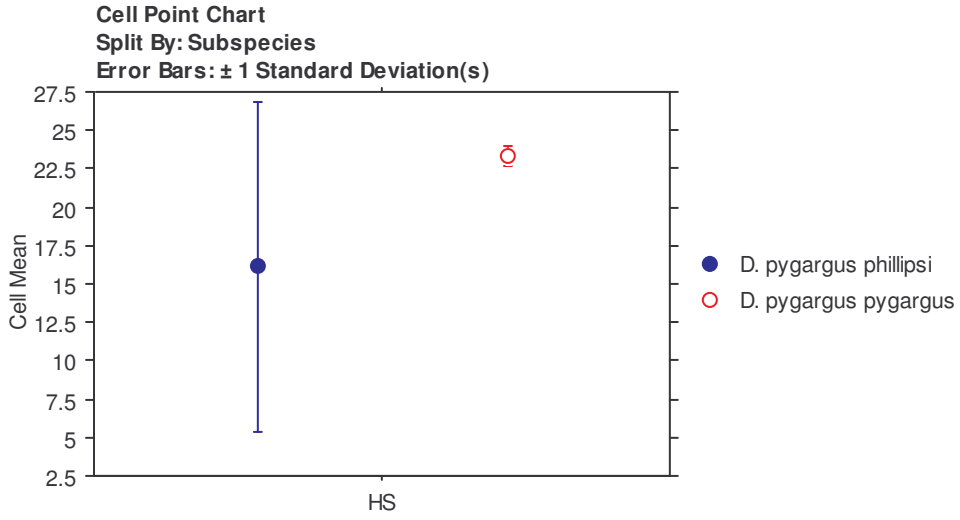


Figure 79: Standard error cell plot of the height along the spine of the scapula (error bars: ±1 STD deviation).

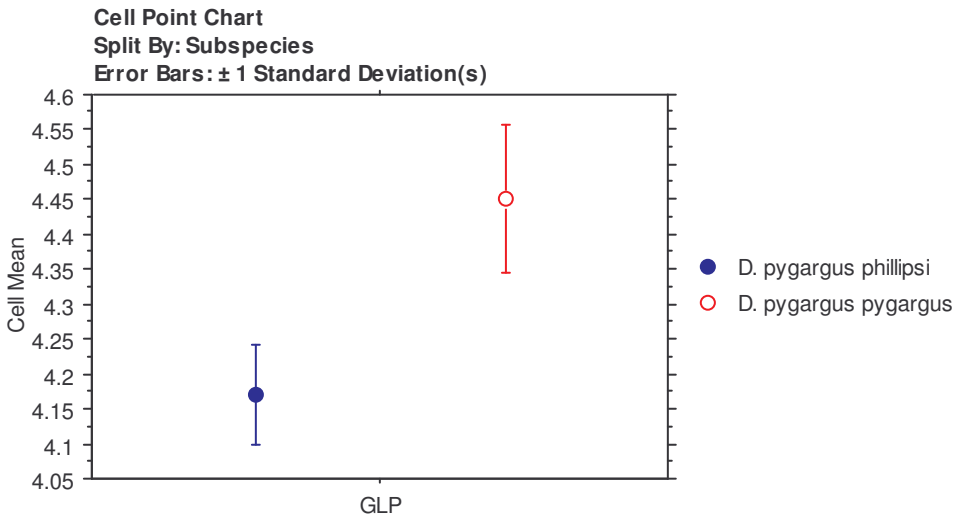


Figure 80: Standard error cell plot of the greatest length of the Processus articularis of the scapula (error bars: ±1 STD deviation).

Figure 80 above shows that there is a difference between the two subspecies when looking at their GLP, whereby bontebok is bigger than blesbok.

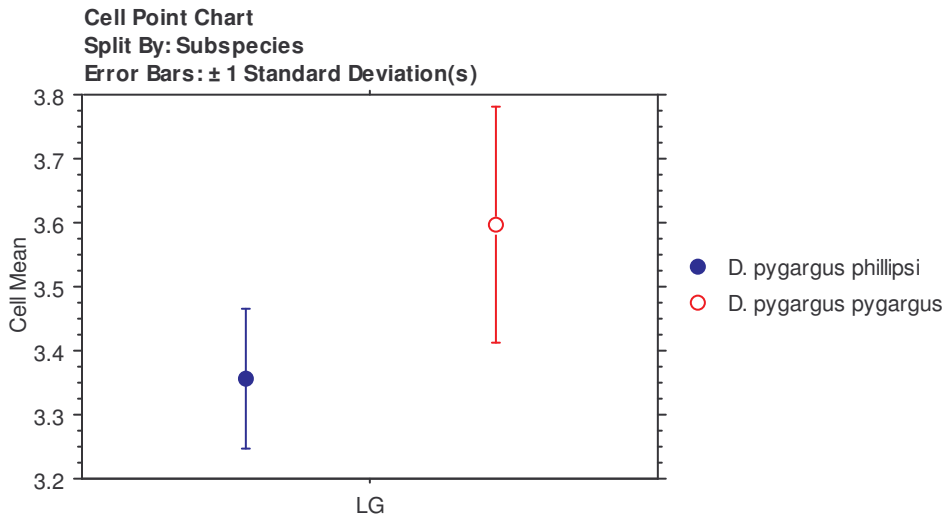


Figure 81: Standard error cell plot of the length of the glenoid cavity of the scapula (error bars: ±1 STD deviation).

3.1.3.4 *Humerus*



Figure 82: Photo showing the lateral view of the humeri of bontebok and blesbok.

When looking at the size, both humeri are nearly equal, but the bontebok humerus is a bit taller than that of the blesbok.

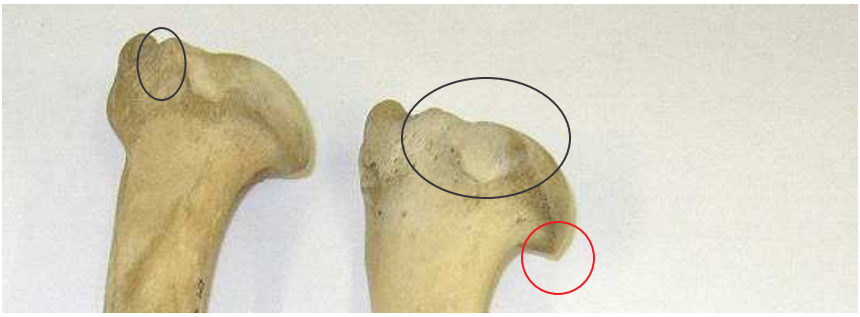


Figure 83: Photo showing the proximal end (craniomedial) of the humerus of bontebok and blesbok.

When looking at the circled *pars cranialis* of blesbok, it is deeper than that of bontebok. The "head" is also bigger than that of bontebok. The lower edge of the caput humeri (circled in red) is also sharper and protrudes more outwards than in bontebok. The

protrusion circled in bontebok is not as pronounced as in blesbok, and in blesbok it is a bit rounder.

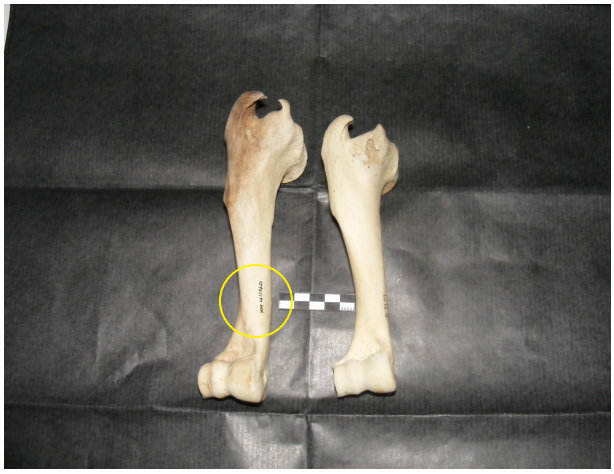


Figure 84: Photo showing the caudo-lateral view of the humerus of bontebok and blesbok.

The picture above shows the differences in size and shape. The humerus of bontebok is more curved (circled above) than that of the blesbok.



Figure 85: Photo showing the lateral view of the proximal end of the humerus of bontebok and blesbok.

Bontebok has a flatter *trochanter maius* than blesbok (marked with a horizontal line).



Figure 86: Photo showing the side view of the humerus of bontebok and blesbok

Again this picture shows the size difference whereby bontebok's humerus is smaller than that of blesbok.

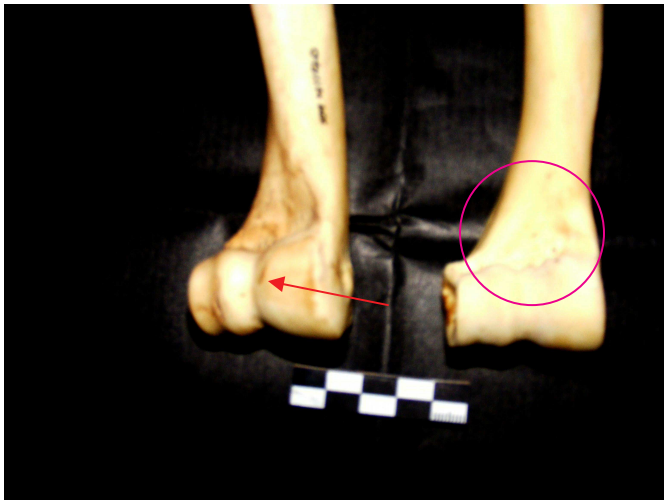


Figure 87: Photo showing the distal end of the humerus (*condylus humeri*) of bontebok and blesbok.

When looking at the *fossa radialis* (circled above), blesbok has a deeper valley than bontebok. Looking at the trochlea; the "divisions" found are clearer in bontebok than in blesbok; blesbok is smoother (illustrated by an arrow).



Figure 88: Photo showing the side view of the distal end of the humerus of the bontebok and blesbok.

When looking at the picture above, the medial *epicondylus* (pointed with an arrow) is rounder in bontebok, whilst in blesbok it is flatter.

Metric statistical analysis

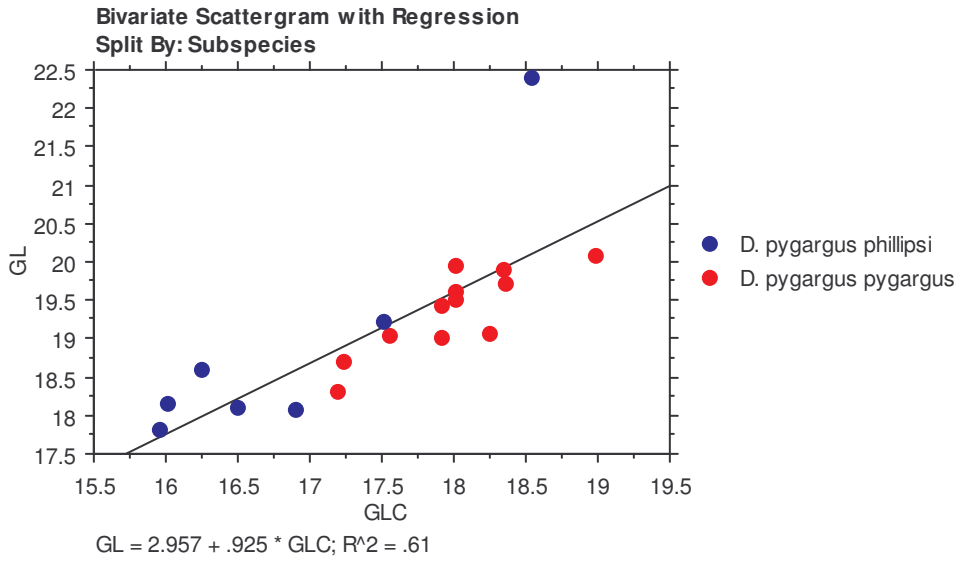


Figure 89: Bivariate plot of the greatest length from the caput (head) versus the greatest length of the humerus showing regression of both groups.

Figure 85 shows a clear distinction between the two subspecies in that blesbok is further down the regression line. This was not expected in that as it was said earlier on, older literature refers to blesbok as being bigger than bontebok (Smithers, 1983).

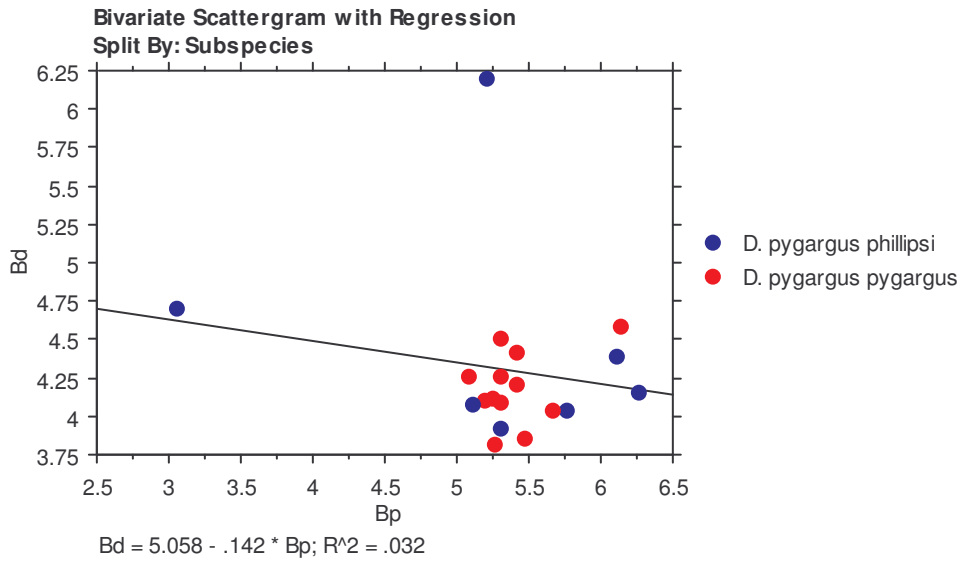


Figure 90: Bivariate plot of the breadth of the proximal end versus the breadth of the *condylus humeri* showing regression of both groups.

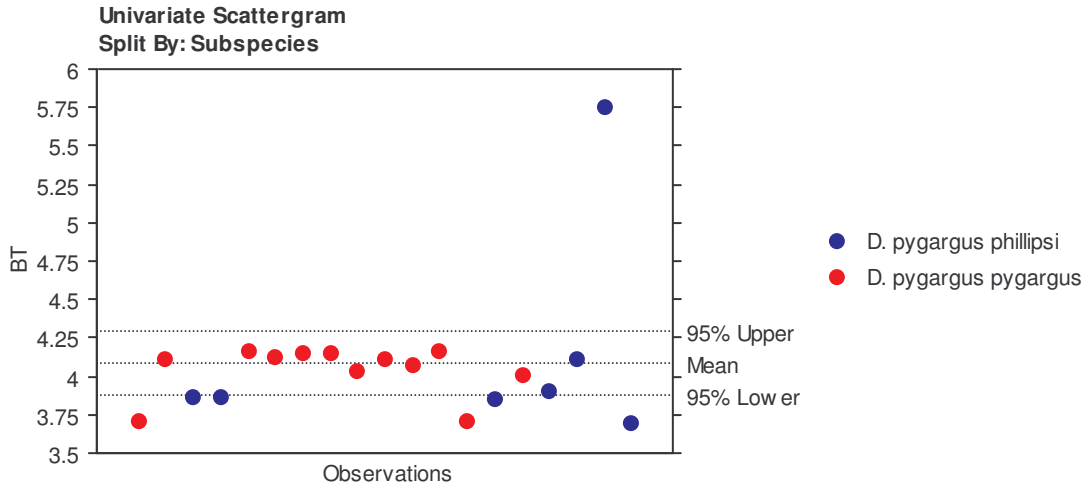


Figure 91: Univariate plot of the breadth of *condylus humeri* showing the mean at 95% confidence interval.

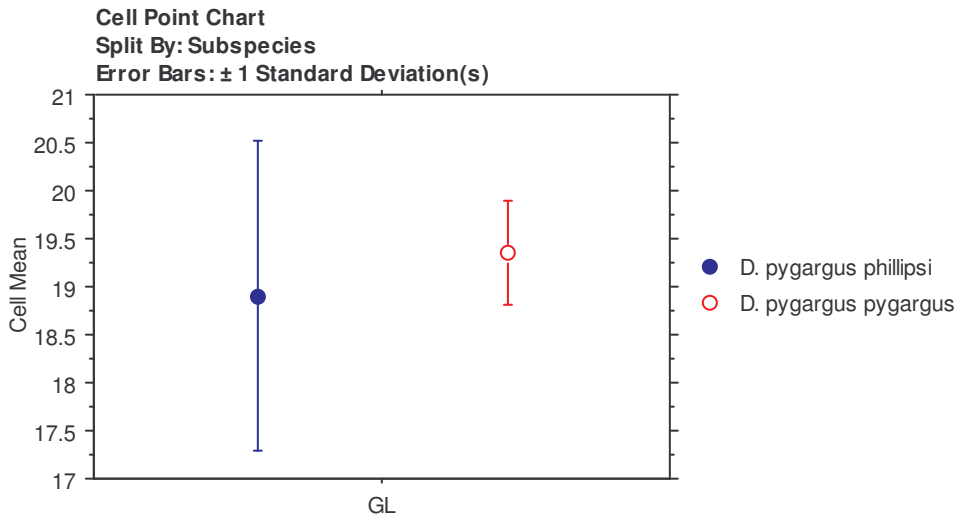


Figure 92: Standard error cell plot of the greatest length of the humerus (error bars: ±1 STD deviation).

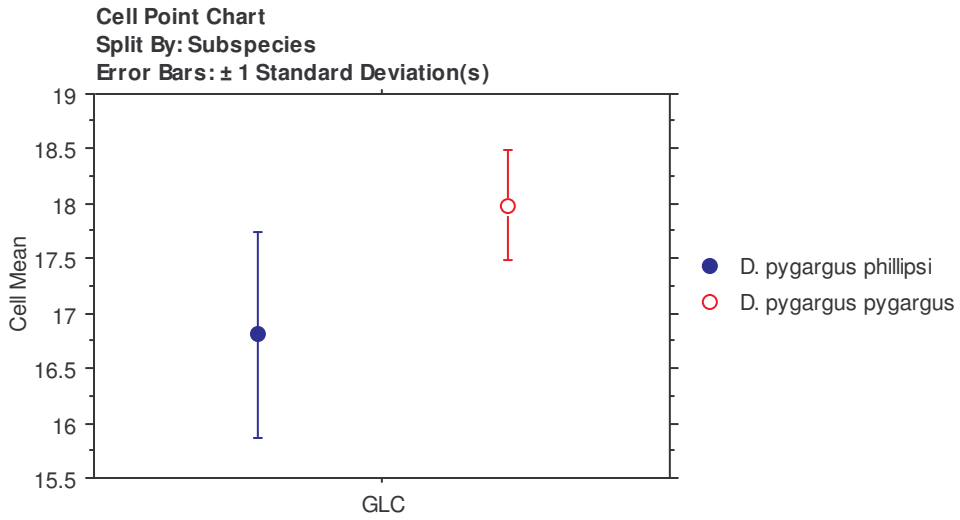


Figure 93: Standard error cell plot of the greatest length from the caput of the humerus (error bars: ±1 STD deviation).

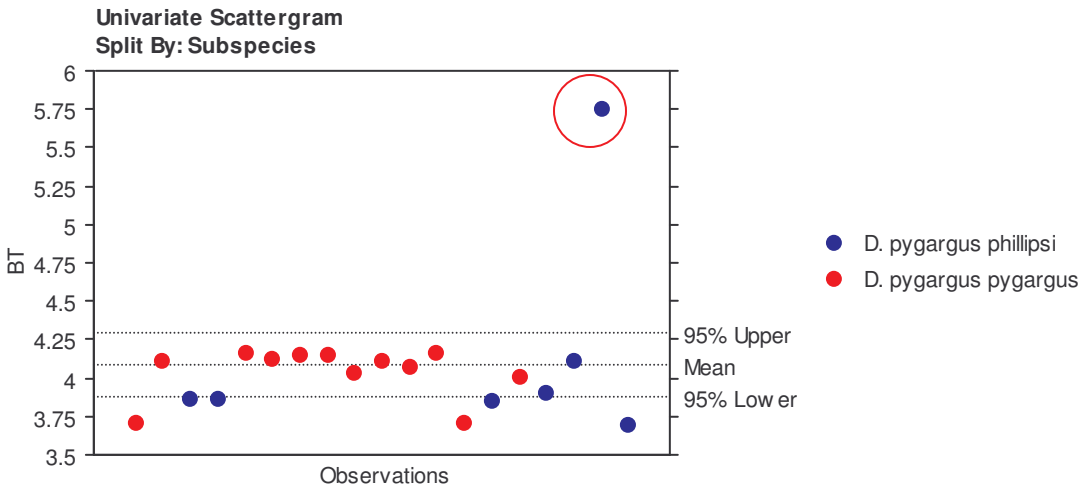


Figure 94: Univariate analysis of the breadth of the *condylus humeri* of the humerus with an outlier.

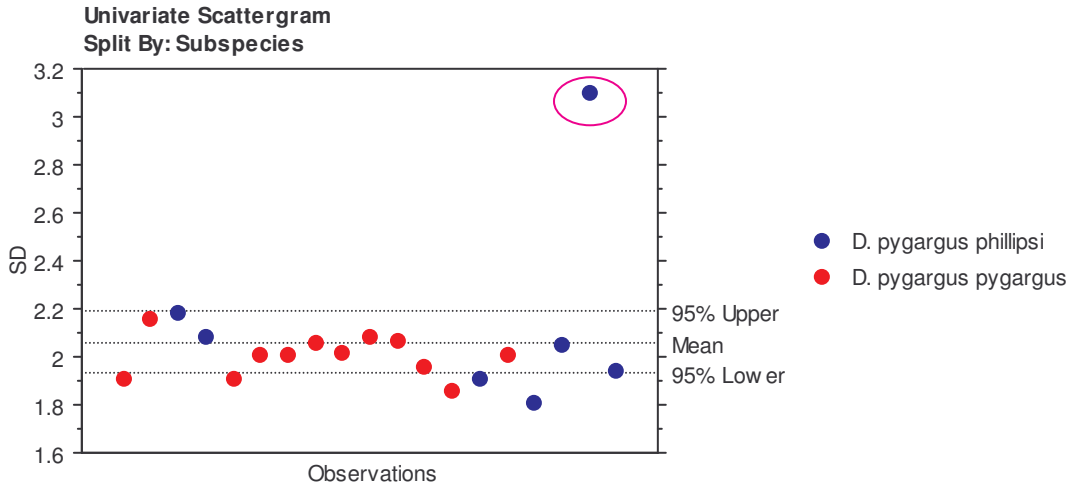


Figure 95: Univariate analysis of the smallest breadth of the diaphysis of the humerus with an outlier.

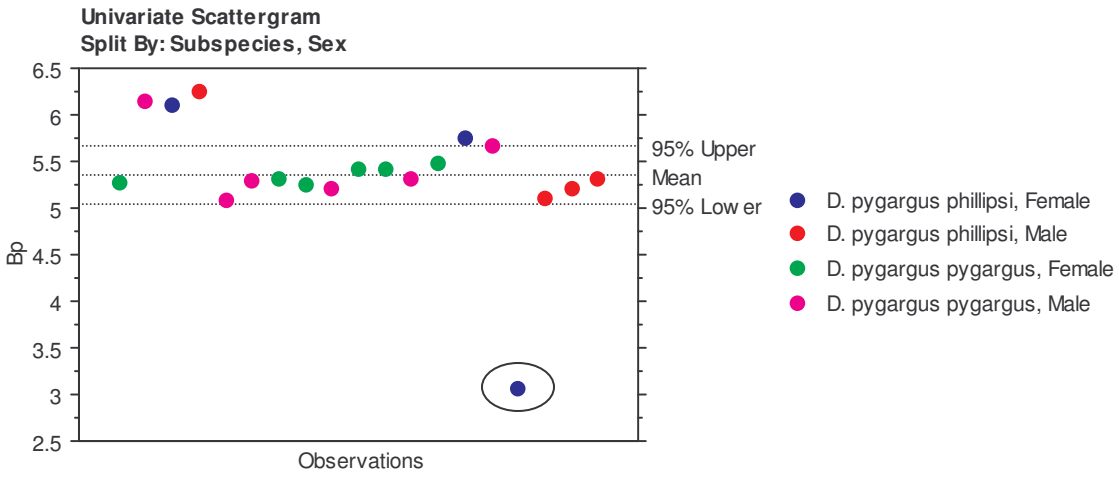


Figure 96: Univariate analysis of the breadth of the proximal end of the humerus split by subspecies and sex of the specimens with an outlier.

3.1.3.5 *Ulna*



Figure 97: Photo showing the ulna of both bontebok and blesbok.

The figure above shows that bontebok is bigger in terms of size than blesbok.

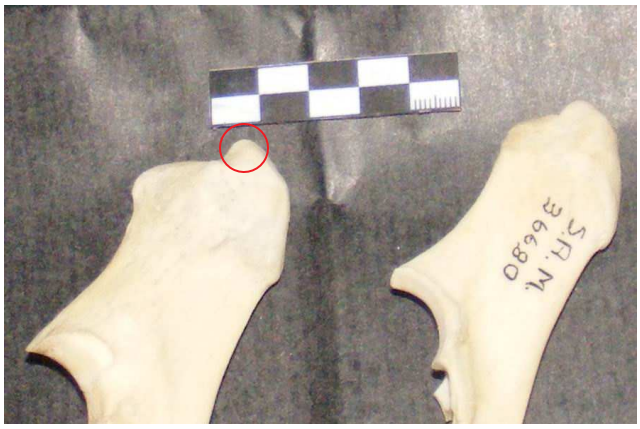


Figure 98: Photo showing the proximal end of the ulna of both bontebok and blesbok.

When looking at these specimens, it is clear that bontebok has a broader proximal end and it is a bit flatter than blesbok. The edge of the *proc. anconaeus* (circled above in red) is also a bit sharper in bontebok, whilst almost rounded in blesbok.

Metric statistical analysis

The statistical analyses below show that the differences between these two subspecies are not that significant. This was expected because of what was mentioned earlier on about these groups being subspecies.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
DPA	3.324	.104	.035	9	3.120	3.430	8
SDO	2.627	.198	.048	17	2.130	2.970	0

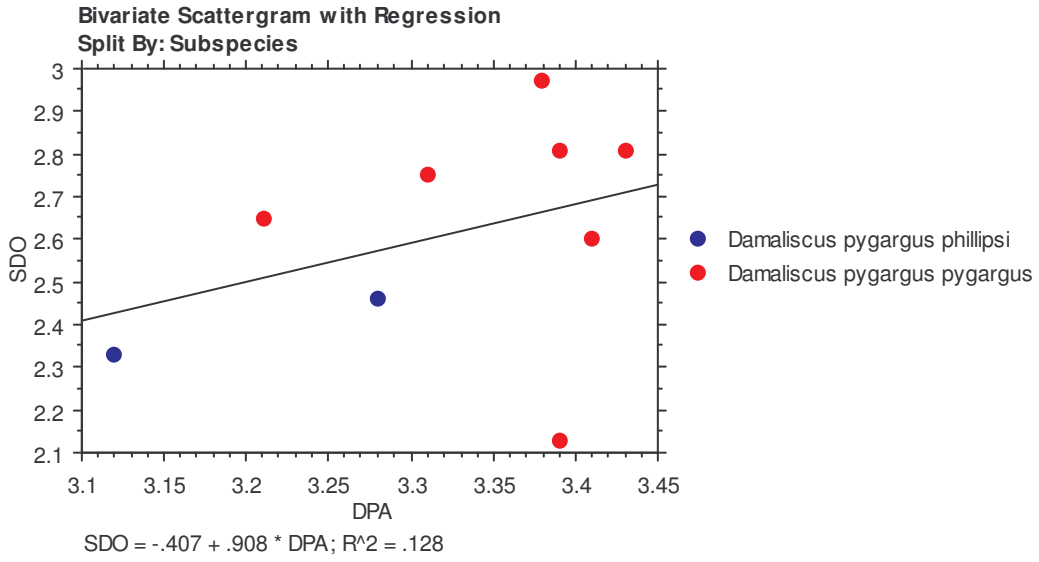


Figure 99: Bivariate plot of the depth across the Processus anconaeus versus the smallest depth of the olecranon of the ulna showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GL	28.341	.725	.201	13	26.880	29.330	4
LO	5.740	.241	.058	17	5.310	6.220	0

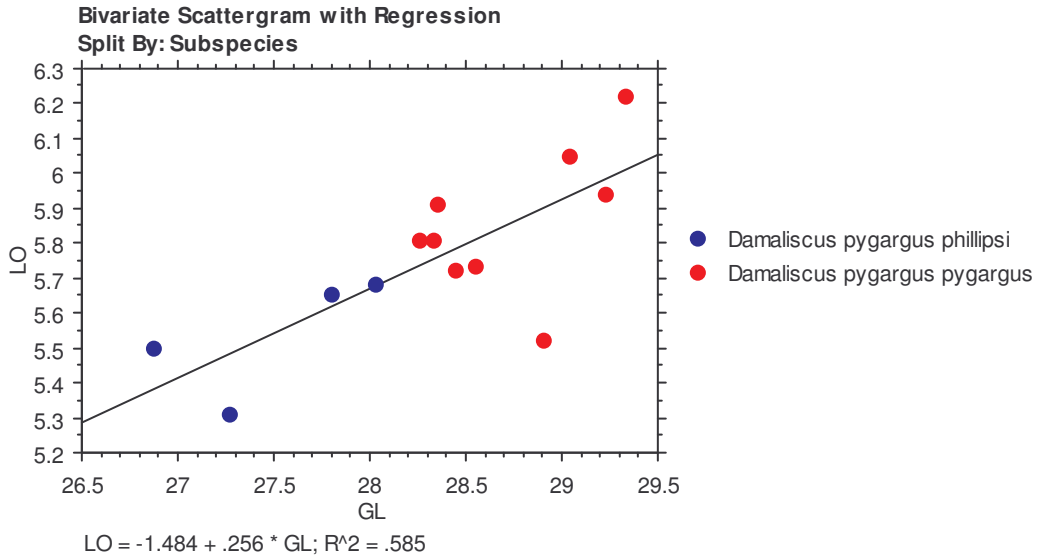


Figure 100: Bivariate plot of the greatest length versus the length of the olecranon of the ulna showing regression of both groups.

Descriptive Statistics

	GL
Mean	28.341
Std. Dev.	.725
Std. Error	.201
Count	13
Minimum	26.880
Maximum	29.330
# Missing	4

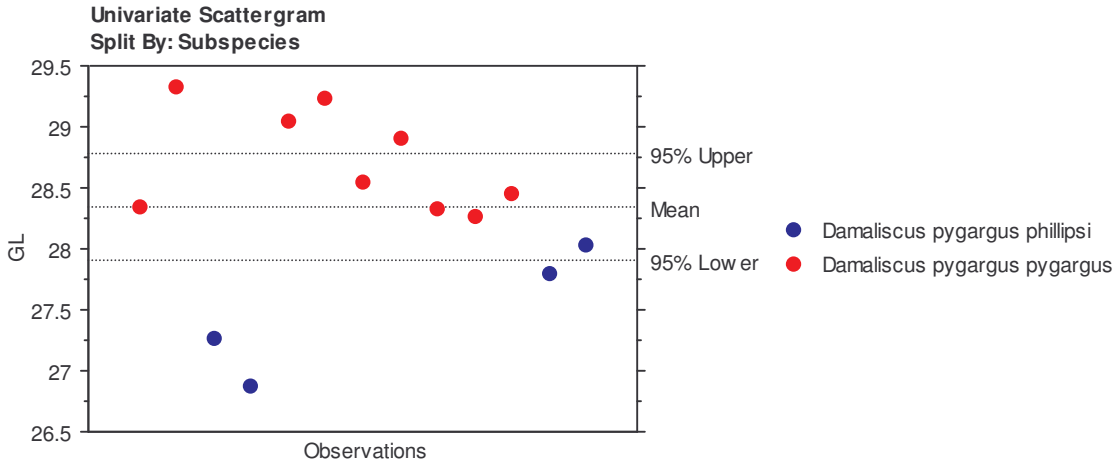


Figure 101: Univariate plot of the greatest length showing the mean at 95% confidence interval.

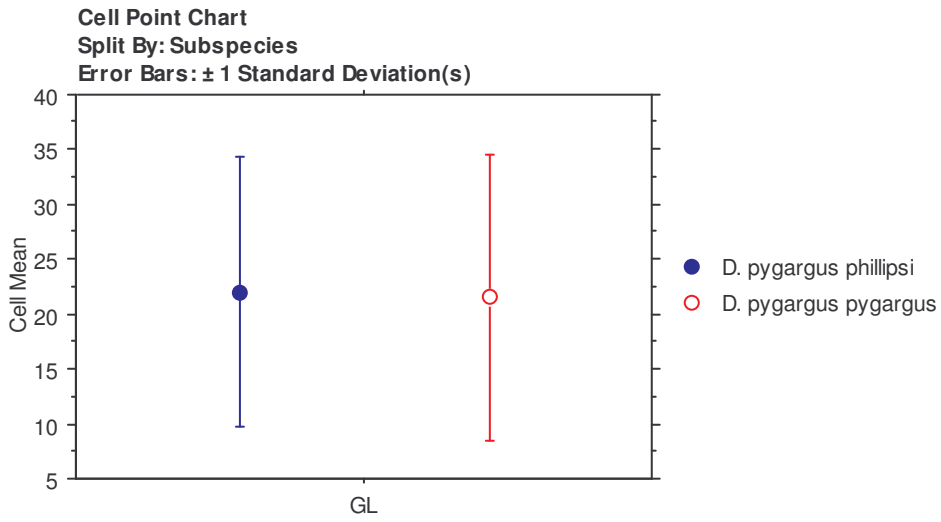


Figure 102: Standard error cell plot of the greatest length of the ulna (error bars: ±1 STD deviation).

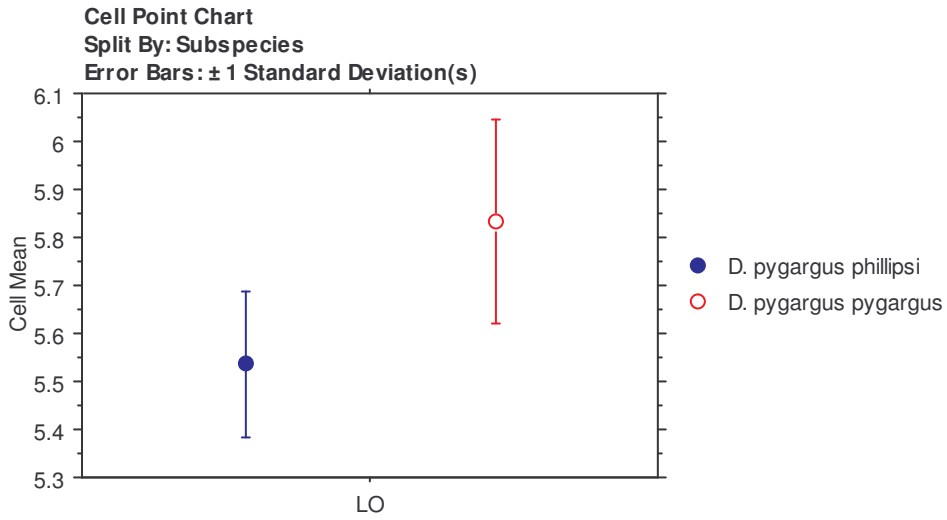


Figure 103: Standard error cell plot of the length of the olecranon of the ulna (error bars: ±1 STD deviation).

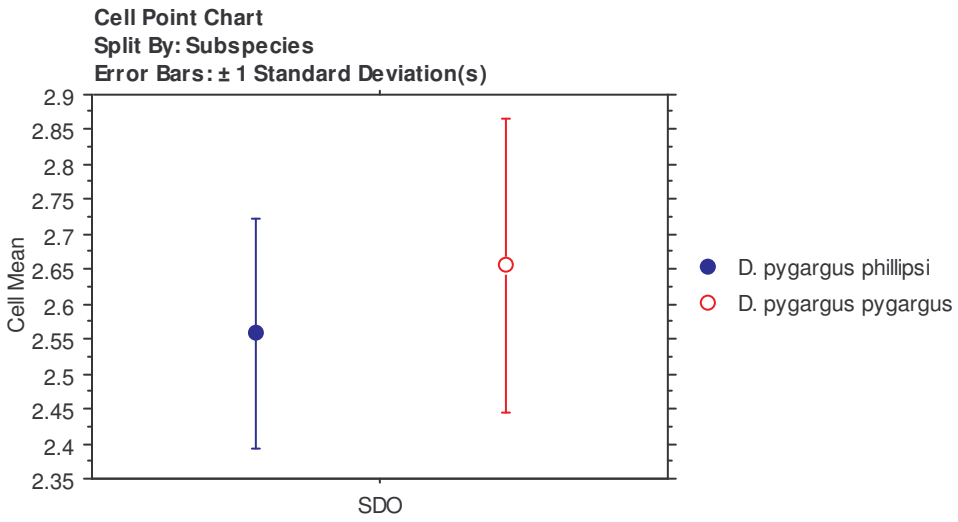


Figure 104: Standard error cell plot of the smallest depth of the olecranon of the ulna (error bars: ±1 STD deviation).

Descriptive Statistics

	DPA
Mean	3.324
Std. Dev.	.104
Std. Error	.035
Count	9
Minimum	3.120
Maximum	3.430
# Missing	8

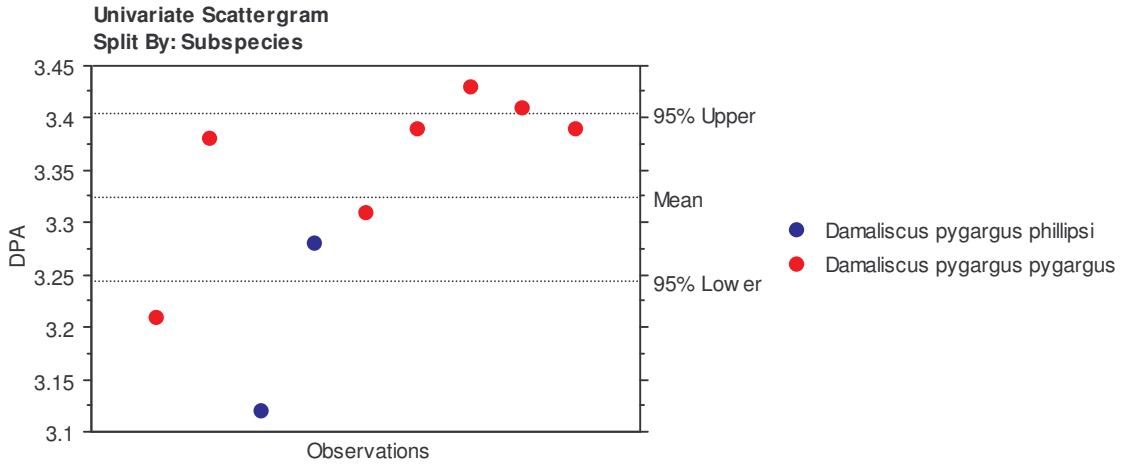


Figure 105: Univariate analysis of the depth across the Processus anconaeus of the ulna with outliers.

Descriptive Statistics

	BPC
Mean	2.159
Std. Dev.	.103
Std. Error	.034
Count	9
Minimum	2.000
Maximum	2.280
# Missing	8

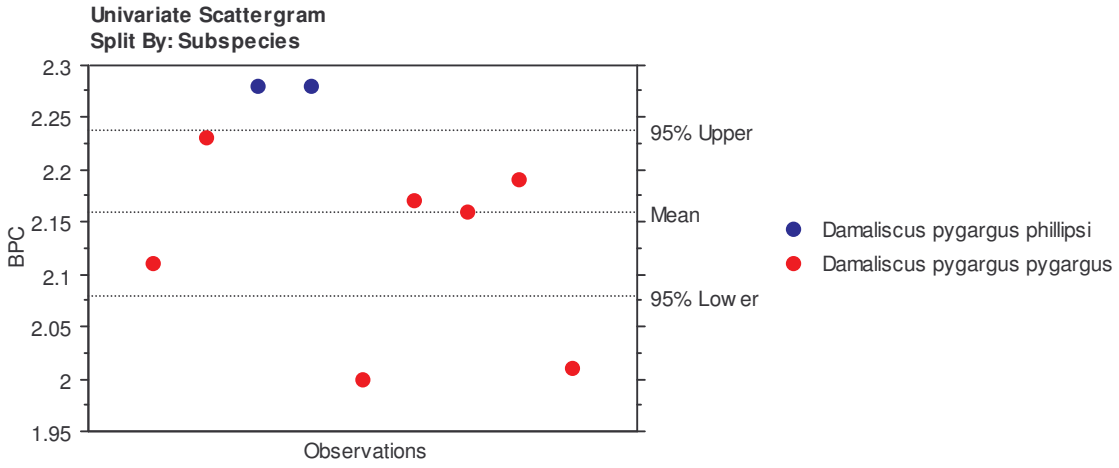


Figure 106: Univariate analysis of the breadth across the coronoid process of the ulna.

3.1.3.6 *Radius*



Figure 107: Photo showing the radii of bontebok and blesbok.

The specimens above are almost equal in height; but bontebok has a longer radius than blesbok.



Figure 108: Photo showing the distal end of the radii of bontebok and blesbok.

When looking at the photo above, it is clear that there are certain differences between the two radii of bontebok and blesbok. The most noticeable difference is that of the distal

end of the radius, whereby bontebok has a noticeable protrusion (circled above), whilst blesbok does not have.

Metric statistical analysis

The statistical analyses below show both similarities and differences found in these subspecies.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GL	23.868	.918	.216	18	22.430	25.060	0
PL	23.571	1.000	.236	18	22.010	24.960	0

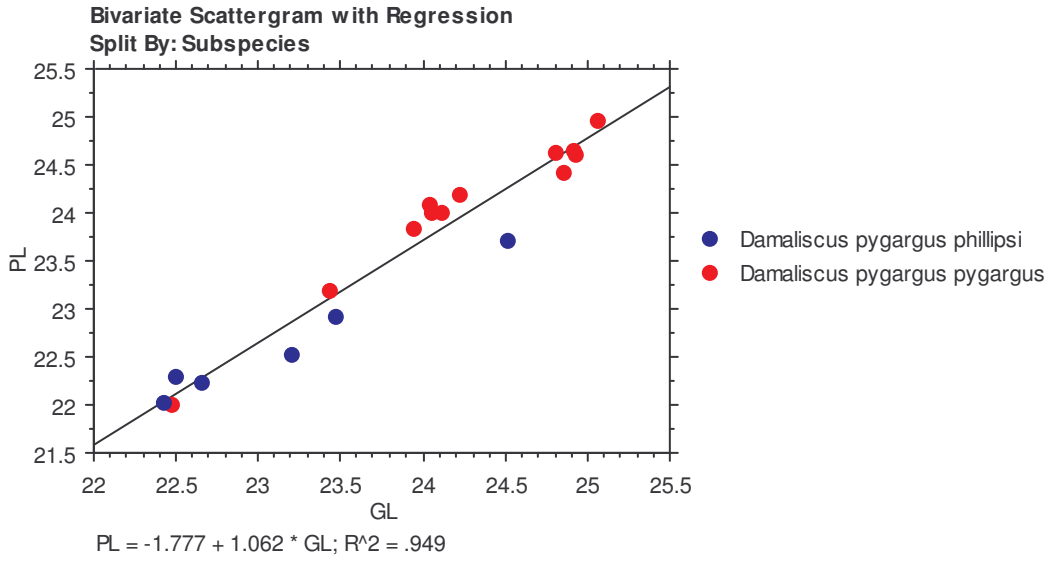


Figure 109: Bivariate plot of the greatest length versus the physiological length of the radius showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
Bp	4.251	.134	.039	12	4.090	4.500	6
Bd	3.644	.136	.039	12	3.410	3.840	6

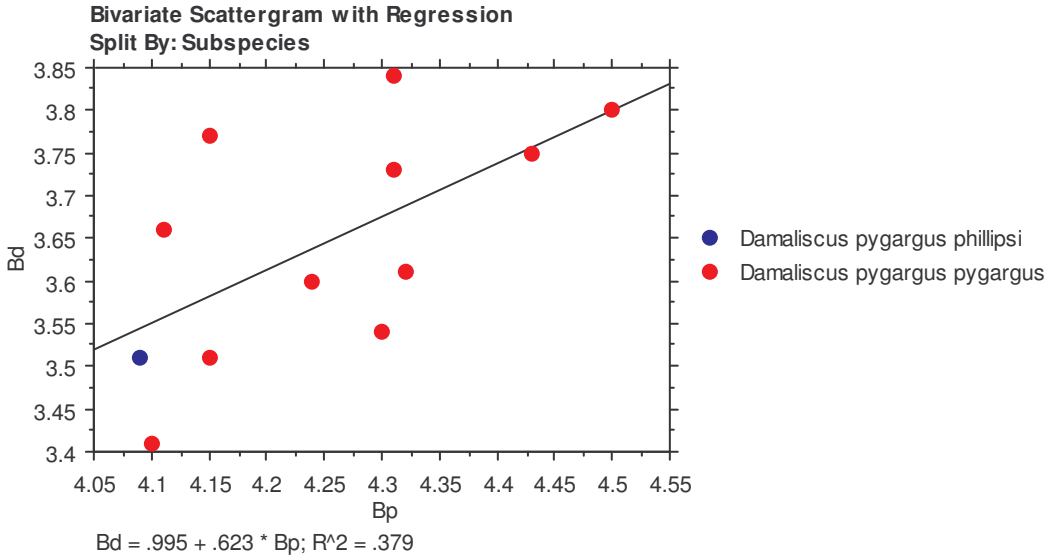


Figure 110: Bivariate plot of the breadth of the proximal end versus the breadth of the distal end of the radius showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
Depth of Articular	1.726	.256	.060	18	1.320	2.010	0
Depth of lateral	1.591	.381	.090	18	1.060	2.070	0

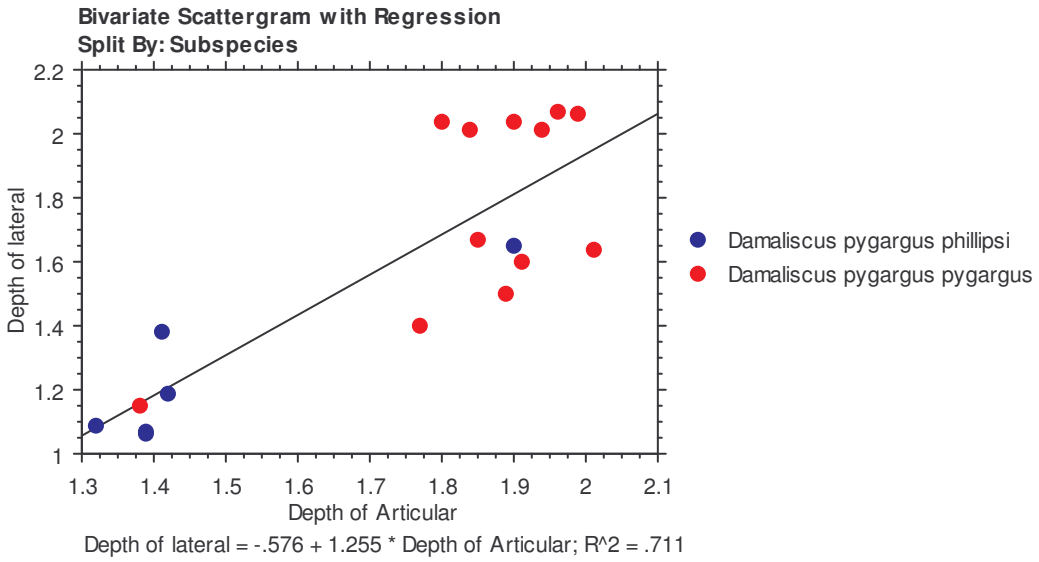


Figure 111: Bivariate plot of the depth of the articular versus the depth of the lateral of the distal end of the radius showing regression of both groups.

Figure 111 shows a clear distinction between the two groups. Blesbok is shown to be smaller than bontebok in this case.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
BFd	3.337	.241	.070	12	3.010	3.710	6
BFp	3.853	.337	.097	12	3.060	4.160	6

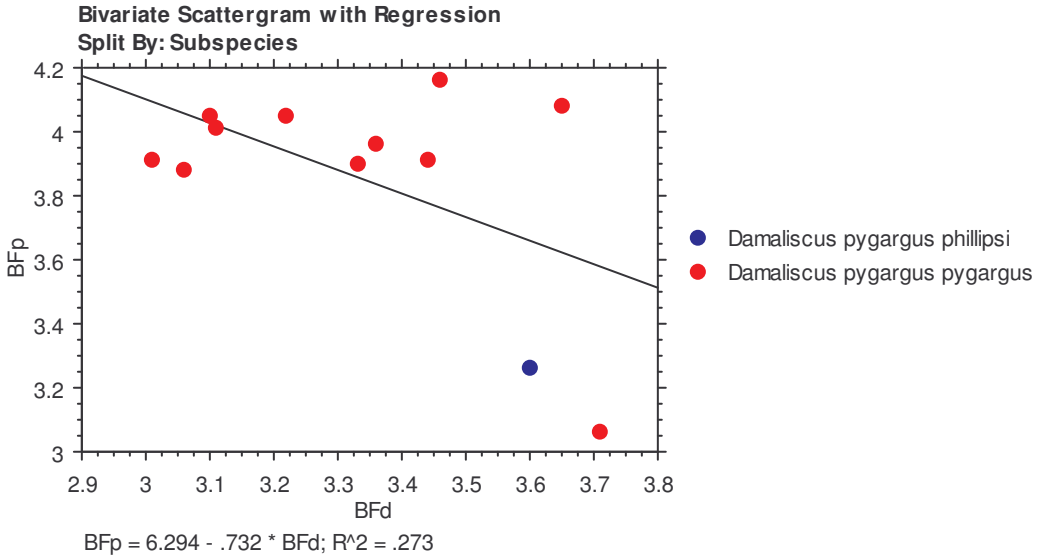


Figure 112: Bivariate plot of the breadth of the Facies articularis distalis versus the breadth of the Facies articularis proximalis of the radius showing regression of both groups.

Descriptive Statistics

	GL
Mean	23.868
Std. Dev.	.918
Std. Error	.216
Count	18
Minimum	22.430
Maximum	25.060
# Missing	0

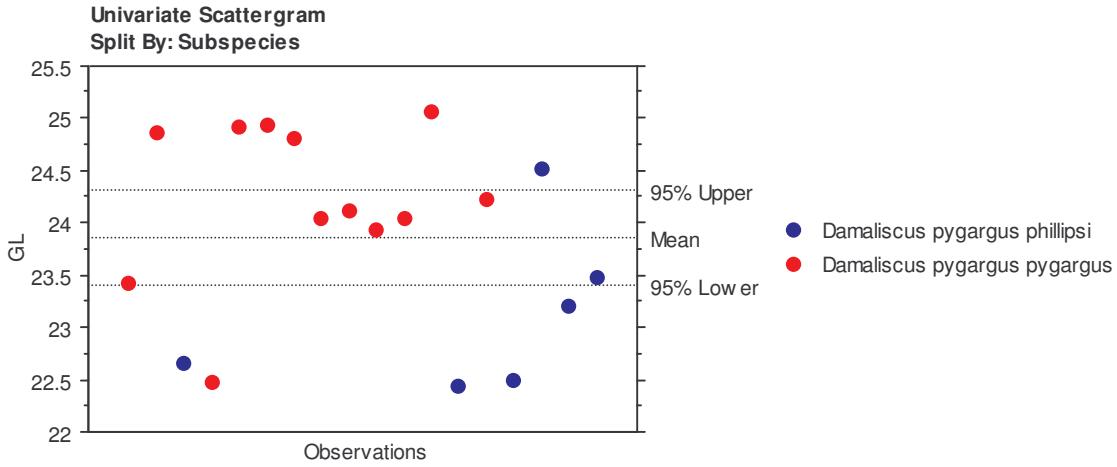


Figure 113: Univariate analysis of the greatest length of the radius with an outlier.

Descriptive Statistics

	PL
Mean	23.571
Std. Dev.	1.000
Std. Error	.236
Count	18
Minimum	22.010
Maximum	24.960
# Missing	0

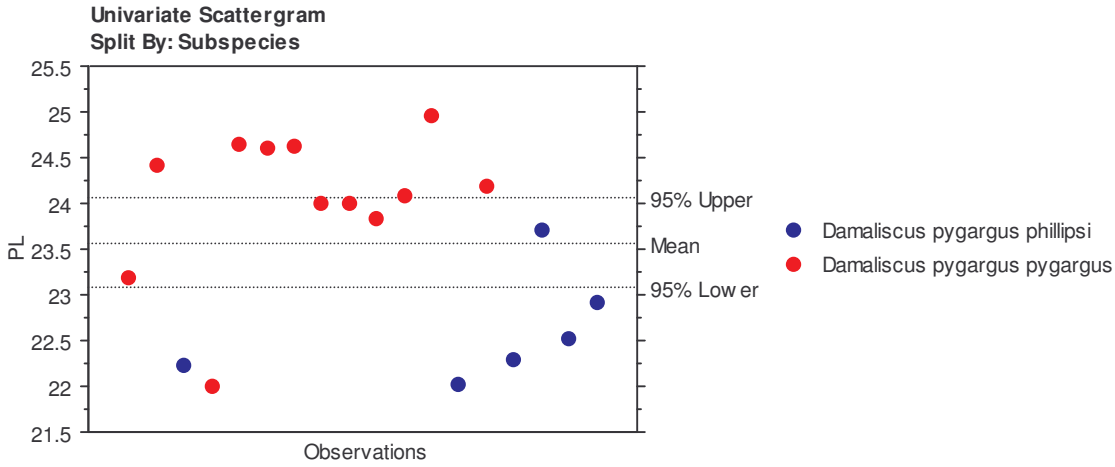


Figure 114: Univariate analysis of the physiological length of the radius.

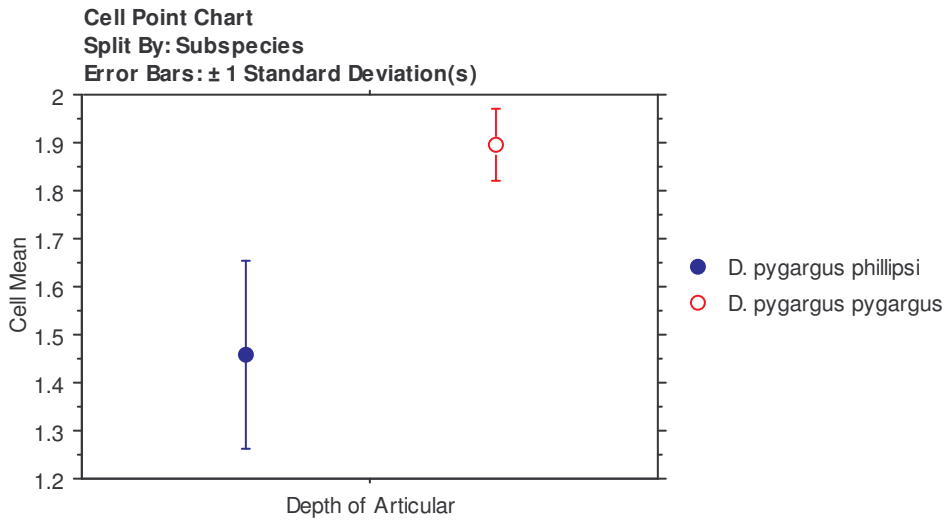


Figure 115: Standard error cell plot of the depth of the articular at the distal end of the radius (error bars: ±1 STD deviation).

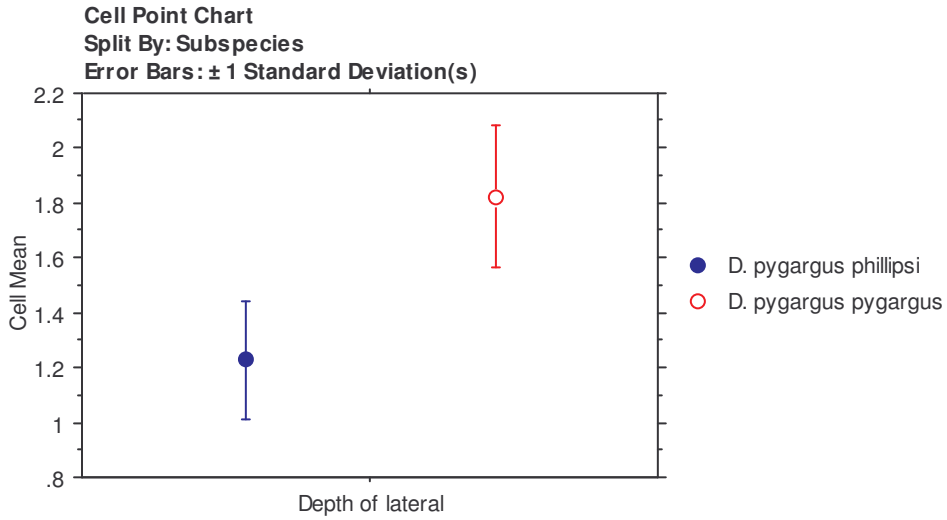


Figure 116: Standard error cell plot of the depth of the lateral at the distal end of the radius (error bars: ±1 STD deviation).

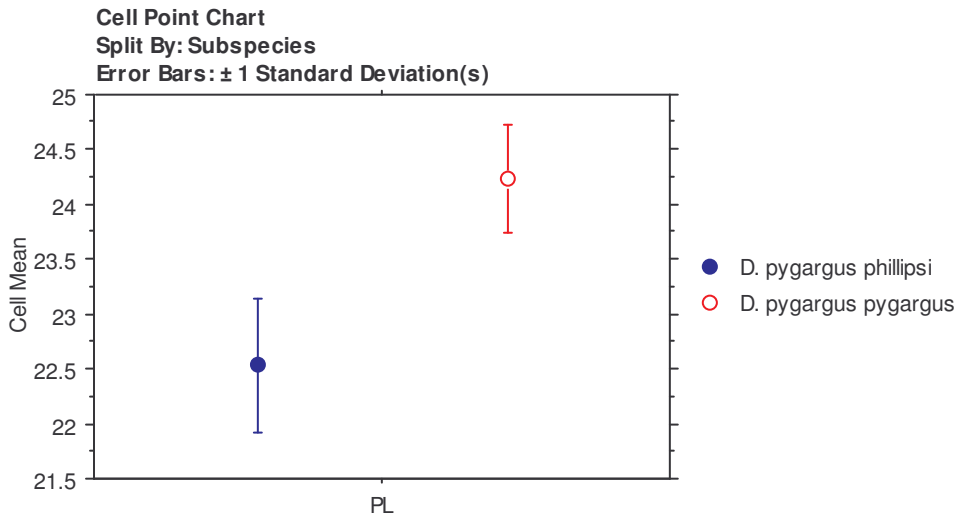


Figure 117: Standard error cell plot of the physiological length of the radius (error bars: ±1 STD deviation).

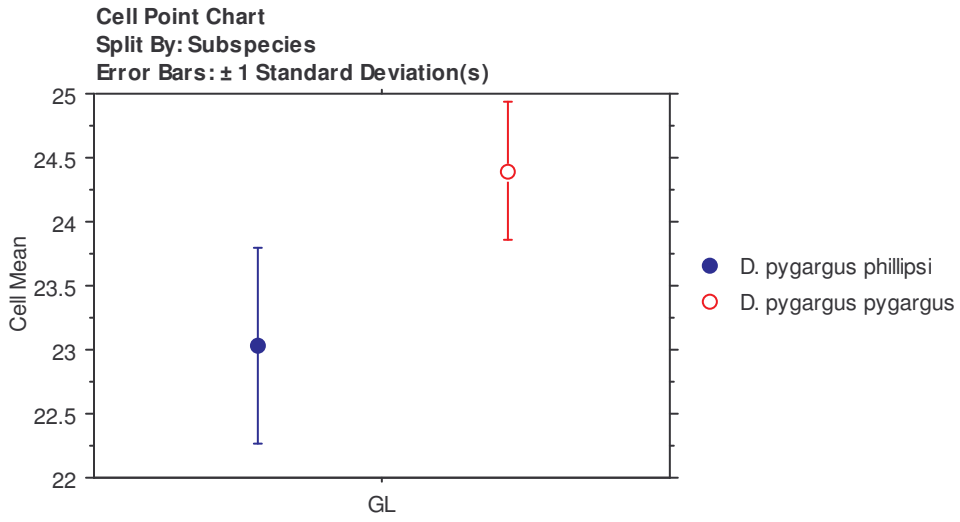


Figure 118: Standard error cell plot of the greatest length of the radius (error bars: ±1 STD deviation).

3.1.3.7 *Metacarpal*

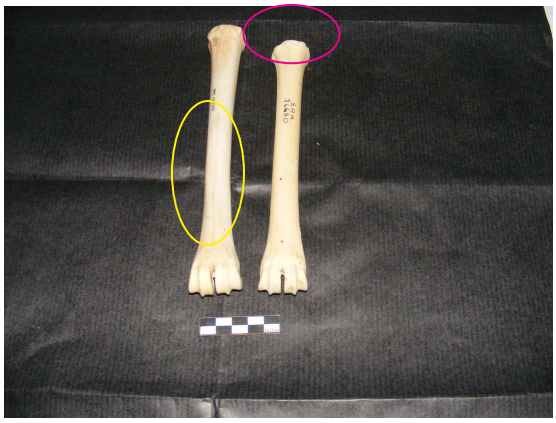


Figure 119: Photo showing the dorsal view of the metacarpals of bontebok and blesbok.

Figure 119 shows that these two specimens are not equal in length (bontebok is longer than blesbok) and that bontebok (circled above in yellow) is a bit thinner than blesbok. It also shows that the proximal view of the two is also different in that blesbok (circled in purple) has a more rounded proximal end (when looking at it from the top) than bontebok.

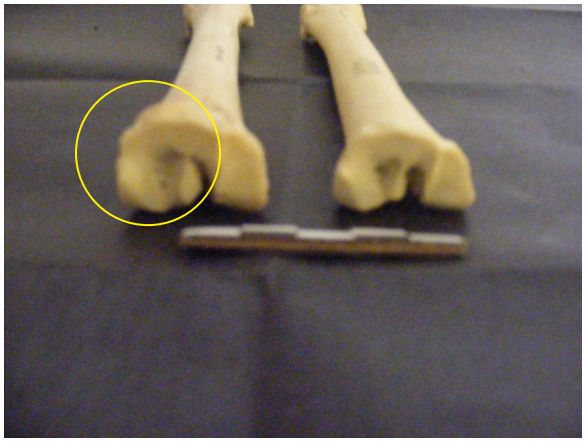


Figure 120: Photo showing the proximal view of the metacarpals of bontebok and blesbok.

Figure 120 shows that bontebok upper part of the proximal end (circled above) is a bit higher than that of bontebok.

Metric statistical analysis

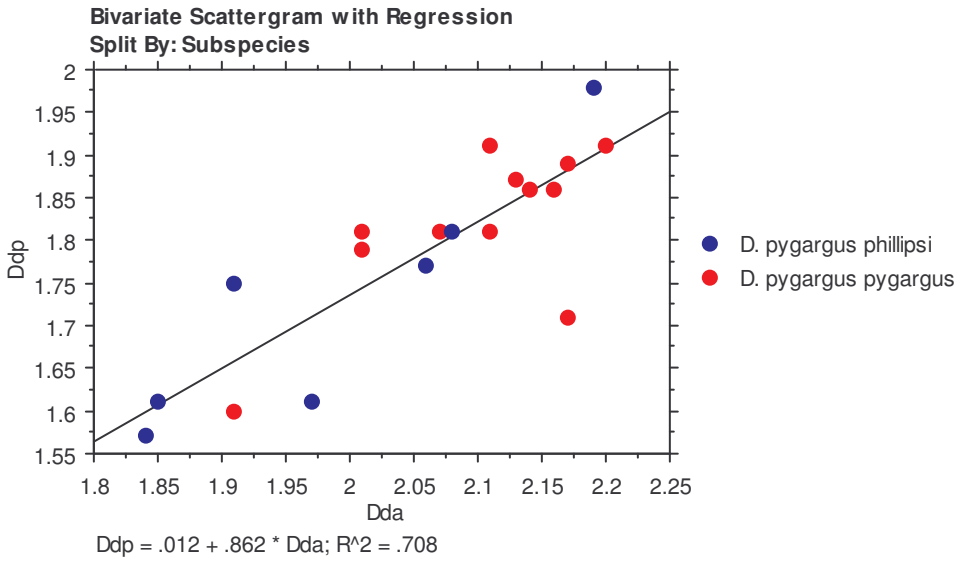


Figure 121: Bivariate plot of the axial versus the peripheral of the metacarpal showing regression of both groups.

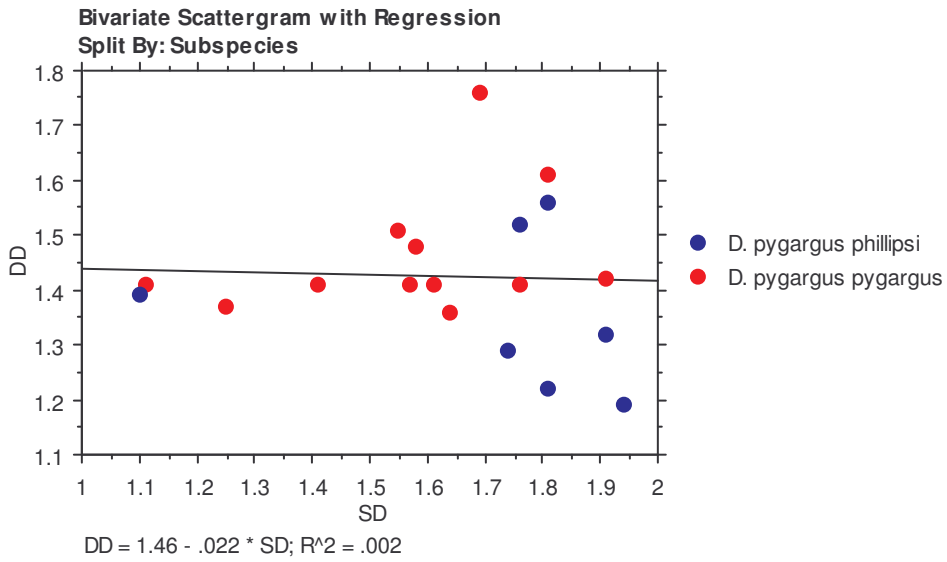


Figure 122: Bivariate plot of the smallest breadth of the diaphysis versus the depth of the diaphysis of the metacarpal showing regression of both groups.

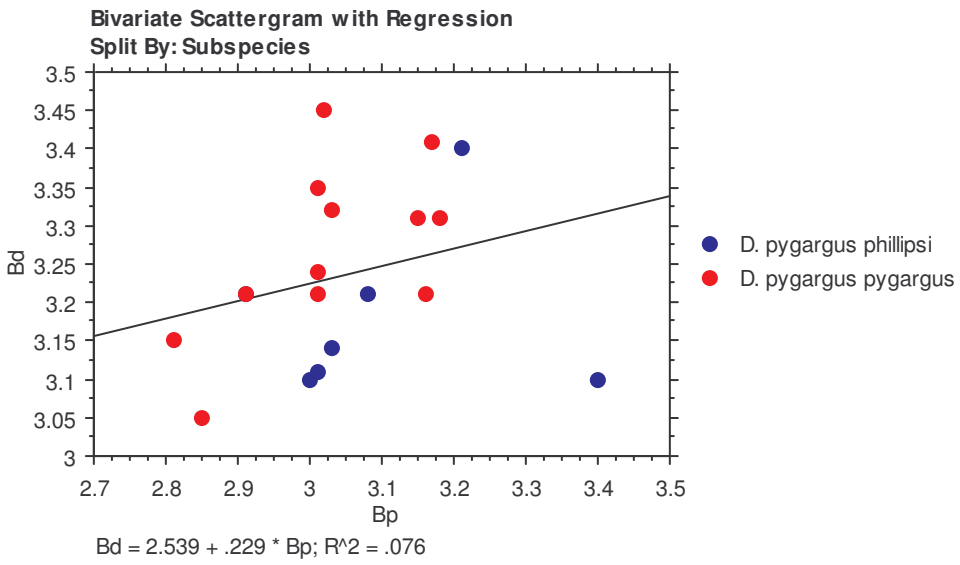


Figure 123: Bivariate plot of the breadth of the proximal end versus the breadth of the distal end of the metacarpal showing regression of both groups.

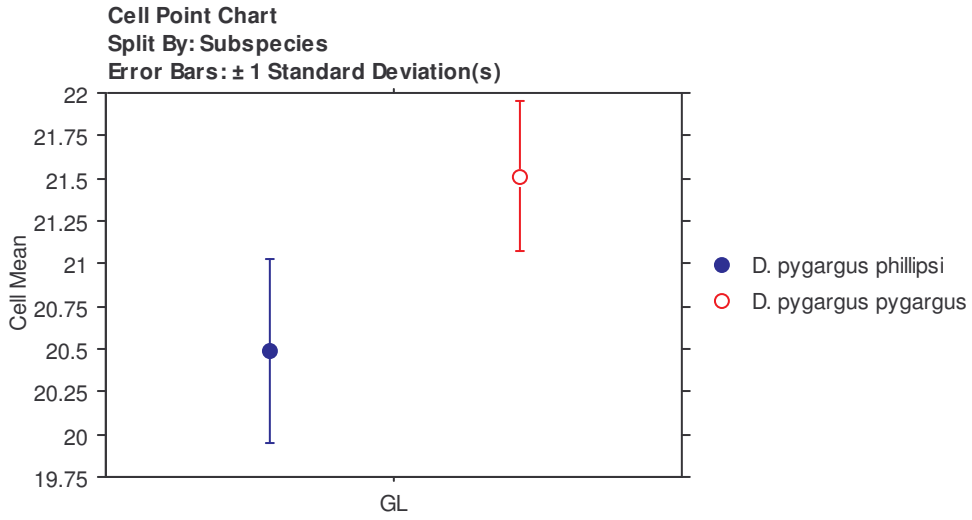


Figure 124: Standard error cell plot of the greatest length of the metacarpal (error bars: ±1 STD deviation).

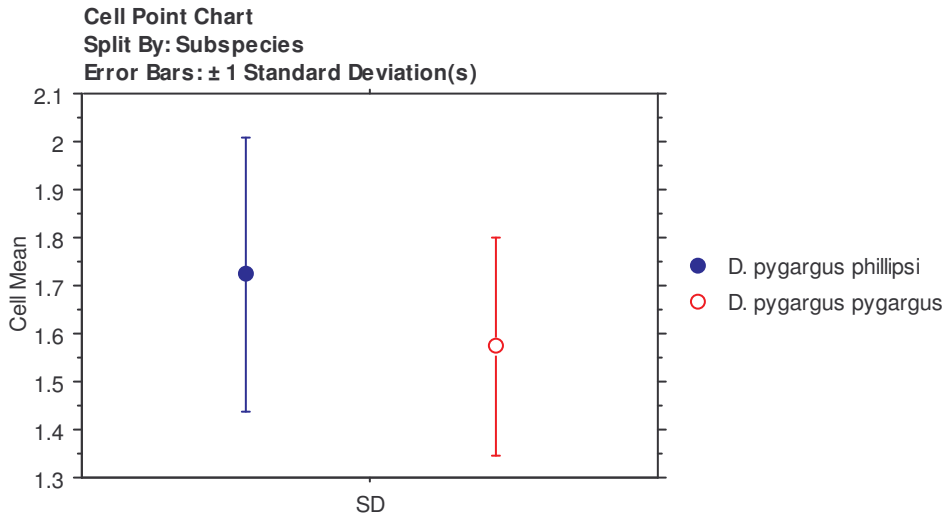


Figure 125: Standard error cell plot of the smallest breadth of the diaphysis of the metacarpal (error bars: ±1 STD deviation).

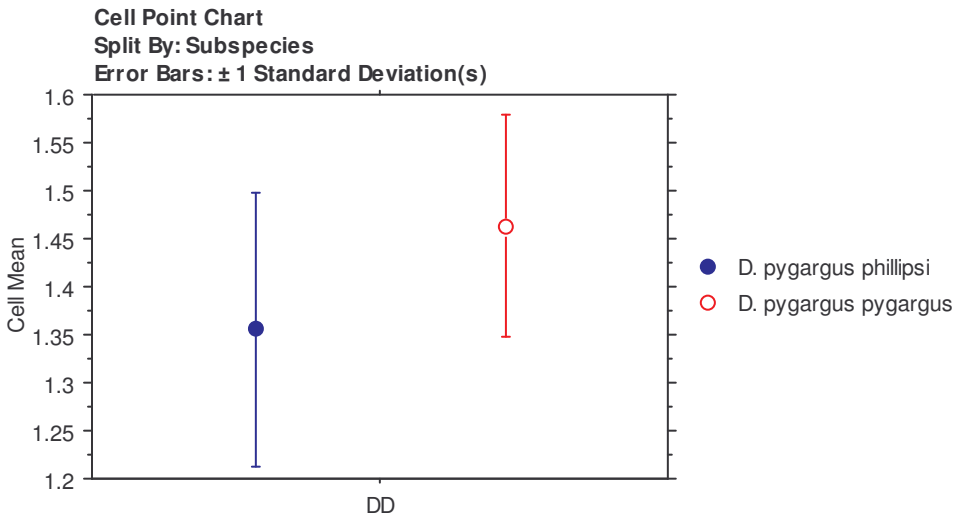


Figure 126: Standard error cell plot of the depth of the diaphysis of the metacarpal (error bars: ±1 STD deviation).

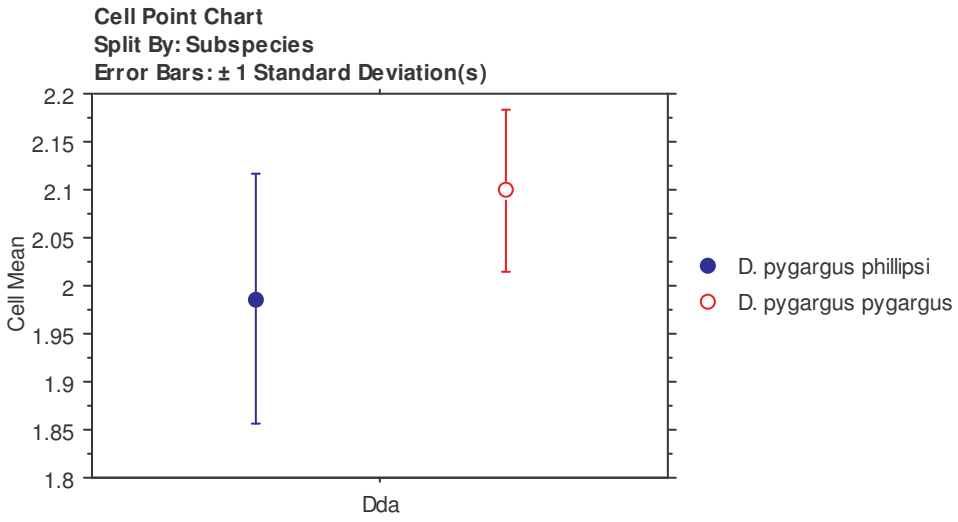


Figure 127: Standard error cell plot of the axial at the distal end of the metacarpal (error bars: ±1 STD deviation).

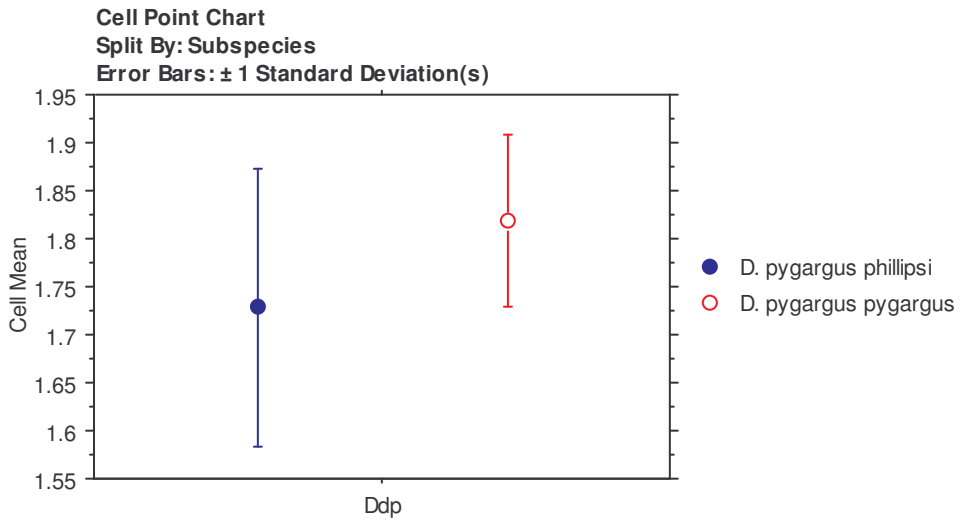


Figure 128: Standard error cell plot of the peripheral at the distal end of the metacarpal (error bars: ±1 STD deviation).

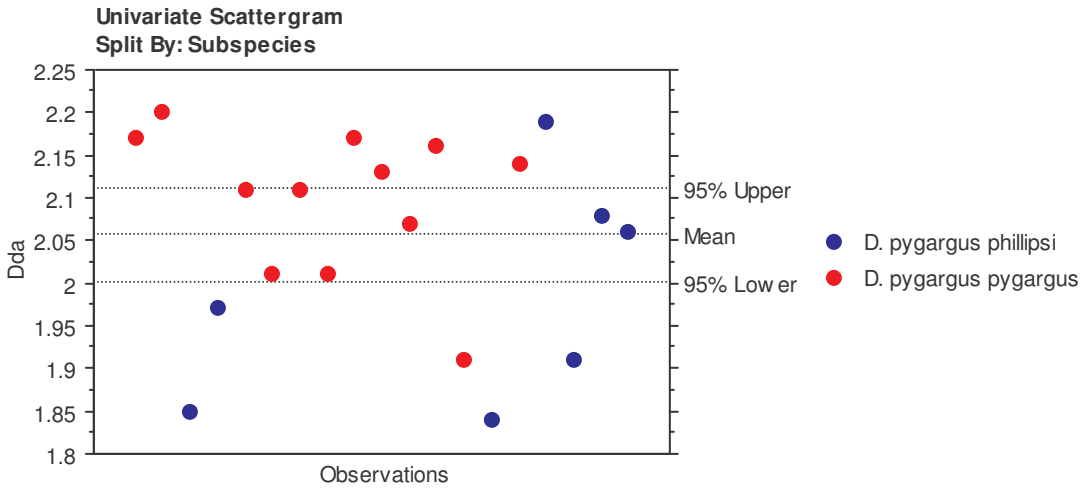


Figure 129: Univariate analysis of the axial at the distal end of the metacarpal.

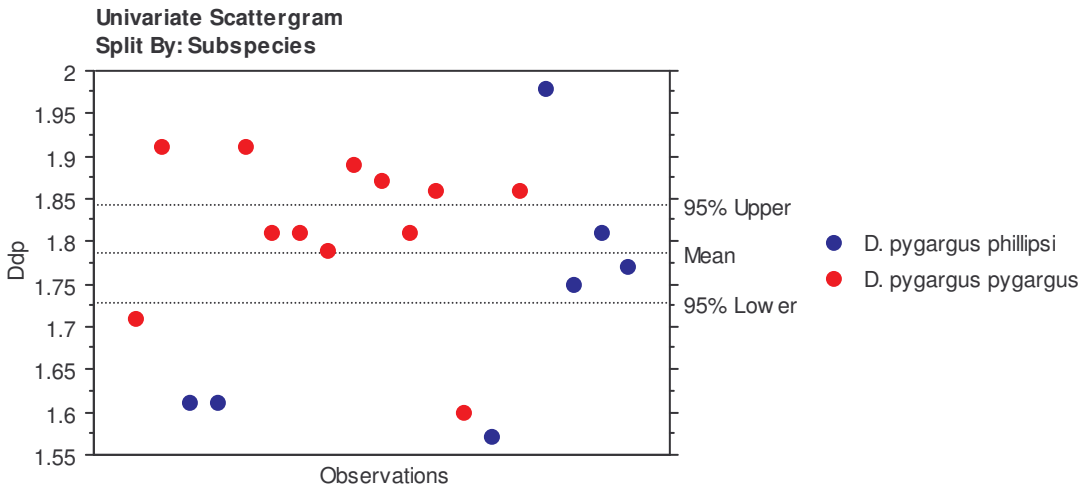


Figure 130: Univariate analysis of the peripheral at the distal end of the metacarpal.

Hind Limb

3.1.3.8 *Pelvis*

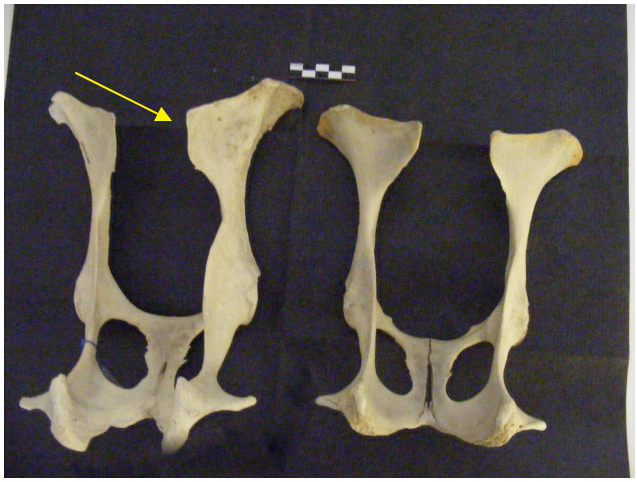


Figure 131: Photo showing the dorsal view of the pelvis of bontebok and blesbok.

Figure 131 shows the size difference between the two pelvises, whereby bontebok is greater than blesbok. Another difference is that of the Tubera coxarum; bontebok has sharper Tubera coxarum (shown above in yellow).



Figure 132: Photo showing the ventral view of the pelvis of bontebok and blesbok.

The Tuber ischiadicum of bontebok is sharper (shown above in yellow) than that of blesbok and this is visible in figure 132. The acetabula of bontebok are bigger than those of blesbok (shown above in red).

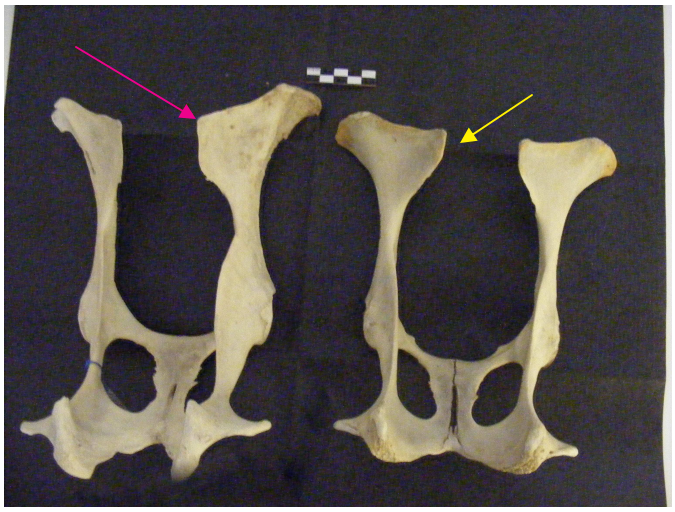


Figure 133: Photo showing the dorsal view of the pelvis of bontebok and blesbok.

Figure 133 shows the sharp angle in the interior part of the Tubera coxarum of bontebok (shown above in pink), while the angle in blesbok is less acute (shown above in yellow).

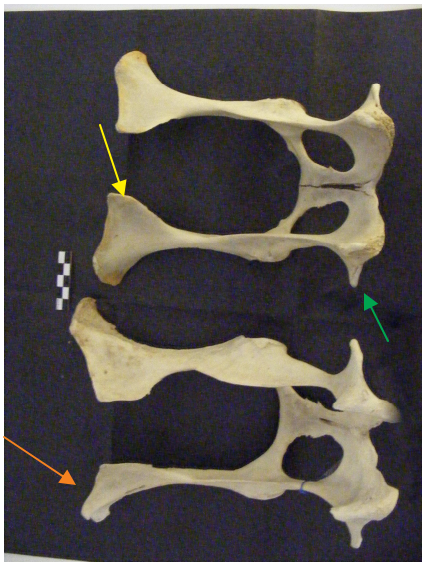


Figure 134: Photo showing the side view of the dorsal view of the pelvis of bontebok (at the bottom) and blesbok (at the top).

Figure 134 shows the angular shape of the inner part of the Tubera coxarum of blesbok (shown in yellow). It also shows the thinness of the pelvis of bontebok (shown in orange). It also shows the protrusion on the *ossis ischii* of the pelvis of blesbok (shown above in green) being sharper than that of bontebok.

Metric statistical analysis

The statistical analysis shows that the pelvises of these animals show significant differences in that bontebok is found on one side, and blesbok is found on the other (see figure 135).

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GL	25.999	1.364	.365	14	23.850	28.040	0
SB	1.486	.274	.073	14	1.110	2.020	0

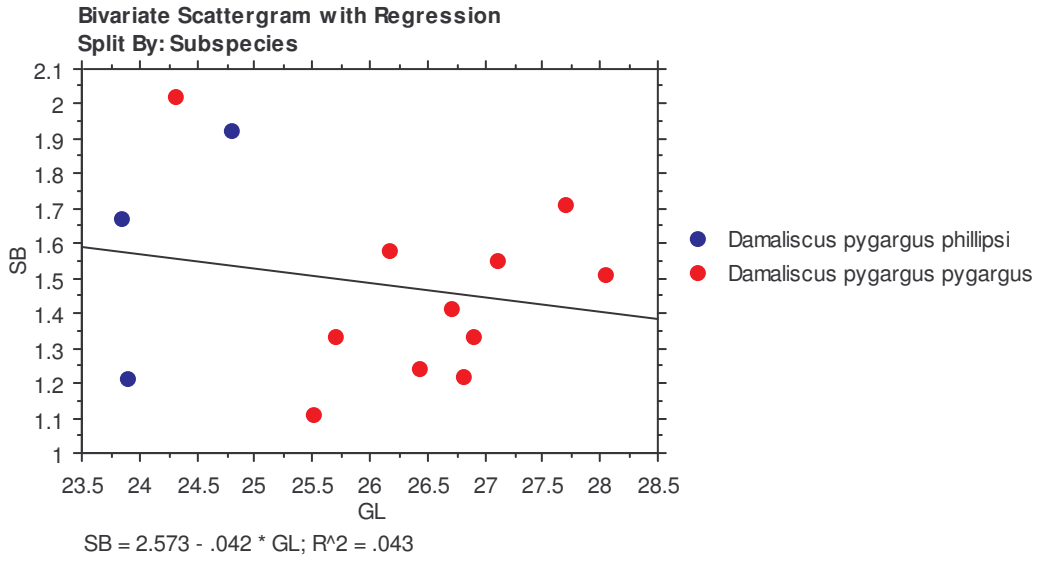


Figure 135: Bivariate plot of the greatest length versus the smallest breadth of the shaft of the ilium showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GBTi	14.320	.577	.192	9	13.440	15.010	5
GBTc	16.697	8.282	2.497	11	0.000	21.510	3

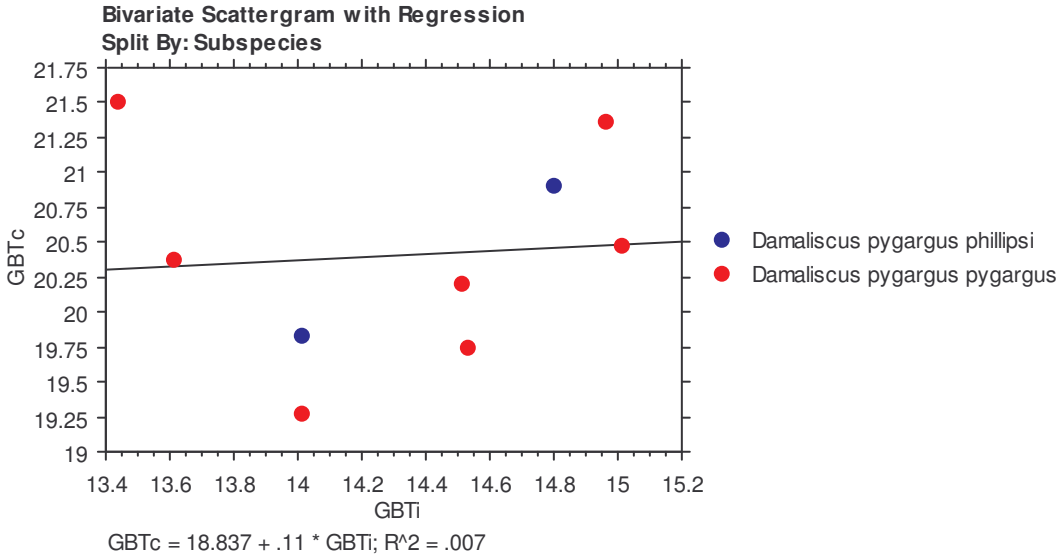


Figure 136: Bivariate plot of the greatest breadth across the Tubera ischiadica versus the greatest breadth across the Tubera coxarum of the pelvis showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
SB	1.486	.274	.073	14	1.110	2.020	0
SBI	9.728	.341	.114	9	9.210	10.230	5

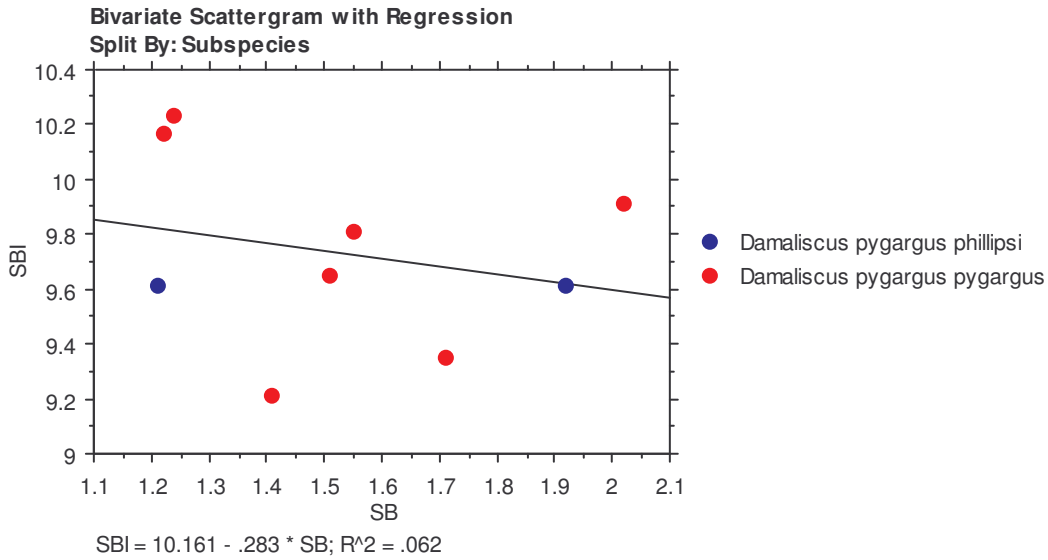


Figure 137: Bivariate plot of the smallest breadth of the shaft of the ilium versus the smallest breadth across the bodies of the ischia showing regression of both groups.

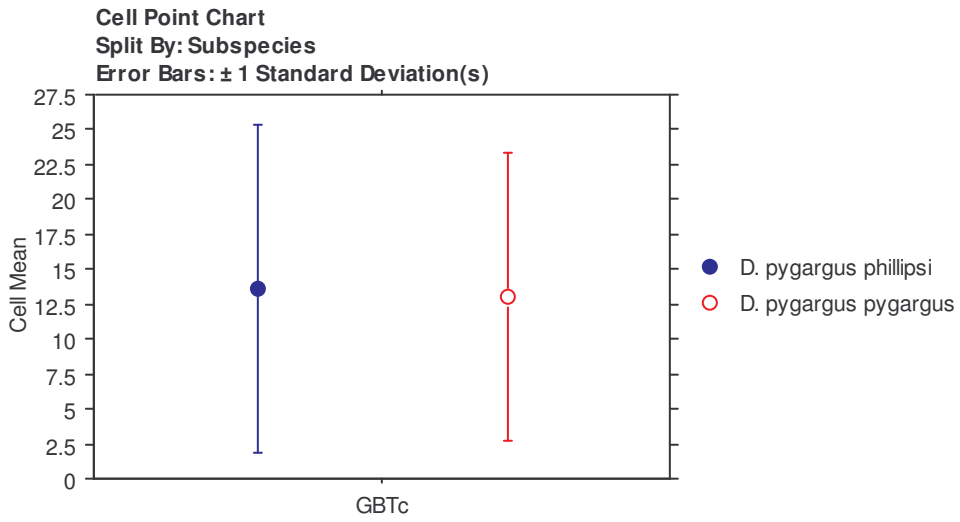


Figure 138: Standard error cell plot of the greatest breadth across the Tubera coxarum of the pelvis (error bars: ±1 STD deviation).

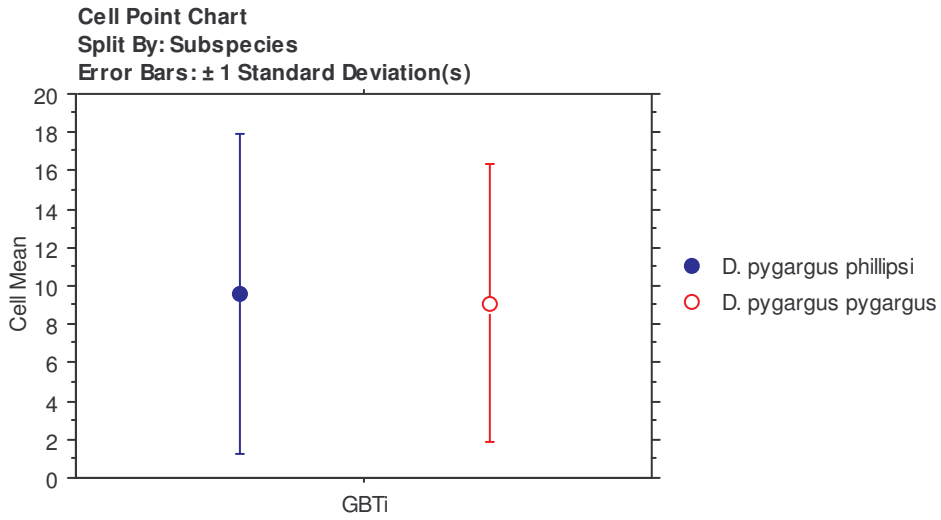


Figure 139: Standard error cell plot of the greatest breadth across the Tubera ischiadica of the pelvis (error bars: ±1 STD deviation).

3.1.3.9 *Femur*



Figure 140: Photo showing the caudal view of the femur of bontebok and blesbok.



Figure 141: Photo showing the caudal view of the femur of bontebok and blesbok.

Figures 140 and 141 indicate that bontebok has a longer femur than blesbok.

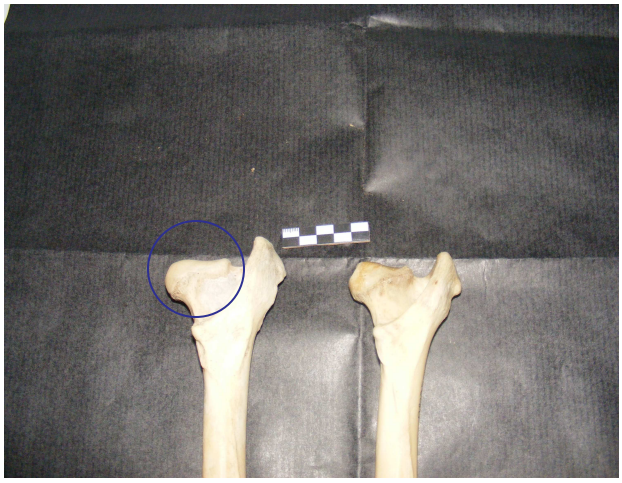


Figure 142: Photo showing the proximal view of the femur of bontebok and blesbok in detail.

When looking at the head of the femur (figure 142), there are differences between the two; that of bontebok (circled above) is rounder than that of blesbok, whilst that of blesbok is a bit edgy.



Figure 143: Photo showing the side view (medial) of the femur of bontebok and blesbok.

Metric statistical analysis

When looking at the statistical analysis of the femur of both subspecies, there are differences in that bontebok is found at the bottom end of the graph, whilst blesbok is found at the top end of the graph.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GL	23.581	.918	.216	18	22.050	24.870	0
GLC	22.776	1.109	.261	18	20.750	24.360	0

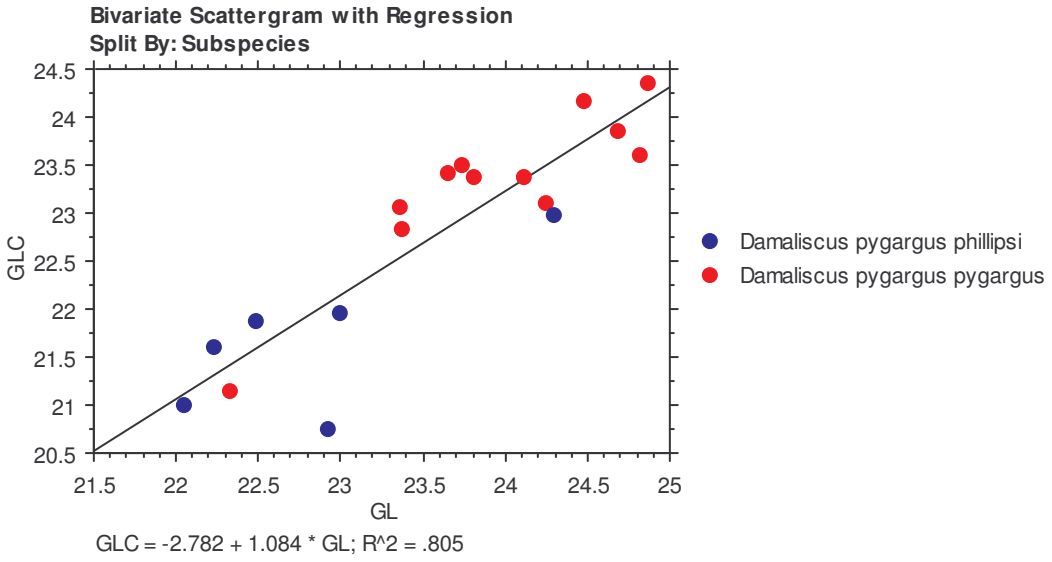


Figure 144: Bivariate plot of the greatest length versus the greatest length from the caput femoris (head) of the femur showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
Dld	1.597	.212	.067	10	1.320	2.050	8
Dmd	1.898	.192	.061	10	1.600	2.250	8

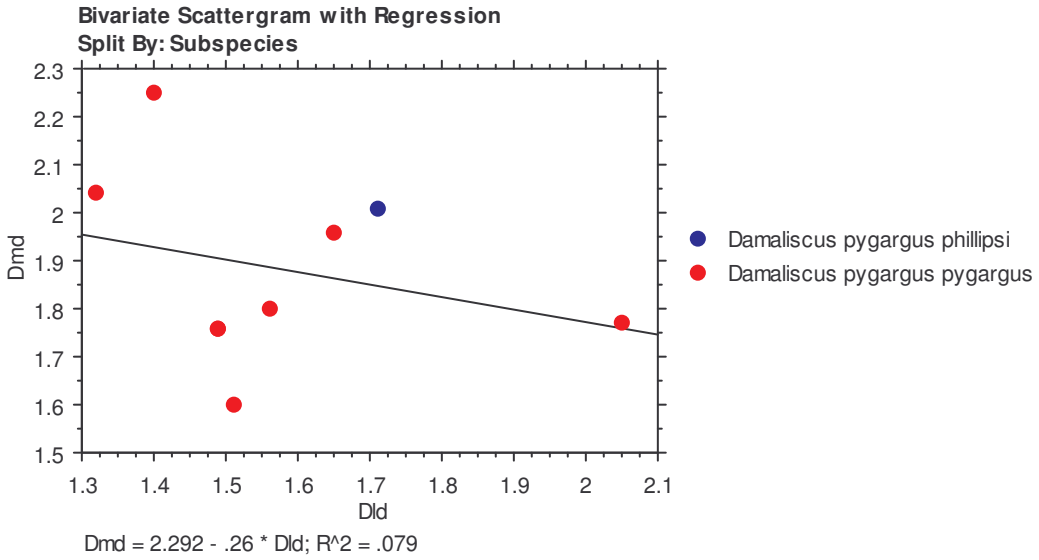


Figure 145: Bivariate plot of distal lateral of the diaphysis versus distal medial of the diaphysis of the femur showing regression of both groups.

Figure 145 shows a clear distinction between the two subspecies whereby the results show that bontebok is bigger than blesbok, even though there is an outlier of bontebok (it is found within the range of blesbok).

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
Bp	6.153	.320	.092	12	5.730	6.800	6
Bd	4.854	.329	.088	14	3.860	5.140	4

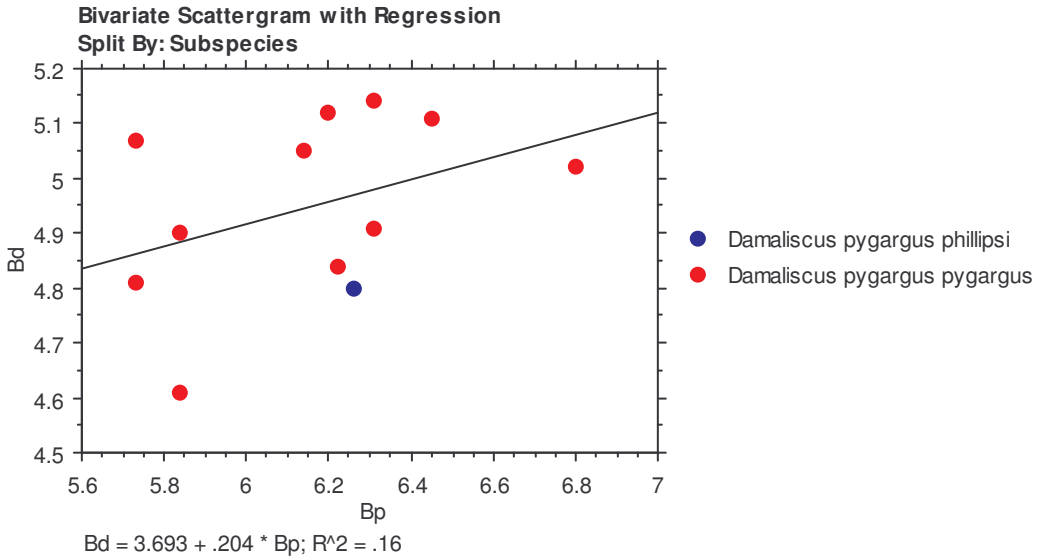


Figure 146: Bivariate plot of the breadth of the proximal end versus the breadth of the distal end of the femur showing regression of both groups.

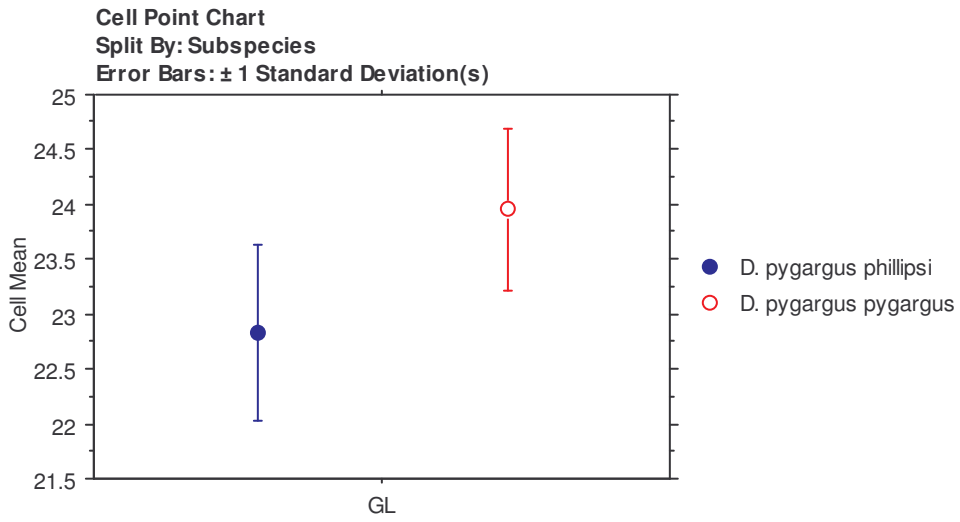


Figure 147: Standard error cell plot of the greatest length of the femur (error bars: ±1 STD deviation)

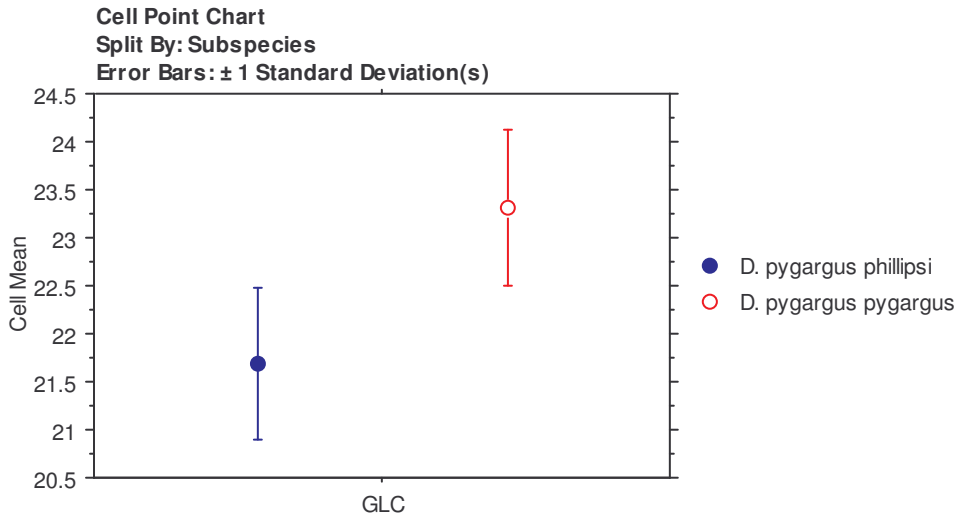


Figure 148: Standard error cell plot of the greatest length from the caput of the femur (error bars: ±1 STD deviation).

Descriptive Statistics

	GLC
Mean	22.776
Std. Dev.	1.109
Std. Error	.261
Count	18
Minimum	20.750
Maximum	24.360
# Missing	0

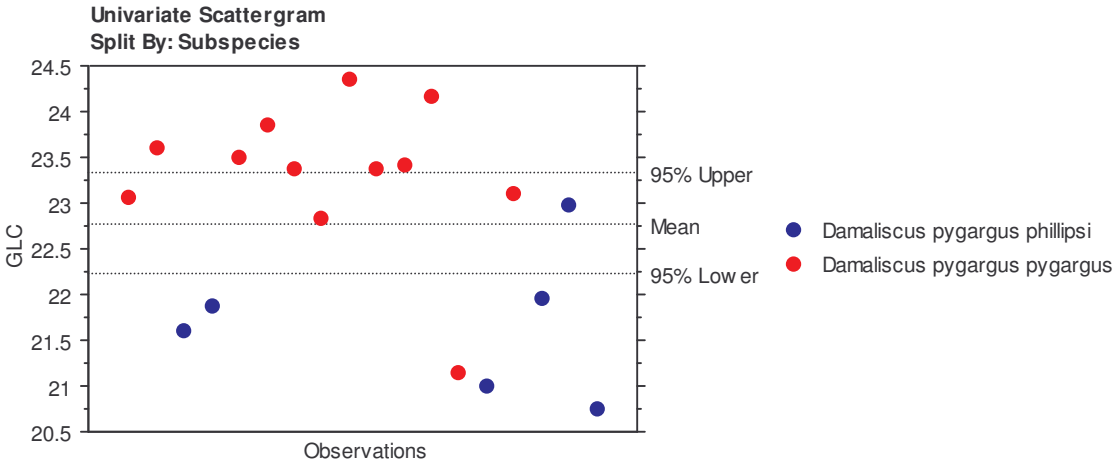


Figure 149: Univariate analysis of the greatest length of the caput of the femur split by subspecies and sex of the specimens.

Descriptive Statistics

	Bp
Mean	6.153
Std. Dev.	.320
Std. Error	.092
Count	12
Minimum	5.730
Maximum	6.800
# Missing	6

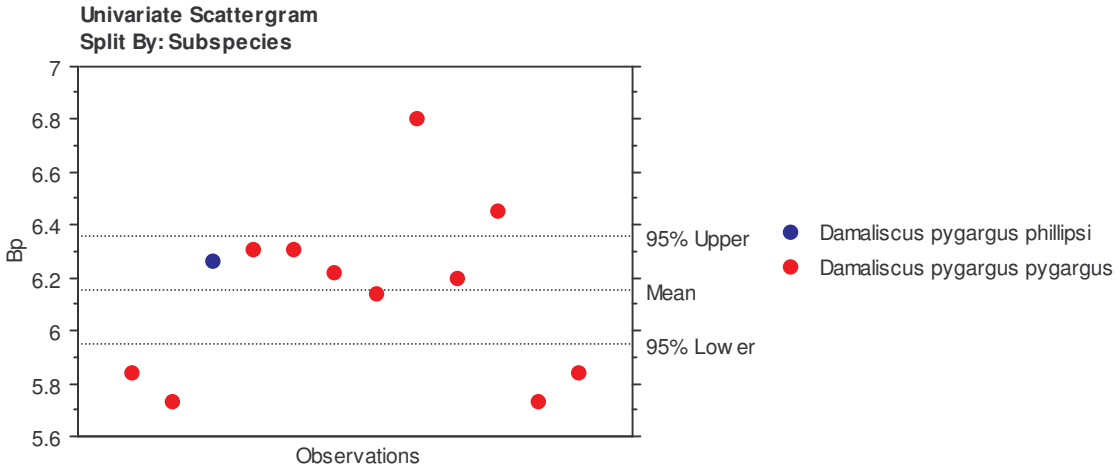


Figure 150: Univariate analysis of the breadth of the proximal end of the femur of bontebok and blesbok.

Descriptive Statistics

	Bd
Mean	4.854
Std. Dev.	.329
Std. Error	.088
Count	14
Minimum	3.860
Maximum	5.140
# Missing	4

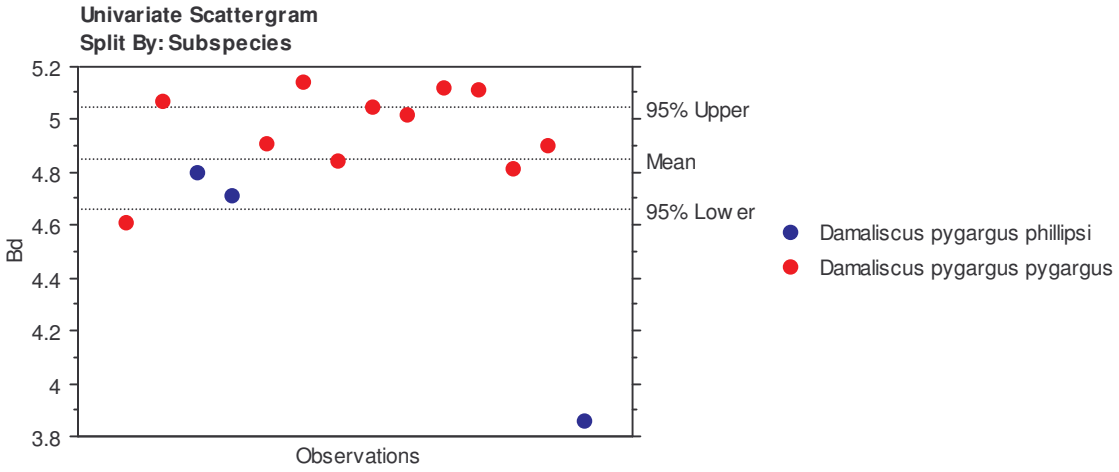


Figure 151: Univariate analysis of the breadth of the distal end of the diaphysis of the femur.

Descriptive Statistics

	SD
Mean	2.233
Std. Dev.	.075
Std. Error	.022
Count	12
Minimum	2.100
Maximum	2.310
# Missing	6

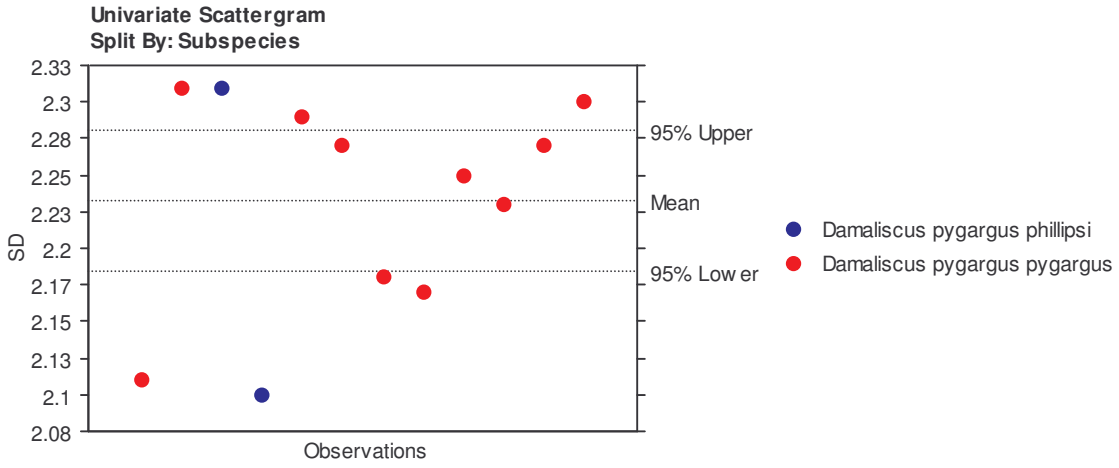


Figure 152: Univariate analysis of the smallest breadth of the diaphysis of the femur.

3.1.3.10 *Patella*



Figure 153: Photo showing the cranial view of the patella of bontebok and blesbok.

The patella of bontebok is broader than that of the blesbok.



Figure 154: Photo showing the plantar view of the patella of bontebok and blesbok.

Figure 154 shows that the outlines of the patella are sharper defined in the bontebok. It can be seen also that the edge on the side of the patella (pointed in red) is also more pronounced, i.e. it can be seen more clearly in bontebok than in blesbok.

Metric statistical analysis

When looking at the statistical analysis, the patella shows no differences between these subspecies (bontebok and blesbok) (see figure 155). Differences were expected as these animals are exposed to different stresses since they are found in different terrains. These results show some overlap, supporting what has just been mentioned above about no differences.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GL	3.287	.162	.043	14	3.060	3.550	0
GB	3.240	.229	.061	14	2.910	3.580	0

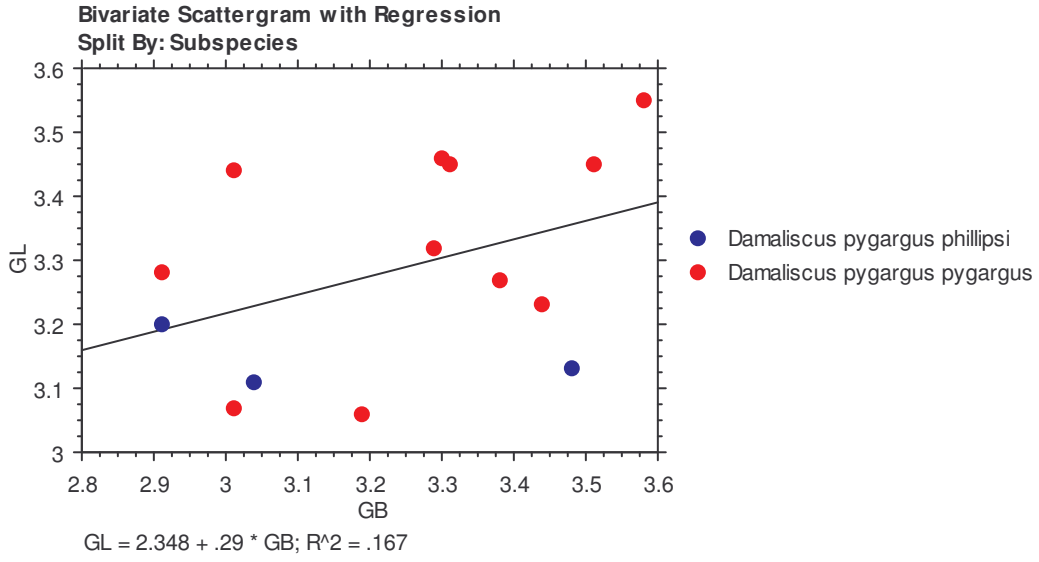


Figure 155: Bivariate plot of the greatest breadth over the wings versus the greatest length of the patella showing regression for both groups

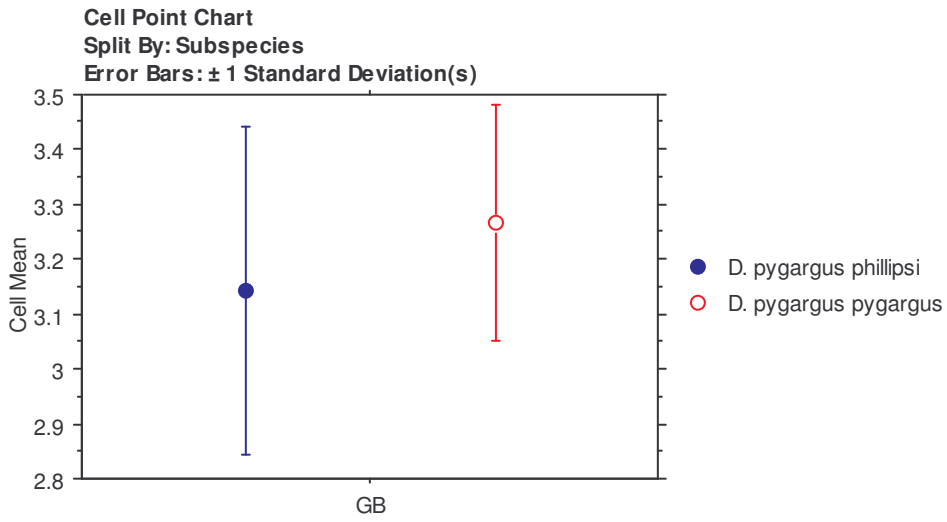


Figure 156: Standard error cell plot of the greatest breadth of the patella (error bars: ±1 STD deviation).

Figure 156 shows that there is a clear distinction between the two subspecies, whereby bontebok has a greater breadth than blesbok. This was unexpected because blesbok is thought to be bigger than bontebok.

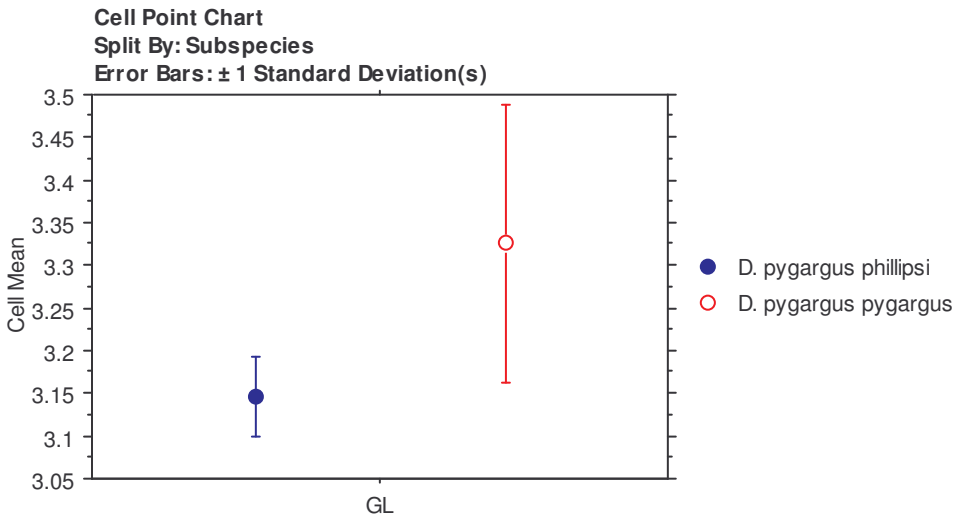


Figure 157: Standard error cell plot of the greatest length of the patella (error bars: ±1 STD deviation).

Descriptive Statistics

	GB
Mean	3.240
Std. Dev.	.229
Std. Error	.061
Count	14
Minimum	2.910
Maximum	3.580
# Missing	0

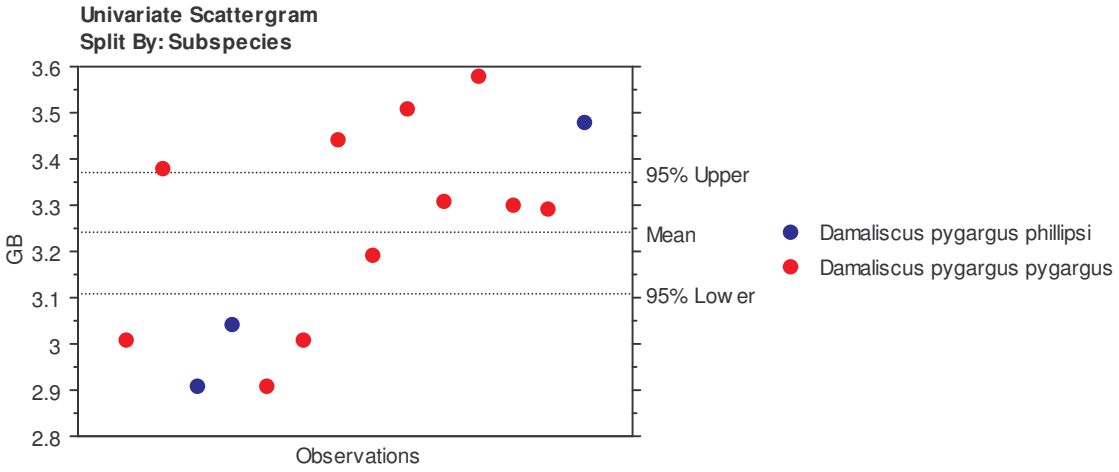


Figure 158: Univariate plot of the greatest breadth of the patella showing outliers.

Descriptive Statistics

	GB
Mean	3.240
Std. Dev.	.229
Std. Error	.061
Count	14
Minimum	2.910
Maximum	3.580
# Missing	0

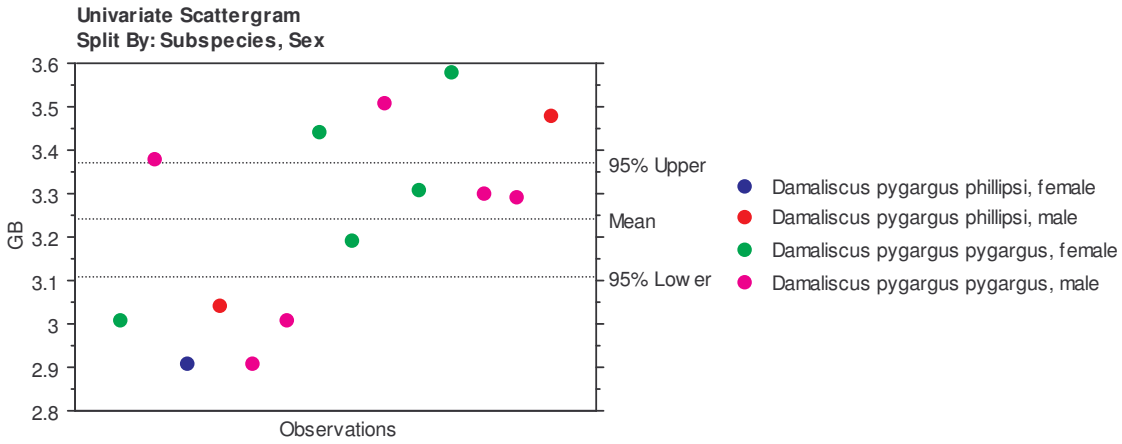


Figure 159: Univariate plot of the greatest breadth of the patella showing some outliers of both sexes of both subspecies.

Descriptive Statistics

	GL
Mean	3.287
Std. Dev.	.162
Std. Error	.043
Count	14
Minimum	3.060
Maximum	3.550
# Missing	0

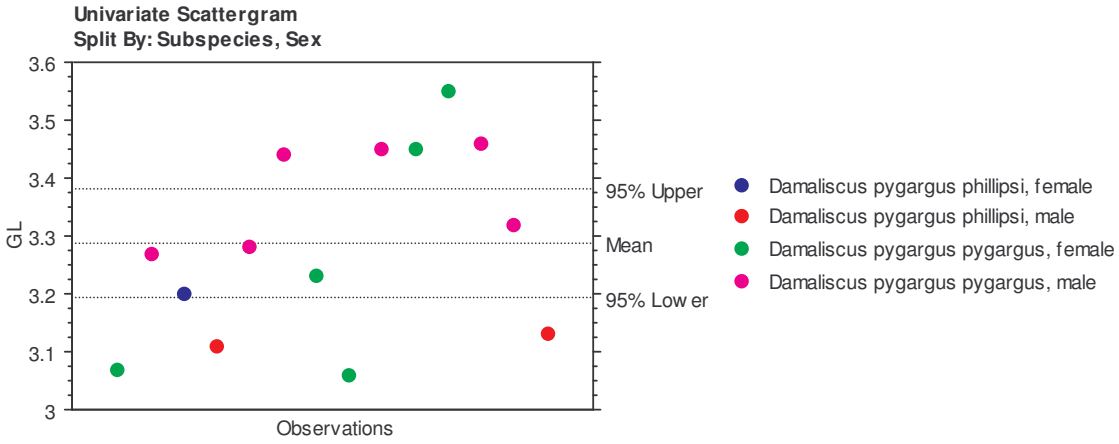


Figure 160: Univariate plot of the greatest length of the patella showing outliers.

3.1.3.11 *Tibia*



Figure 161: Photo showing craniolateral view of the tibia of bontebok and blesbok.

When looking at the photos, there are differences in the proximal end; the remnant of the fibula in blesbok (circled above) is a bit sharper than that of bontebok. That is the only significant difference as they are almost equal in size.



Figure 162: Photo showing the craniolateral view of the tibia of bontebok and blesbok.

When looking at figure 162 above, the tibia of blesbok is much bigger and longer than that of bontebok and it is also a bit slender than that of bontebok.

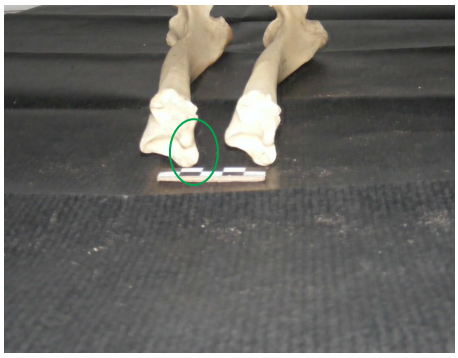


Figure 163: Photo showing the distal end of the tibia of bontebok and blesbok.

Figure 163 shows differences in the distal end of the tibia; the plantolateral articular facet in bontebok is more outward than in blesbok (circled above) than blesbok which is a bit rounder.



Figure 164: Photo showing the craniolateral view of the tibia of bontebok and blesbok (in relation to size).

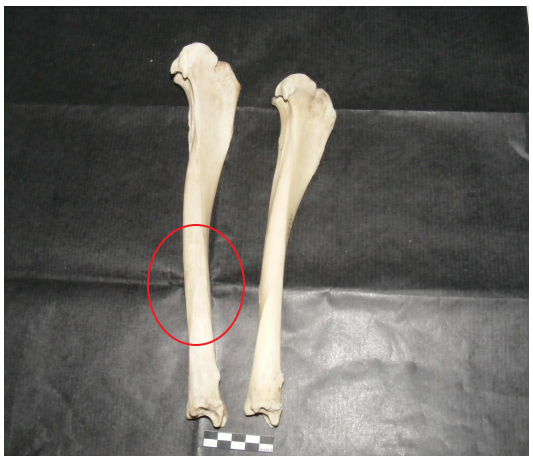


Figure 165: Photo showing dorsal view of the tibia of bontebok and blesbok.

The curvature of the tibia is near the distal end in bontebok (circled above) and a bit higher in blesbok (figures 164 & 165). It is also clear that the tibia of bontebok is a bit longer than that of blesbok in these figures.

Metric statistical analysis

In this instance, the statistical analysis shows that these subspecies show differences. This was expected as they are found in different terrains, and therefore, experience different stresses, and their stressors are also different. When looking at figure 166, blesbok seems to be above the regression line while blesbok is under the regression line.

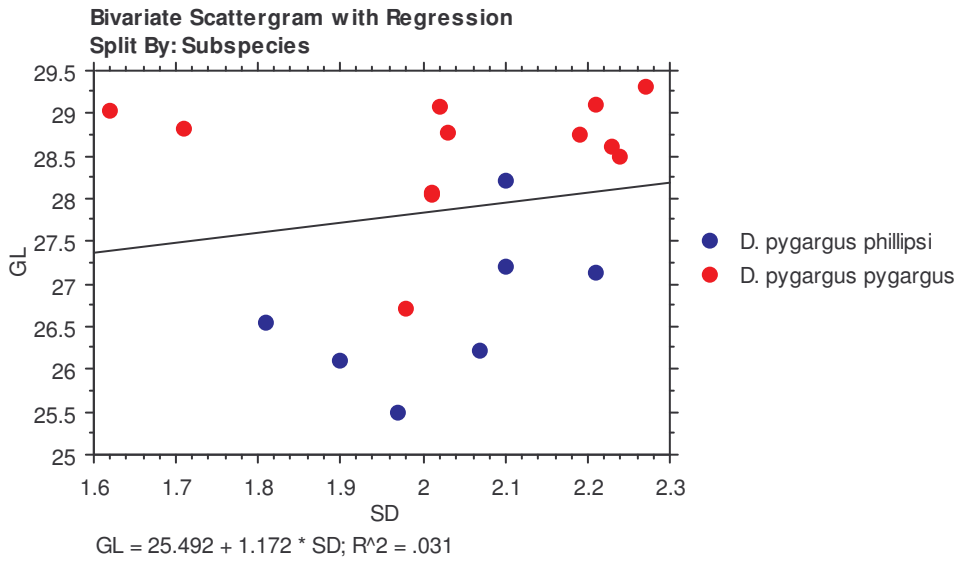


Figure 166: Bivariate plot showing smallest breadth of diaphysis versus the greatest length of the tibia showing regression of both groups.

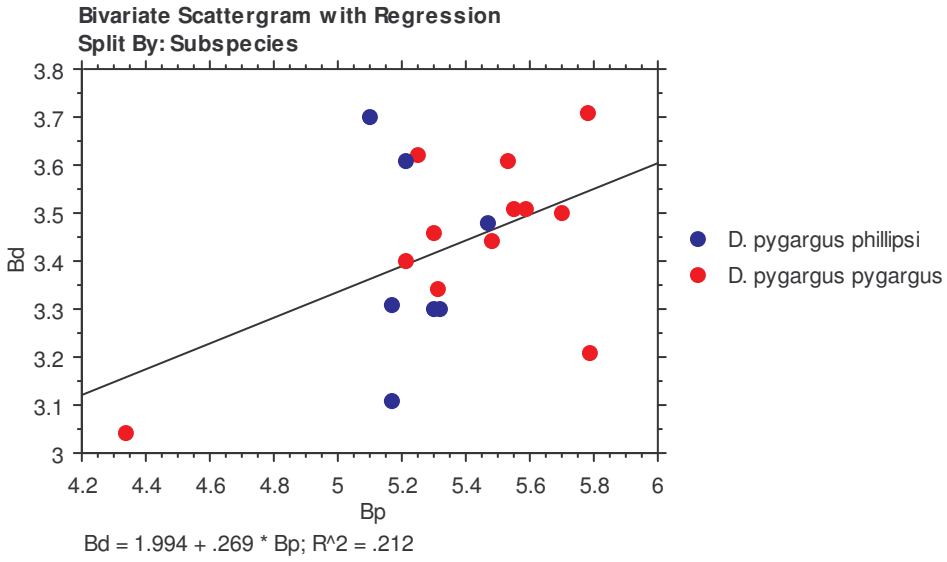


Figure 167: Bivariate plot showing the breadth of proximal end versus the breadth of the distal end of the tibia showing regression of both groups.

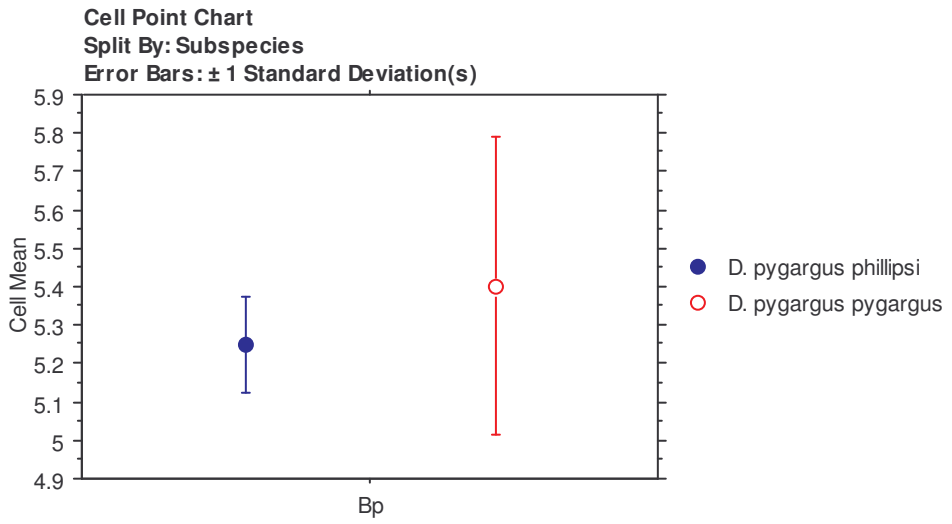


Figure 168: Standard error cell plot of the greatest length of the tibia (error bars: ±1 STD deviation).

Figure 168 shows a very clear distinction between the two subspecies in that bontebok is shown to have a smaller length than bontebok, which is highly unexpected.

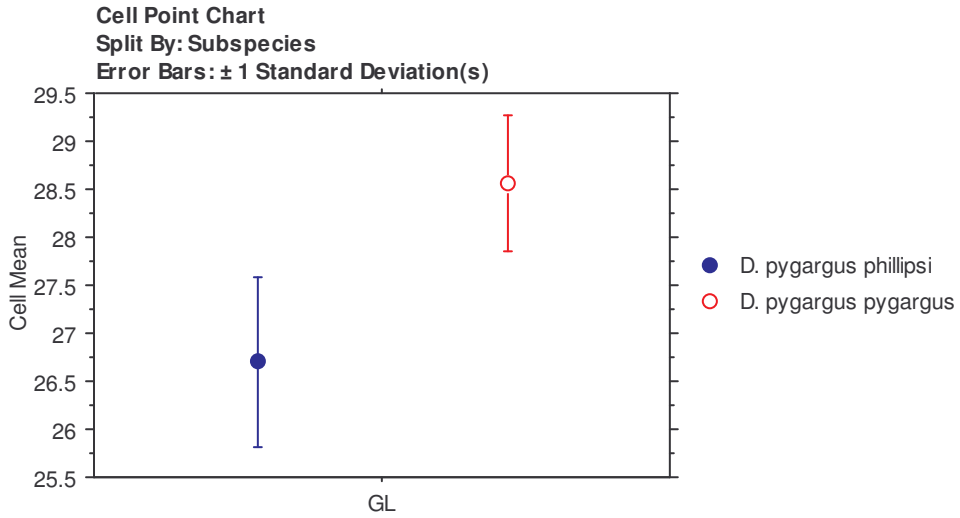


Figure 169: Standard error cell plot of the breadth of the proximal end of the tibia (error bars: ±1 STD deviation).

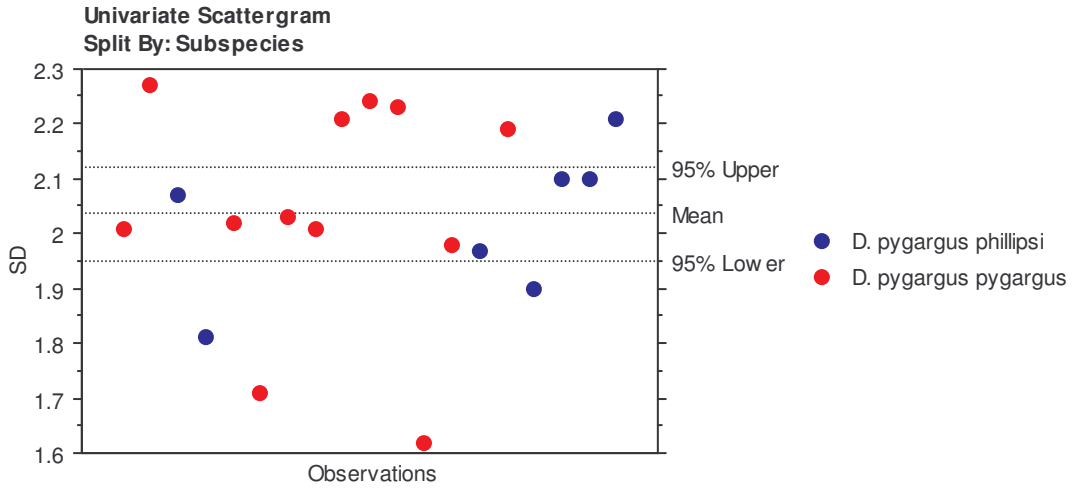


Figure 170: Univariate plot of the smallest breadth of the diaphysis of the tibia.

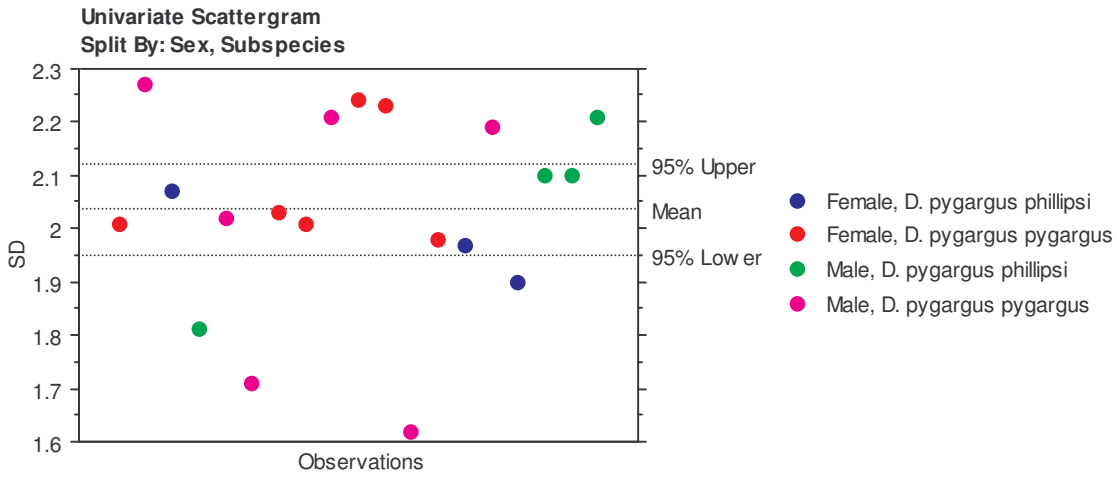


Figure 171: Univariate plot of the smallest breadth of the diaphysis of the tibia split by sex and subspecies.

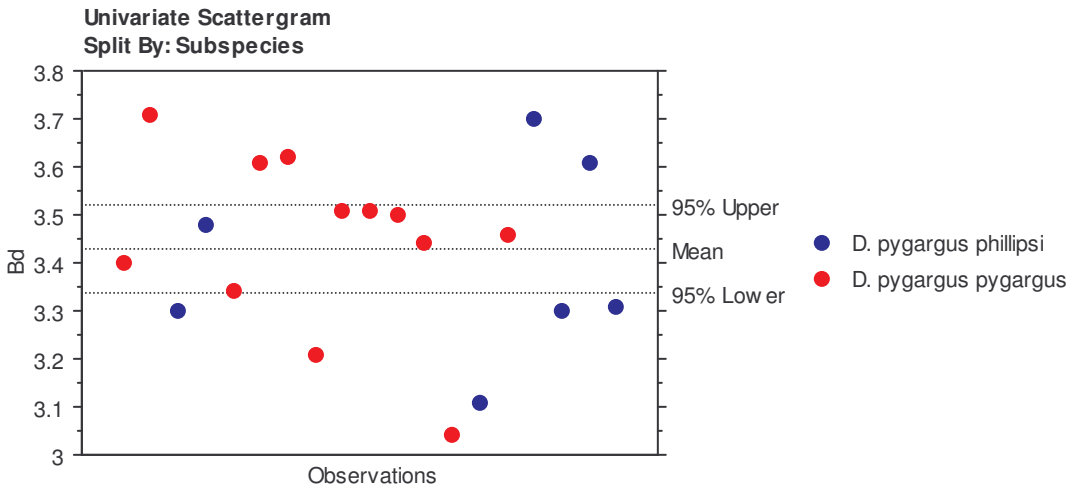


Figure 172: Univariate plot of the breadth of the distal end of the tibia.

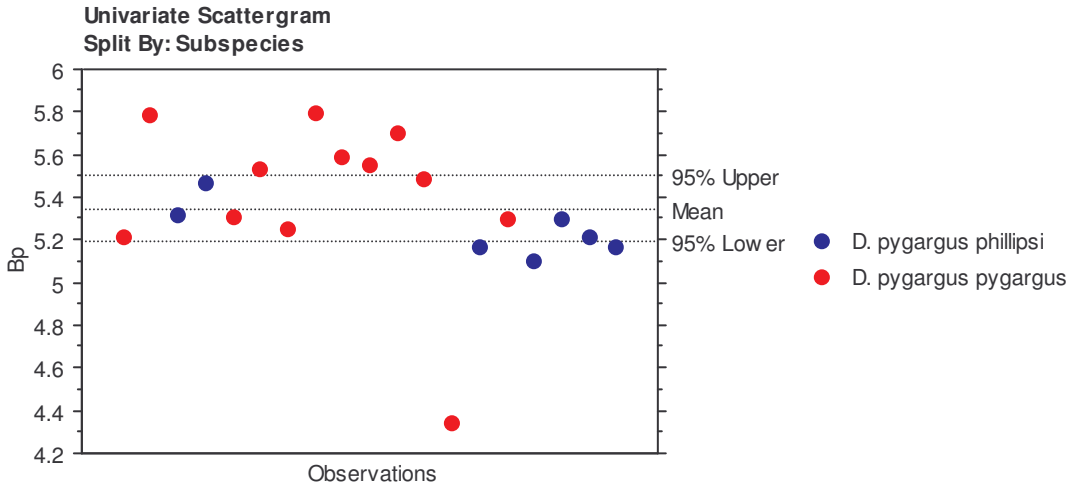


Figure 173: Univariate plot of the breadth of the proximal end of the tibia.

3.1.3.12 *Metatarsal*

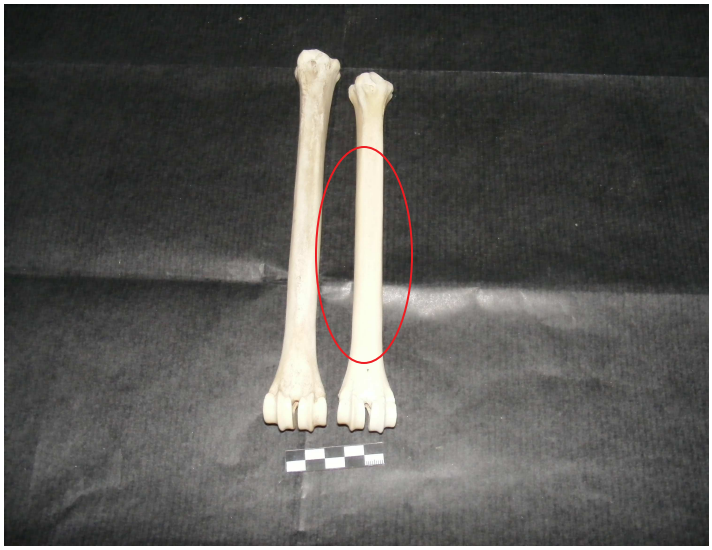


Figure 174: Photo showing the dorsal view of the metatarsals of bontebok and blesbok.

Figure 174 shows that there are differences between the metatarsals of the two animals. The metatarsal of bontebok is a bit broader near the distal end and narrow near the proximal end, whilst that of blesbok (circled above) is almost the same from the distal end to the proximal end.

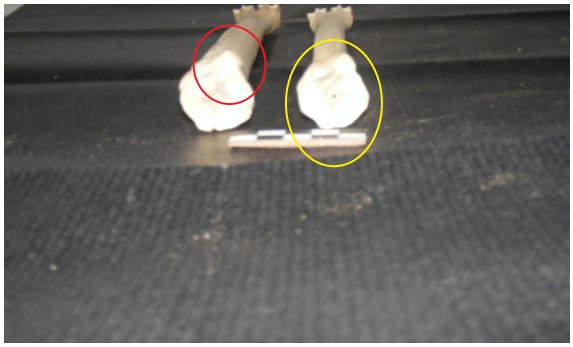


Figure 175: Photo showing the proximal view of the metatarsals of bontebok and blesbok.

The proximal end of blesbok (circled above in yellow) is a bit broader than that of bontebok, and the plantolateral articular facet of bontebok (circled above in red) is sharper than that of blesbok.

Metric statistical analysis

When comparing the metatarsals of bontebok and blesbok, no difference is documented; they are basically the same.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
Dda	1.950	.088	.021	18	1.800	2.080	0
Ddp	1.651	.101	.024	18	1.400	1.800	0

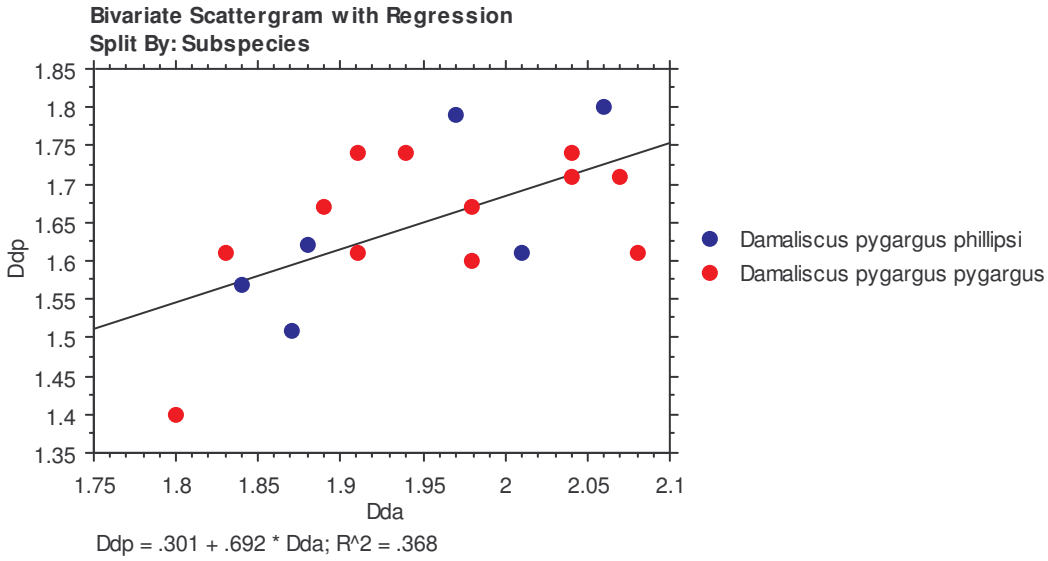


Figure 176: Bivariate plot of the axial versus the peripheral of the metatarsal bones showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
SD	1.615	.205	.048	18	1.100	1.940	0
DD	2.071	.772	.223	12	1.410	3.120	6

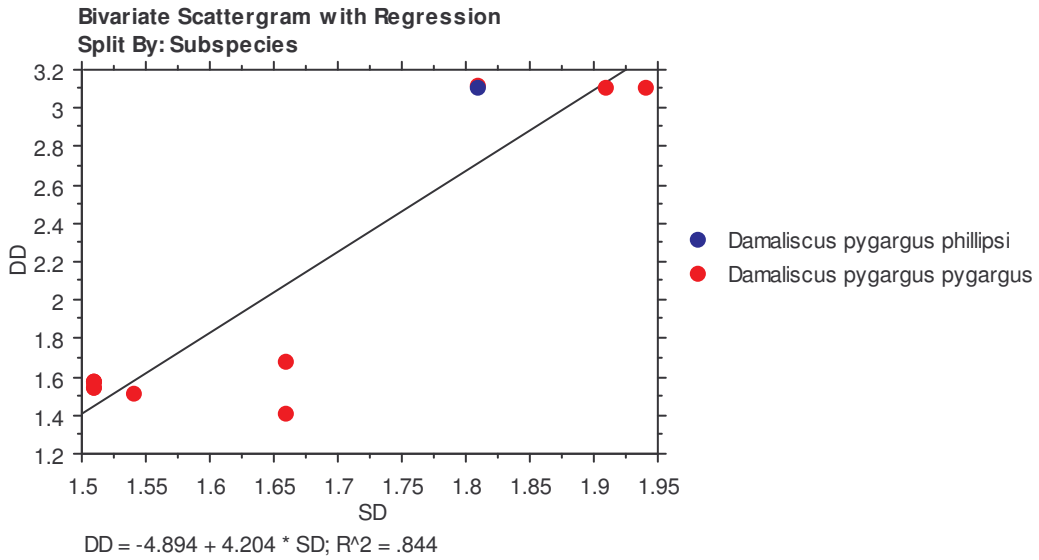


Figure 177: Bivariate plot of the smallest breadth of the diaphysis versus the smallest depth of the diaphysis of the metatarsal showing regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
Bp	2.867	.176	.051	12	2.610	3.230	6
Bd	3.137	.064	.018	12	3.050	3.250	6

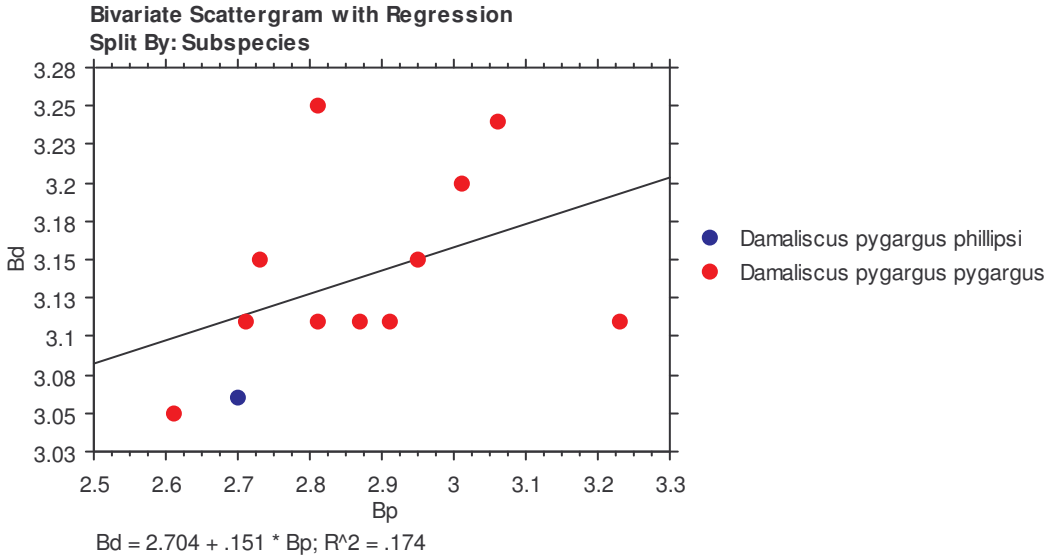


Figure 178: Bivariate plot of the breadth of the proximal end versus the breadth of the distal end of the metatarsal bone showing regression of both groups.

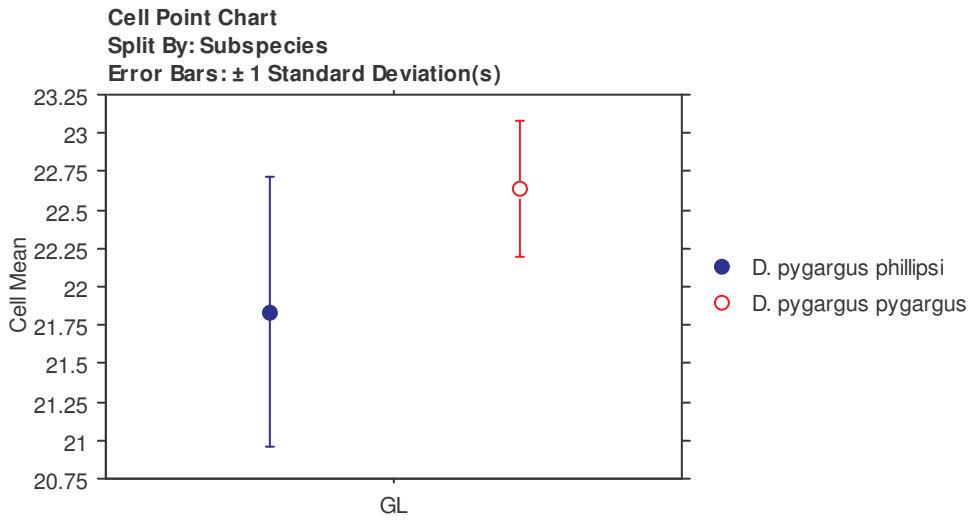


Figure 179: Standard error cell plot of the greatest length of the metatarsal (error bars: ±1 STD deviation).

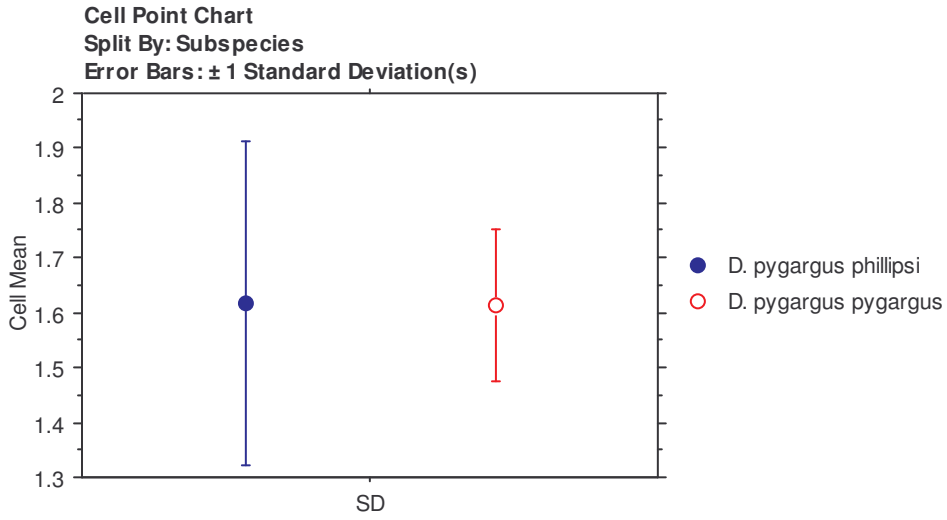


Figure 180: Standard error cell plot of the smallest breadth of the diaphysis of the metatarsal (error bars: ±1 STD deviation).

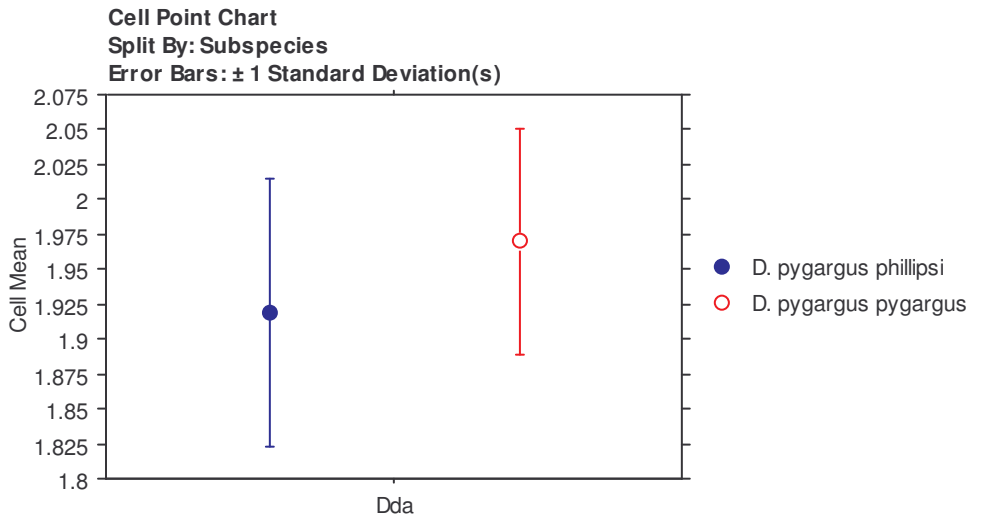


Figure 181: Standard error cell plot of the axial of the distal end of the metatarsal (error bars: ±1 STD deviation).

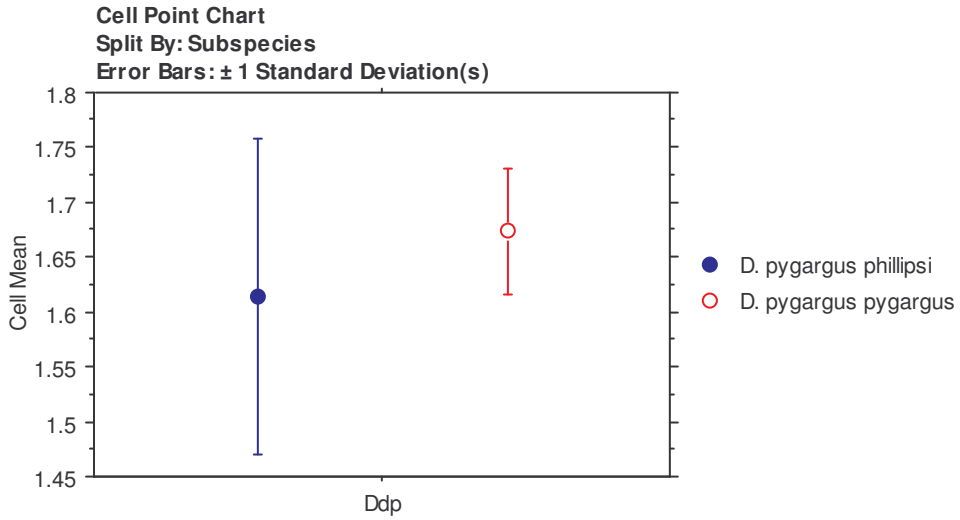


Figure 182: Standard error cell plot of the peripheral of the distal end of the metatarsal (error bars: ±1 STD deviation).

Descriptive Statistics

	Ddp
Mean	1.651
Std. Dev.	.101
Std. Error	.024
Count	18
Minimum	1.400
Maximum	1.800
# Missing	0

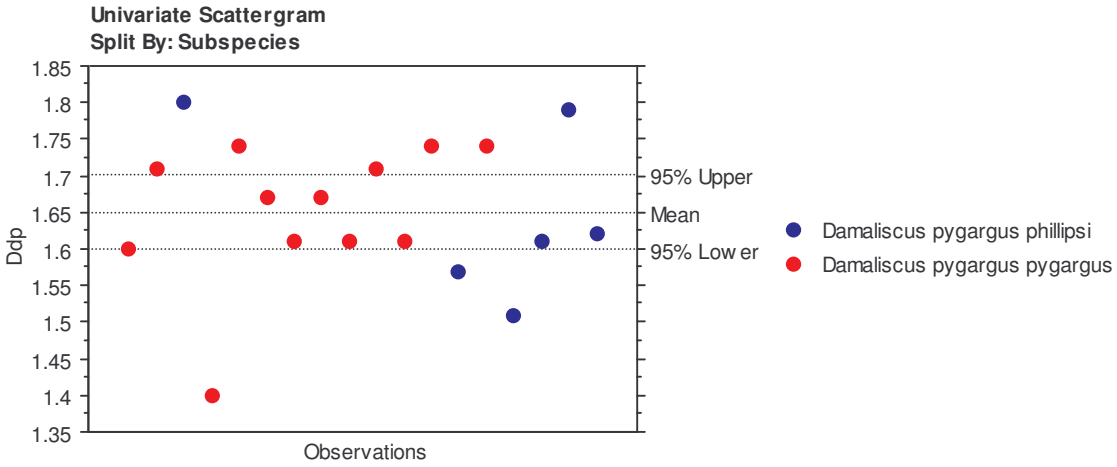


Figure 183: Univariate analysis of the peripheral of the distal end of the metatarsal with an outlier.

Descriptive Statistics

	SD
Mean	1.615
Std. Dev.	.205
Std. Error	.048
Count	18
Minimum	1.100
Maximum	1.940
# Missing	0

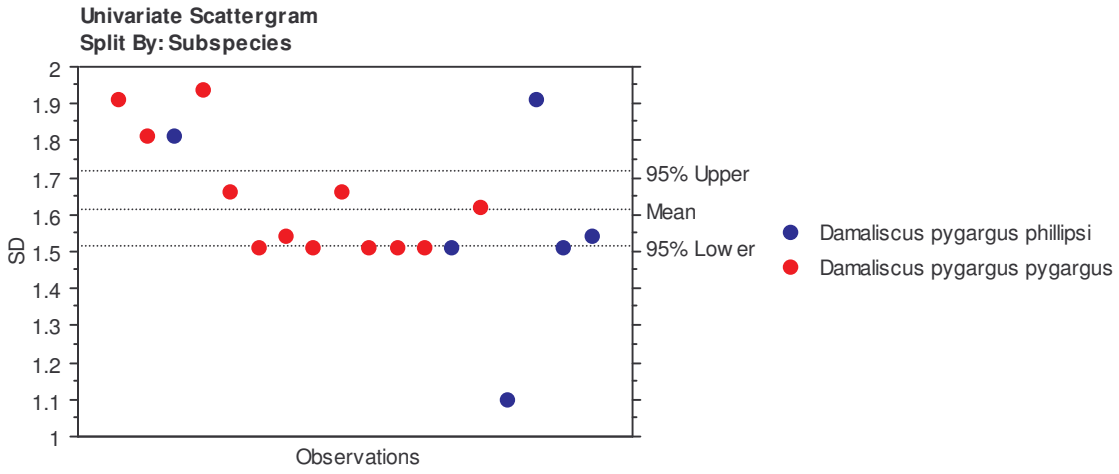


Figure 184: Univariate analysis of the smallest breadth of the diaphysis of the metatarsal with an outlier.

Descriptive Statistics

	DD
Mean	2.071
Std. Dev.	.772
Std. Error	.223
Count	12
Minimum	1.410
Maximum	3.120
# Missing	6

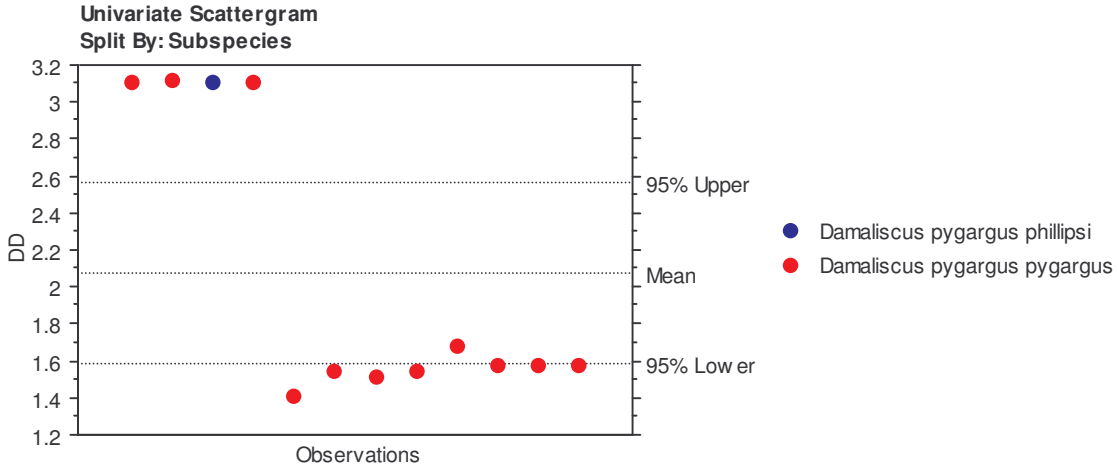


Figure 185: Univariate plot of the depth of the diaphysis of the metatarsal.

3.1.3.13 *Talus (astragalus)*

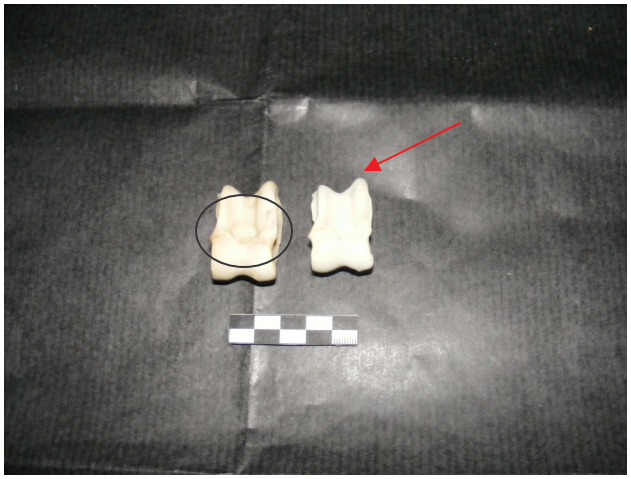


Figure 186: Photo showing the dorsal view of the talus bone of bontebok and blesbok.

The deep part found in the middle of the talus bone is much deeper in bontebok (circled above) than in blesbok. The other difference is pointed above (with an arrow). This shows that the lateral ridge is a bit higher in blesbok than in bontebok.

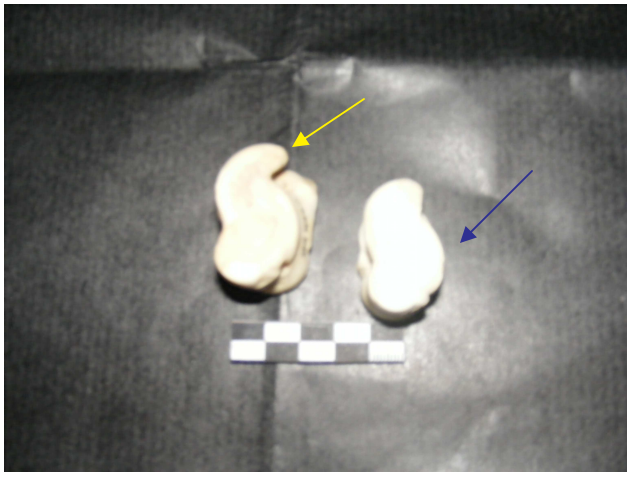


Figure 187: Photo showing the lateral view of the talus bone of bontebok and blesbok.

Figure 187 shows the differences found in the two specimens. The first difference is pointed above with a yellow arrow (the lateral ridge). It can be seen that the bone of bontebok is curvier and more pronounced than in bontebok. Another difference is also pointed above in blesbok with a blue arrow. These bones differ in that blesbok is curvier than bontebok in this instance.

Metric statistical analysis

The talus bone shows no differences between the two species even though they are found in different terrains (see both figures 188 & 189).

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GLI	3.854	.092	.022	18	3.710	4.080	0
GLm	3.581	.124	.029	18	3.410	3.770	0

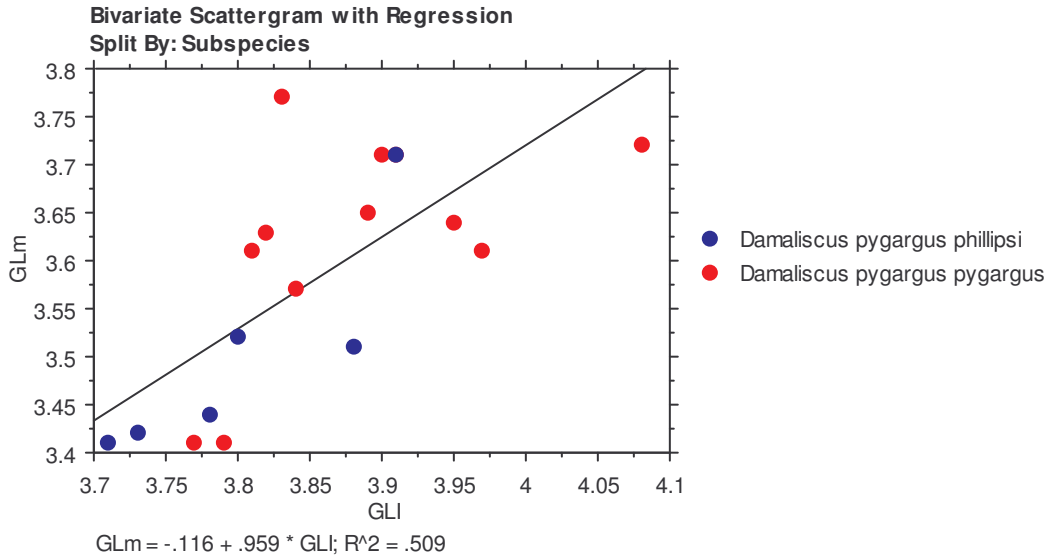


Figure 188: **Bivariate plot of the greatest length of the lateral half versus the greatest length of the medial half of the talus bone showing a regression for both groups.**

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
Dl	2.235	.089	.026	12	2.110	2.350	6
Dm	2.305	.083	.024	12	2.110	2.410	6

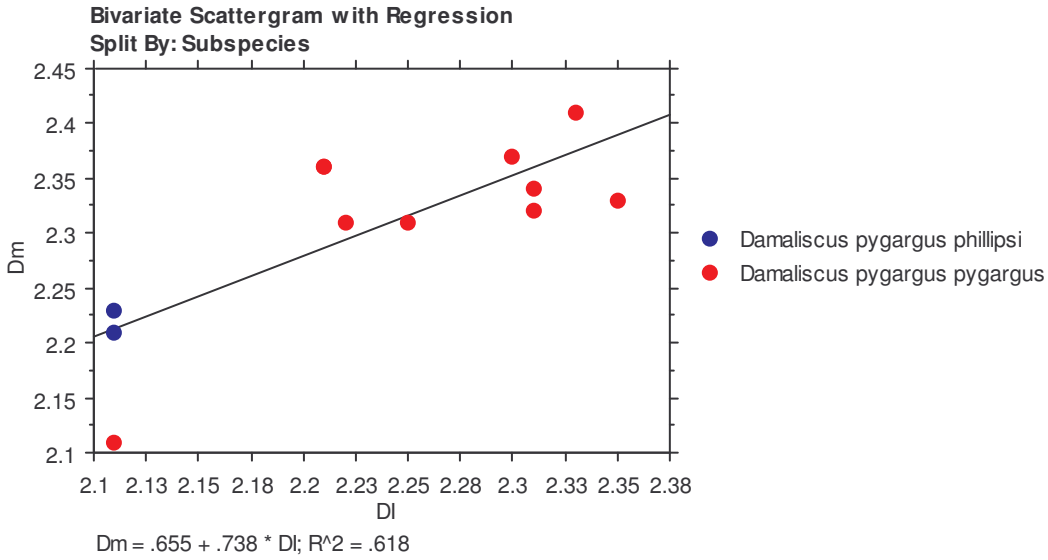


Figure 189: Bivariate plot of the depth of the lateral half versus the depth of the medial half of the talus bone showing regression for both groups.

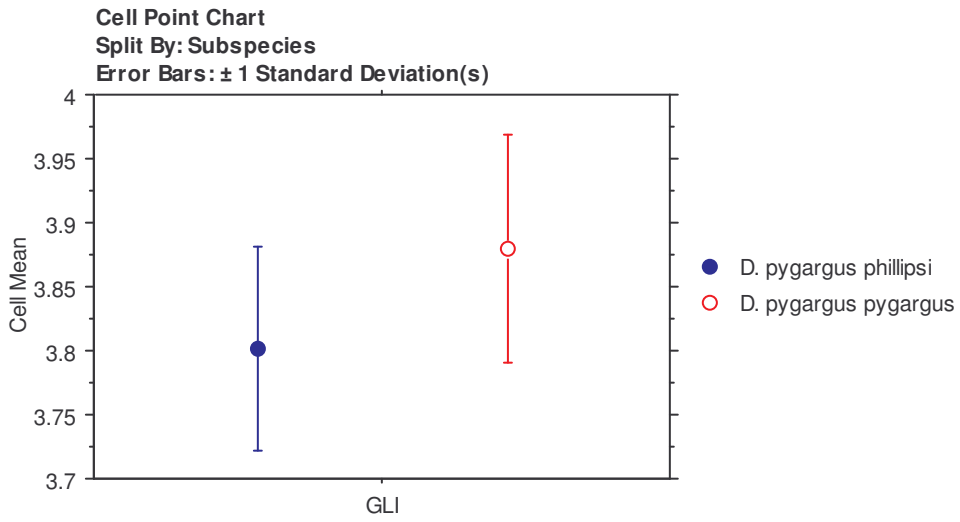


Figure 190: Standard error cell plot of the greatest length of the lateral half of the talus (astragalus) (error bars: ±1 STD deviation).

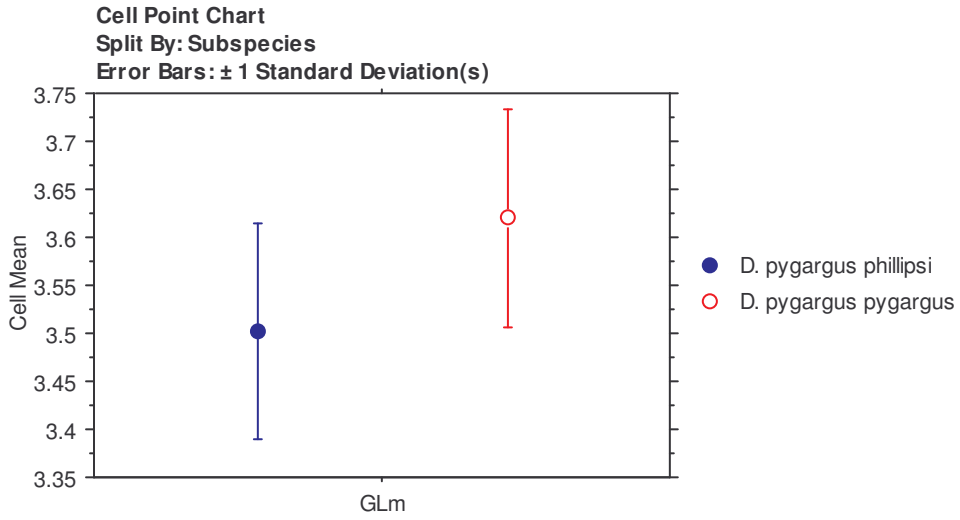


Figure 191: Standard error cell plot of the greatest length of the medial half of the talus (error bars: ±1 STD deviation).

Descriptive Statistics

	Dm
Mean	2.305
Std. Dev.	.083
Std. Error	.024
Count	12
Minimum	2.110
Maximum	2.410
# Missing	6

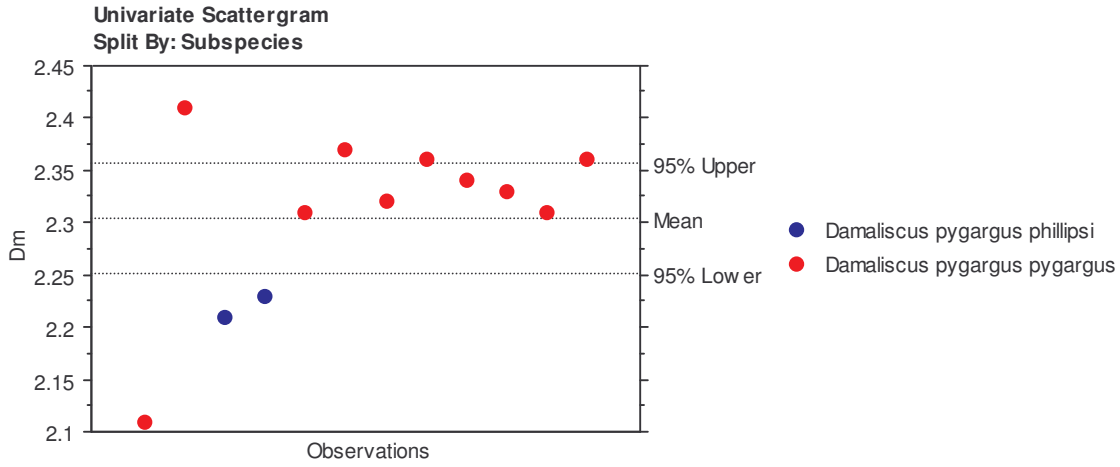


Figure 192: Univariate analysis of the depth of the medial half of the talus showing outliers.

Descriptive Statistics

	DI
Mean	2.235
Std. Dev.	.089
Std. Error	.026
Count	12
Minimum	2.110
Maximum	2.350
# Missing	6

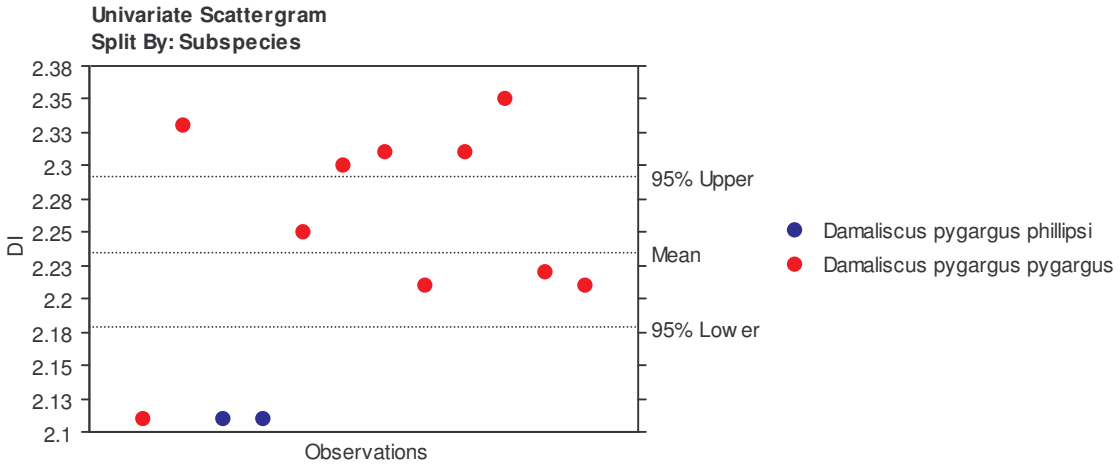


Figure 193: Univariate analysis of the depth of the lateral half of the talus showing outliers.

Descriptive Statistics

	Bd
Mean	2.416
Std. Dev.	.080
Std. Error	.023
Count	12
Minimum	2.310
Maximum	2.560
# Missing	6

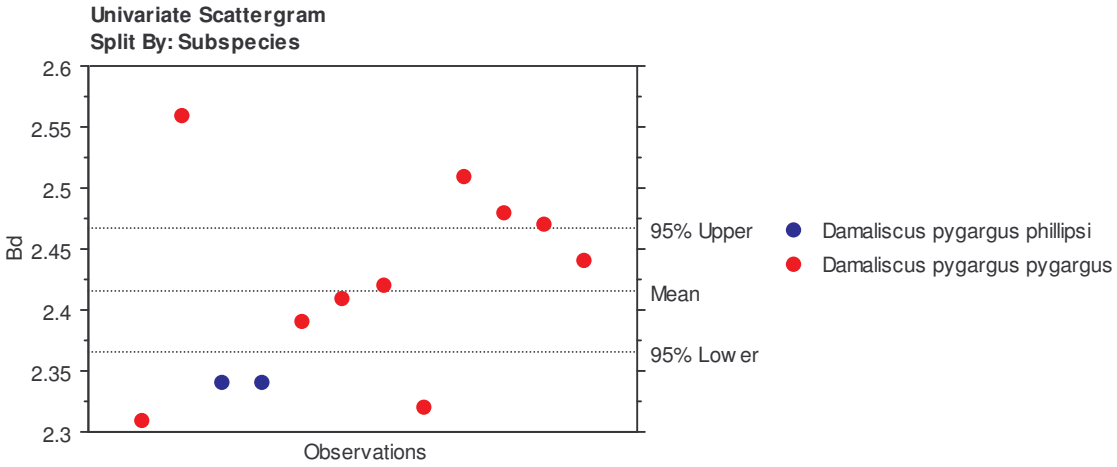


Figure 194: Univariate plot of the breadth of the distal end of the talus.

3.1.3.14 *Calcaneus*



Figure 195: Photo showing the plantar view of the calcaneus of bontebok and blesbok.

There are several differences when one looks at the two bones in figure 195. The first difference is (pointed above with a black arrow) that bontebok is almost round than blesbok. The second difference can be seen at the tip of the calcaneus whereby blesbok is sharper than bontebok (pointed above with a blue arrow).

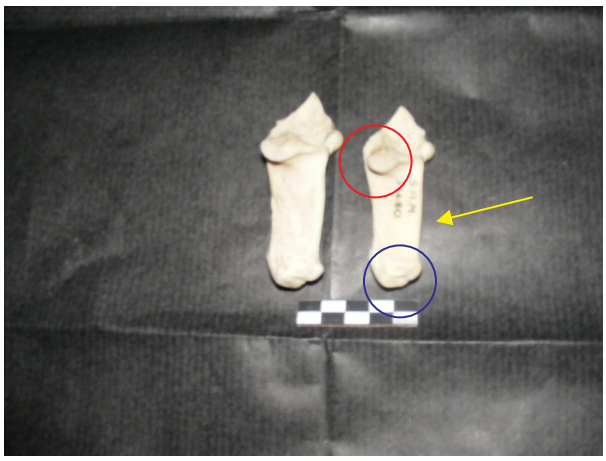


Figure 196: Photo showing the dorsal view of the calcaneus of bontebok and blesbok.

The first difference noticed in figure 196 is pointed above in blue whereby blesbok is smaller than bontebok (blesbok rounder than bontebok). Another difference is pointed above in yellow whereby blesbok is thinner than bontebok. The protrusion (pointed in red) is bigger in blesbok than in bontebok and almost rounder in blesbok.

Metric statistical analysis

Limb bones are supposed to be showing off differences but this particular limb bone does not show any. Both these subspecies are found under, below and on the regression line.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GB	2.423	.199	.048	17	2.130	2.970	0
GL	8.435	.235	.057	17	8.030	8.990	0

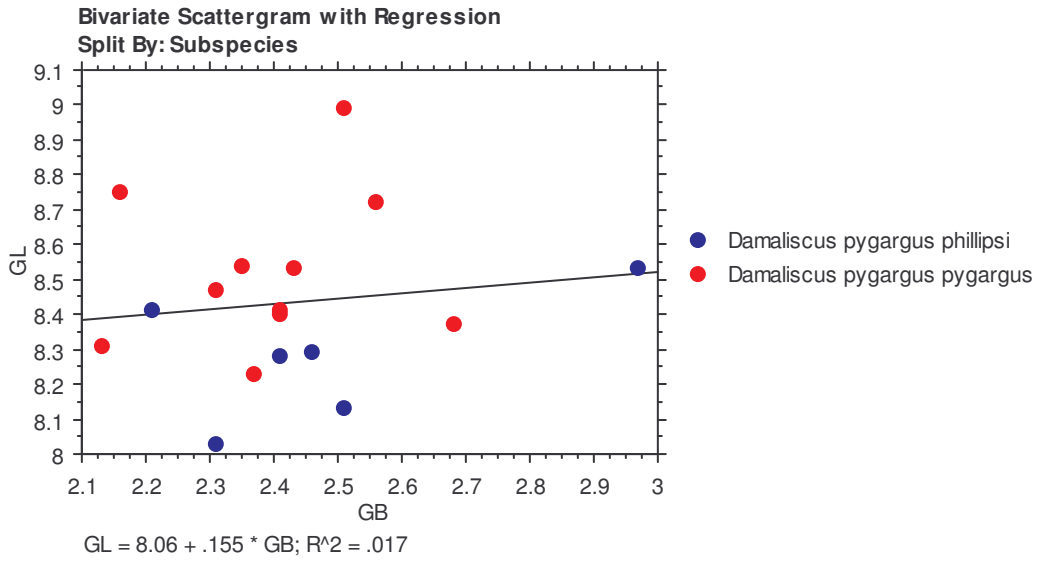


Figure 197: Bivariate plot of the greatest breadth over the *sustenaculum* versus the greatest length of the calcaneus showing regression for both groups.

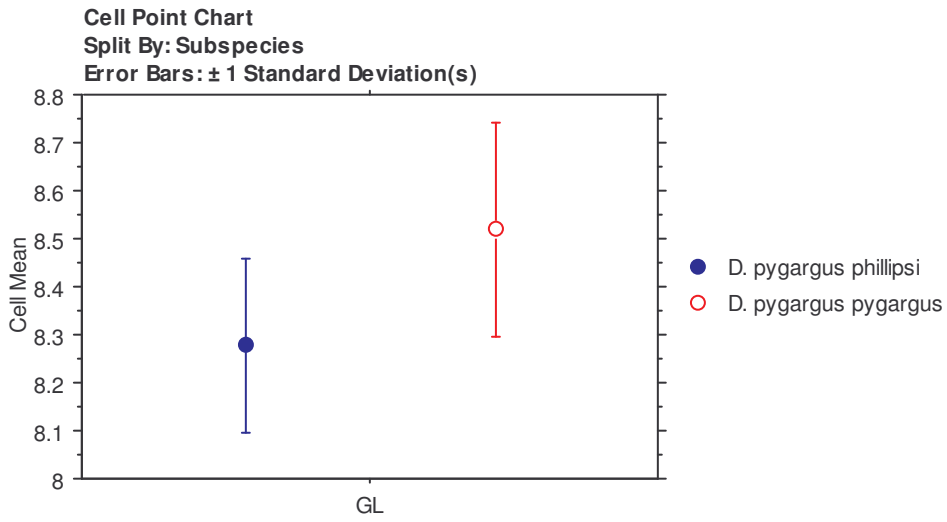


Figure 198: Standard error cell plot of the greatest length of the calcaneus (error bars: ±1 STD deviation).

Figure 198 shows that the cell mean is higher in bontebok than blesbok. This was unexpected since blesbok is run faster than bontebok (Smithers, 1983).

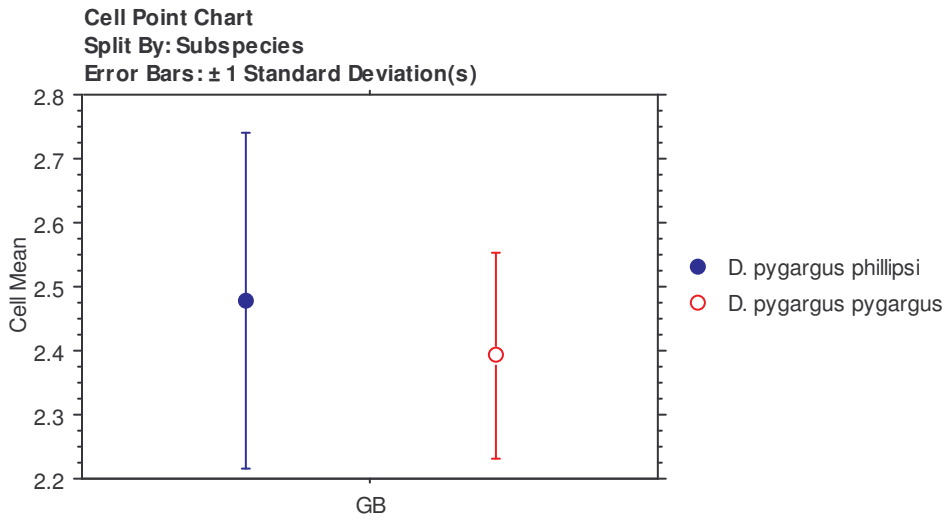


Figure 199: Standard error cell plot of the greatest breadth of the calcaneus (error bars: ±1 STD deviation).

Descriptive Statistics

	GB
Mean	2.423
Std. Dev.	.199
Std. Error	.048
Count	17
Minimum	2.130
Maximum	2.970
# Missing	0

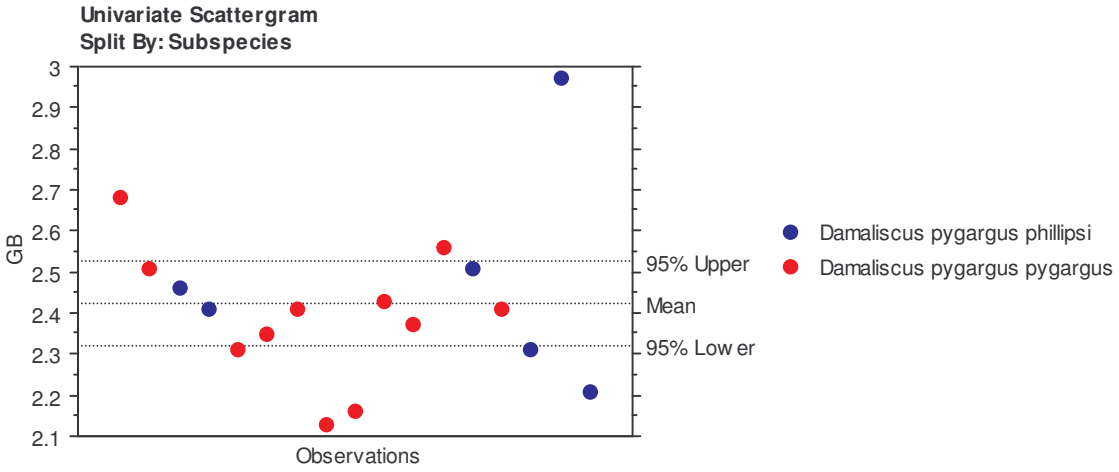


Figure 200: Univariate plot of the greatest breadth of the calcaneus with outliers.

Descriptive Statistics

	GB
Mean	2.423
Std. Dev.	.199
Std. Error	.048
Count	17
Minimum	2.130
Maximum	2.970
# Missing	0

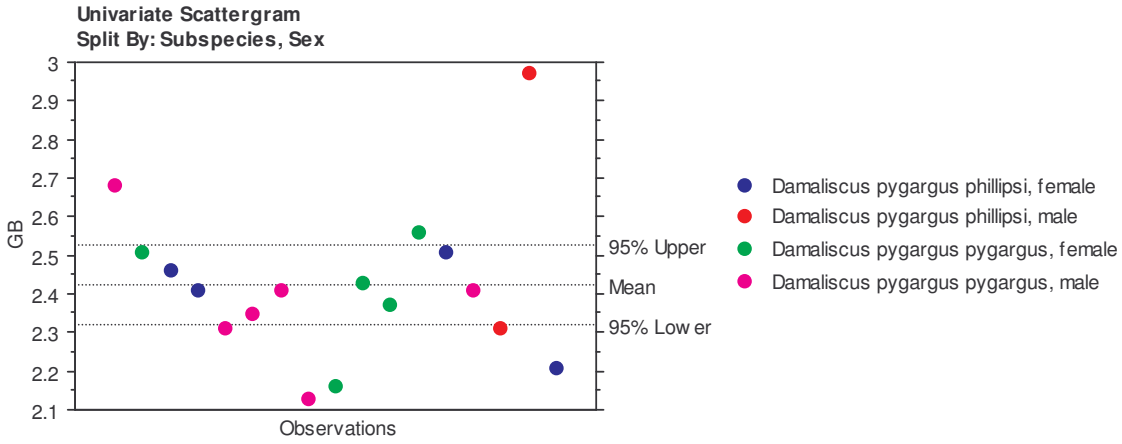


Figure 201: Univariate plot of the greatest breadth split by sex and subspecies.

Descriptive Statistics

	GL
Mean	8.435
Std. Dev.	.235
Std. Error	.057
Count	17
Minimum	8.030
Maximum	8.990
# Missing	0

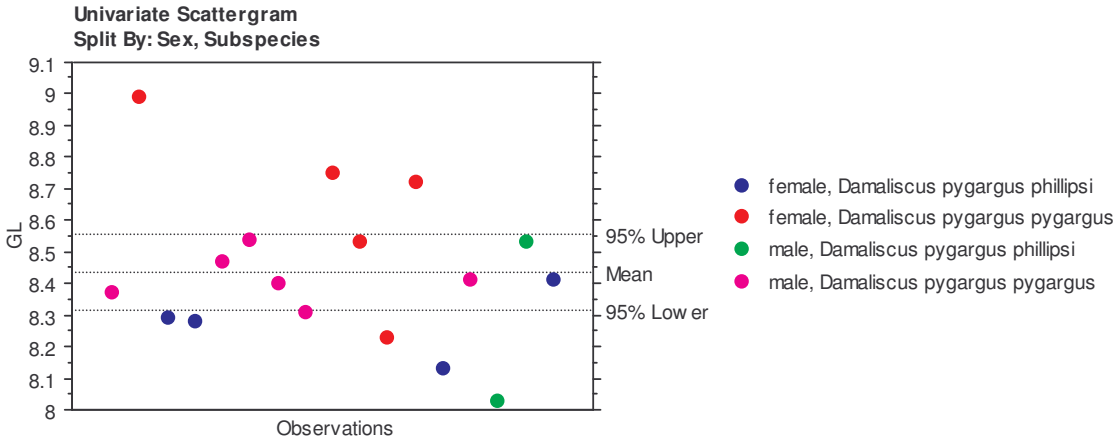


Figure 202: Univariate plot of the greatest length of the calcaneus.

Descriptive Statistics

	GL
Mean	8.435
Std. Dev.	.235
Std. Error	.057
Count	17
Minimum	8.030
Maximum	8.990
# Missing	0

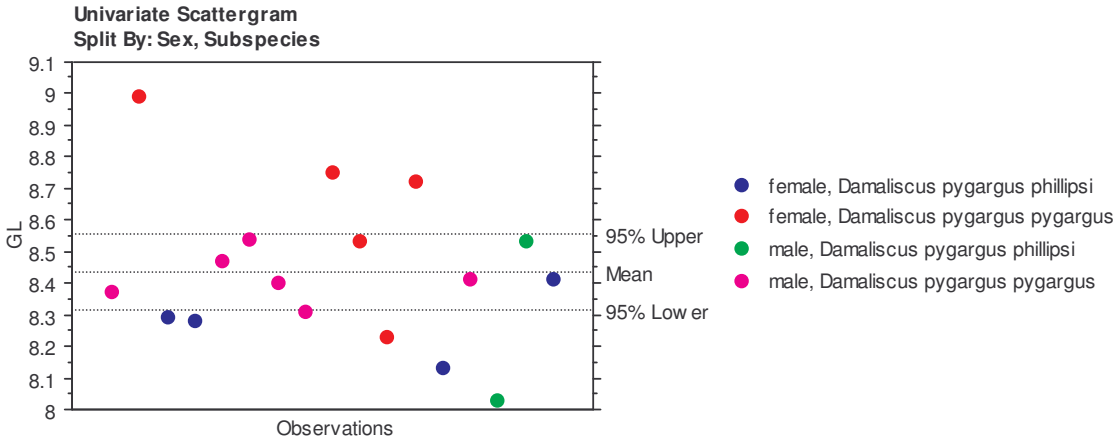


Figure 203: Univariate analysis of the greatest length of the calcaneus split by subspecies and sex of the specimens.

3.1.3.15 *Phalanx 1*



Figure 204: Photo showing the dorsal view of the first phalanx of bontebok and blesbok.

Figure 204 shows that the curvature is not that similar; blesbok is a bit thinner than bontebok on the left. What can also be seen (Fig.204) is that bontebok is smaller than blesbok (in terms of size).

Metric statistical analysis

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
GLpe	5.444	.278	.080	12	4.930	5.780	0
SD	1.070	.102	.029	12	.930	1.290	0

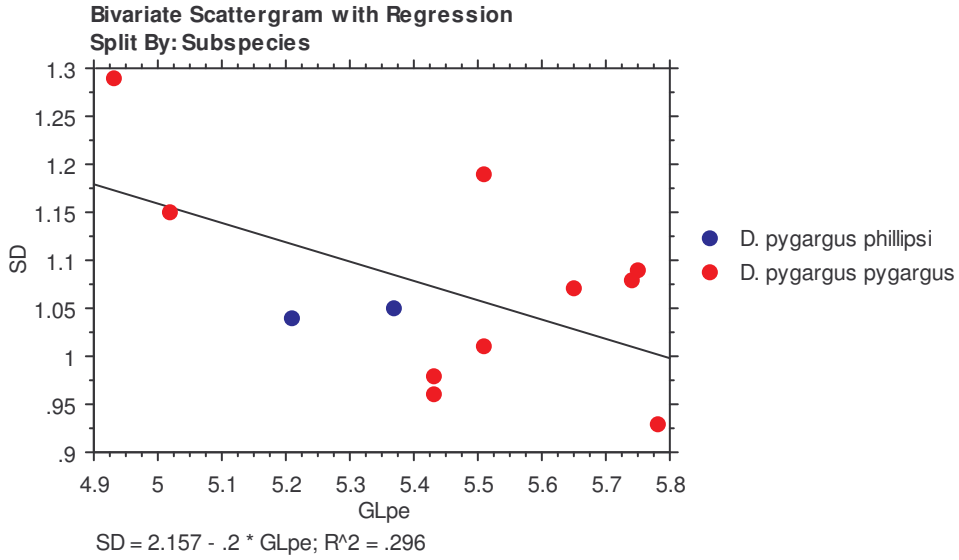


Figure 205: Bivariate analysis showing the greatest length of the peripheral (abaxial) half versus the smallest breadth of the diaphysis of the first phalanx showing the regression of both groups.

Descriptive Statistics

	Mean	Std. Dev.	Std. Error	Count	Minimum	Maximum	# Missing
Bp	1.642	.074	.021	12	1.510	1.770	0
Bd	1.413	.054	.016	12	1.310	1.480	0

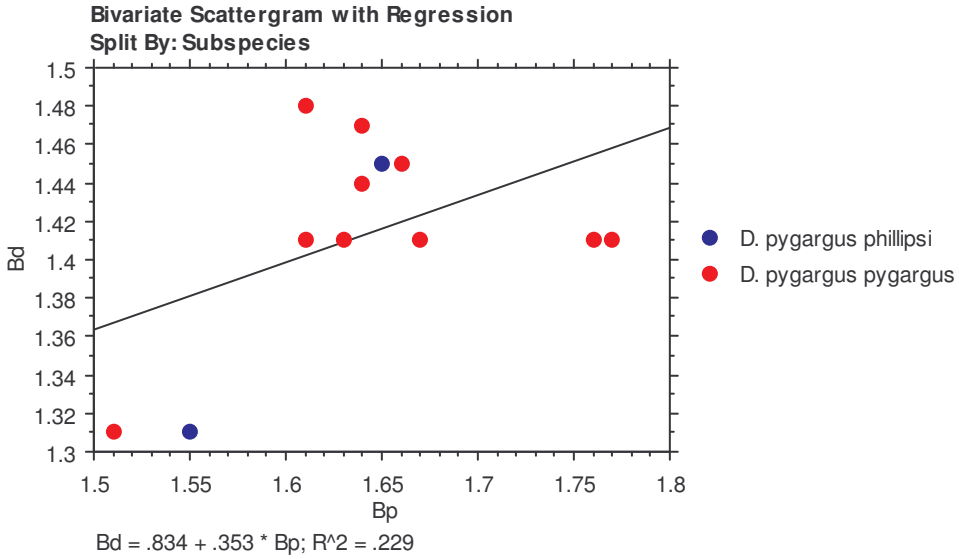


Figure 206: Bivariate analysis of the proximal breadth versus the distal breadth of the first phalanx showing the regression of both groups.

CHAPTER FOUR: DISCUSSION

4.1 Morphological Analysis

When looking at the cranial morphology of both bontebok and blesbok, there are some differences. These differences were expected since these animals are found in different terrains and experience different stresses. They are both grazing animals but eat different kinds of vegetation (bontebok preferring short grass, and blesbok preferring sprouting grass appearing after a burn) (Smithers, 1983). The difference in their cranial morphology could also be due to the fact that these two animals live in different terrains as mentioned earlier on (with bontebok found in the Cape, and blesbok found in the African Highveld) (Smithers, 1983).

Differences can also be seen in their mandibles, and this could partly be due to their diet. That of bontebok has a sharper gonion caudale, and this could be showing their differences in their diet (whereby maybe one of the subspecies has to do a lot of chewing, whilst the other can get away without chewing that much).

The post-cranial morphology, also shows some differences between the two animals, whereby in most cases, bontebok is robust and blesbok a bit small, this was highly unexpected since it has been documented or proposed rather by Smithers (1983) that blesbok is bigger than bontebok. This could again, be due to the different terrains they occupy, and the different stresses they encounter in their habitats. Since blesbok are found in the Highveld, a relatively dry biome, it could have resulted in the blesbok becoming smaller in response to more harsh conditions. Bontebok, on the other hand, is

found in a moist place, and therefore, can afford to be bigger as they don't have to conserve extra energy for survival.

The mean maximum temperature of the Highveld is between 21°C and 25°C, whilst the mean minimum temperature is between 3°C and 6°C (www.routes.co.za). Rainfall occurs in summer and it ranges between 400 mm and 900 mm annually. There have been reports of extreme temperatures in the past, with a record of 38°C in the summer, and -11°C in winter (www.routes.co.za).

Temperature of the Cape Agulhas (Bredasdorp) on the other hand, seldom exceeds 30°C, except in the interior valleys, and rain occurs in winter ranging between 300 mm and 750 mm annually (www.routes.co.za).

While there are minor morphological differences, statistical analyses tell a different story, and this will be discussed below in detail.

4.2 Statistical Analyses

When looking at the analysis of the cranial measurements, it is clear in most graphs (discussed briefly below) that bontebok and blesbok are different, as it was discussed earlier on in the morphological analysis.

Figure 34 shows that the distances from the basion to the prosthion, and that from the basion to the premolare are quite small in *D. pygargus pygargus* as they are below the

regression line, whilst those of *D. pygargus phillipsi* are above the regression line (in some cases, they are clustering together).

However, there is one specimen of *D. pygargus phillipsi* which is below the regression line, and this could mean that the above mentioned lengths are almost similar to those of *D. pygargus pygargus.* This could also mean that, since there has been a problem of hybridisation, this could be one of those specimens, i.e. a hybrid. It could also mean that when this specimen was found, it was wrongly classified, or it could be that it was catalogued wrongly.

The post-cranial statistical analysis, however, tells a different story from the morphological analysis. Since these groups of animals are classified as subspecies in the literature, I assumed that osteological differences between them would be small, but significant enough to distinguish them.

However, slight differences were recorded in the femur, patella, talus, calcaneus, scapula, ulna, atlas, and the axis, outliers include the female blesbok. In the metatarsal, and the radius, the outlier is a female bontebok.

These differences are minor and they occur with regularity presumably in the same individual, and this could be the result of hybridisation, as specimens studied here were presumed to be “pure” though this could not be assured since there is no documented difference between the “pure” ones and the hybrids.

Small differences, however, can be seen in the tibia, humerus, and metacarpal statistical analyses; the results vary quite a lot when looking at the above mentioned elements. Outliers can also be seen within these elements, with the tibia having bontebok as an outlier (male), and both humerus and metacarpal having a female blesbok as an outlier.

The differences found between the two animals are not that significant in other parts of the body. However, some parts like the femur, patella, tibia, scapula, axis, humerus, radius and the metacarpal, show that there are differences in these animals' osteology. However, division into subspecies may be geographically defined, or probably based on the external appearance since some of these animals' bones are not that different. As it has been discussed earlier, geographically, the animals are found in different terrains; bontebok prefers a mountainous habitat whilst blesbok prefers a "flat" habitat, they therefore experience different stresses, which should be reflected in bones (Vrba, 1995).

When one accounts for the size difference (refer to the table above where bontebok stands at 90 cm, and blesbok at 95 cm at the shoulder), there are no significant differences in their distal limb morphology. This is unexpected because one would expect environmental factors to play some role in distinguishing them. At the very least, and in the absence of adaptive evolutionary changes, one would expect pathology in distal limbs of those in a terrain new to them.

When looking at the species concepts, it can be said the best species concept that can describe the division into subspecies, even though there are osteological differences, is the Biological Species Concept, which states that species are organisms that interbreed but are reproductively isolated from other such groups (Coyne & Orr, 2004). Bontebok and blesbok do interbreed, and they produce fertile offspring (Skinner & Chimimba, 2005), and this means that they should be considered as a single species (which

reinforces their designation as subspecies), according to the biological species concept. Even though osteologically indistinguishable, the phenotypic signature in these animals is extremely important, and clearly responsible for mate recognition and the division into subspecies.

The species *D. pygargus* is present in almost all the glacial deposits on the Cape coastal zone, but toward the end of the Late Pleistocene, with the return of high sea levels, all the plains-living forms became extinct because of the reduction of the coastal plains habitat to a narrow strip that it is today (Deacon, *et al.* 1984). *D. pygargus pygargus* is the only plains living form that occurs today in the Cape coastal zone, suggesting that *D. pygargus pygargus* is the surviving form of *D. pygargus* or the glacial relic.

Regarding the two hypotheses posed: the first hypothesis stating that there are osteological differences between the two subspecies is rejected, since the differences are not that significant between the bontebok and blesbok. Subsequently, the second hypothesis, which states that if there are osteological differences, then these differences may be the outcome of speciation, caused by geographical barriers during the Late Pleistocene glaciation does not hold based on osteological information. However, considering that the two groups mate, and produce fertile offspring (Skinner & Chimimba, 2005), shows that in accordance with the biological species concept, they are not distinct. Even though the osteology does not reflect significant differences, the geographical barrier posed by the mountains during glacials remains the most parsimonious explanation for the speciation event.

CHAPTER FIVE: CONCLUSION

Based on the results presented here, differences found in the osteology of these subspecies are not significant. Osteology cannot therefore be relied upon to differentiate between the samples of skeletal remains of these animals. What drove the speciation event is unknown, though the most likely scenario is one of geographical boundaries causing the isolation of the two populations, i.e. Allopatric speciation, most likely caused by the Cape Fold Mountains during the glacials, as proposed by Brink (1993, 2005), where he suggested that bontebok may be the last surviving remnant of dispersals of open grassland ungulates from the interior onto exposed continental platforms during glacials, when sea levels were lower.

In conclusion, it can therefore be said that bontebok and blesbok are similar osteologically but different phenotypically (the outer appearance). It can be assumed that extant animals produce fertile offspring, and therefore, the division into subspecies is questionable. The species concepts cannot be applied to the osteological remains and hence potential fossil record considering the skeletons shows no significant differences. It can also be concluded that even though the specimens collected for this study were assumed to be “pure”, we are not sure about that because of this hybridisation problem amongst these subspecies, and again some of them were probably catalogued incorrectly since there are no differences between the osteological remains of the two subspecies.

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