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Systematics of the Tribe Hippotragini (Cetartiodactyla: Bovidae)

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The tribe Hippotragini consists of the so-called “Horse-like” antelopes, a specious group of large grazing antelopes characterized by striking facial coloration, thick tapering necks, erect manes, and highly specialized for arid regions of Africa and the Arabian Peninsula. Overwhelming genetic, morphological, and paleontological data agree that they consist of a monophyletic group (Lydekker 1908; Shortridge 1934; Simpson 1945; Ansell 1971; Turner and Antón 2004; Price et al. 2005; Wilson and Reeder 2005; Prothero and Foss 2007; Groves and Grubb 2011; Arif et al. 2012; Bibi 2013; Kindgon and Hoffman 2013; Kopecna et al. 2013). Historically, hippotragin antelopes were considered to be a separate subfamily within Bovidae but current molecular evidence suggests that they are best relegated to a tribal level within the subfamily Antilopinae: one of two subfamilies within the Family Bovidae (Mathee and Davis 2001; Kuznetsova et al. 2002; Hassanin and Douzery 2003; Ropiquet 2006; Hassanin et al. 2012; but see Rebholz and Harley 1999; Hernández Fernández and Vrba 2005). Further, the members of this tribe form a clade with the Alcelaphini (wildebeests and hartebeests) and the Caprini (goats and allies) (Hassanin and Douzery 2003; Hernández Fernández and Vrba 2005; Ropiquet 2006; Hassanin et al. 2012; Kopecna et al. 2014).

Hippotragini consists of three genera: *Addax+Oryx*, and *Hippotragus* and currently includes eleven species although that number might increase as more molecular studies are undertaken (Alpers et al. 2004; Pitra et al. 2006; Groves and Grubb 2011; Elmeer et al. 2012). Members of this group are further characterized by the presence of pedal glands on all four feet, 2 pairs of mammae, no inguinal glands, distinct face patterns, and small or absent face glands and ethmoid fissure. In all species, both sexes have horns (Ansell 197; Kindgon and Hoffman 2013). As antelopes specialized in harsh arid conditions, all species have very high-crowned hyspdont teeth and a bending braincase to maximize grazing efficiency (Prothero and Foss 2007) and employ a highly efficient thermoregulation mechanism "nasal sweating" to effectively cool their bodies and prevent water loss (Kingdon and Hoffman 2013). All species are gregarious and form mostly small herds. The IUCN reports that most species are declining; 1 species has become extinct in historic times, 2 more became extinct in the wild, and four are threatened or endangered (IUCN 2014).

Checklist of Hippotragini with Authorities (classification from Groves and Grubb 2011)

Tribe Hippotragini Sundevall 1845

- Genus *Hippotragus* Sundevall 1845
  - *Hippotragus leucophaeus* (Pallas 1766)-Blaubok
  - *Hippotragus equinus** (Desmarest 1804)-Roan Antelope
  - *Hippotragus niger*^ (Harris 1838)-Southern Sable
  - *Hippotragus roosevelti* (Heller 1910)-Roosevelt's Sable
- Genus *Addax* Rafinesque 1815
  - *Addax nasomaculatus* (de Blainville 1816)-Addax
- Genus *Oryx* de Blainville 1816
  - *Oryx beisa* (Rüppell 1835)-Beisa Oryx
  - *Oryx gallarum* Neumann 1902-Galla Oryx
  - *Oryx callotis* Thomas 1892-Fringe-eared Oryx
  - *Oryx gazella* (Linnaeus 1758)-Gemsbok

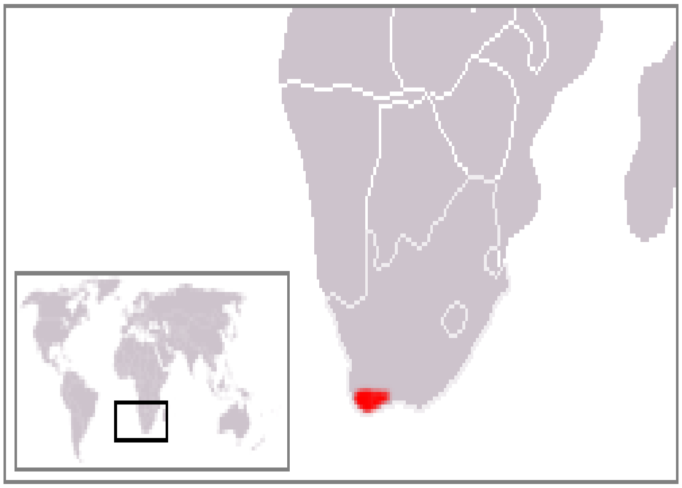
Oryx dammah Cretzschmar 1826-Scimitar-horned Oryx

Oryx leucoryx (Pallas 1777)-Arabian Oryx

*This species may soon be split into 2 species: *Hippotragus equinus* (Eastern Roan Antelope) consisting of populations in eastern, central, and southern Africa and a western species *Hippotragus koba* (Western Roan Antelope) (Robinson and Alpers 2001; Alpers et al. 2004; Groves and Grubb 2011).

^This species includes several distinct genetic/morphological lineages that may represent individual species: *Hippotragus kirkii* (Zambian Sable) and *Hippotragus variani* (Angolan or Giant Sable) (Pitra et al. 2006; Jansen van Vuuren 2010; Kingdon and Hoffman 2013).

***Hippotragus leucophaeus* (Blaubok, Bluebuck or Blue Antelope)**



http://www.wildafrica.sk

http://en.wikipedia.org/wiki

Shoulder Height: 115-120 cm

Total Body Length: 230-300 cm

Weight: approximately 160 kg

The Blaubok or Blue Buck was the smallest member of the genus *Hippotragus*. So named for its distinctive bluish coat, this species was hunted to extinction in 1800. The last know refuge for this species was mountains between Swellendam and Algoa Bay (Lydekker 1908). This species was known to occur in South Africa along the Cape, with prehistoric distributions reaching as far north as Elands Bay (Groves and Grubb 2011). Cytochrome b analyses on one of the few remaining skins found the Blaubok to be sister to the other species of *Hippotragus*. Paleontological evidence suggests that the Blaubok had been naturally declining since the onset of the Pleistocene (Nowak 1991).

***Hippotragus equinus* (Roan Antelope)**

http://www.eg-pic.com

http://www.ultimateungulate.com

Shoulder Height: 126-145cm

Total Body Length: 225-290 cm

Weight: 260-300 kg

A massive antelope, the Roan Antelope is the largest member of Hippotragini and one of the largest species of antelope. In Africa only elands are larger (although the Bongo is more massive) (Kingdon and Hoffmann 2011). This species is characterized by relatively short, heavy horns, large ears, and tufts of long white hair below the eye. It also departs from other hippotragin antelopes by having a reduction of typical face markings (Lydekker 1908). Roan

Antelopes are found primarily in grassland and tree savanna especially in association with *Brachystegia*/*Isoberlinia* wooded savannah. They prefer more open areas than other sympatric *Hippotragus* species and selective graze poor nutrient grasses to prevent competition from other herbivores and avoid predators (Estes 1991). Small herds (5-20) individuals are comprised mostly of cows and young; young males form small bachelor herds which eventually give way to solitary, older, territorial bulls. Under favorable conditions, females birth approximately every 10 months (Kingdon and Hoffman 2011).

Hippotragus niger **(Southern Sable)**

http://ridingsouthafrica.com

http://www.scirecordbook.org

Modifications by Holland

Shoulder Height: 120-140 cm

Total Body Length: 250-320 cm

Weight: 220-260 kg

The Sable Antelope is a striking species with strongly dimorphic coloration and horn size. Males are typically jet black with white markings and massive curved horns, while females are dark brown with white markings and shorter horns although in southern forms the females are also black. This species is prized by hunters for the magnificent horns which reach over 160 cm in some individuals (Kingdon and Hoffmann 2011). Like the Roan antelope, this species is often in association with certain plant communities, in particular *Brachystegia* woodland. Sable

Antelope prefer light canopy and forest edge over open areas and also browse more than any other species of Hippotragini; in this way they avoid competition with the Roan Antelope where they occur sympatrically (Nowak 1991). This species is more gregarious than the Roan Antelope and occurs in larger herds composed of females and young. Otherwise sex structure and reproduction is similar to the Roan Antelope (Estes 1991).

Hippotragus roosevelti **(Roosevelt's Sable)**

http://rickandlynnedwardsphotography.com http://www.scirecordbook.org

Shoulder Height: 110-117 cm Modifications by Holland

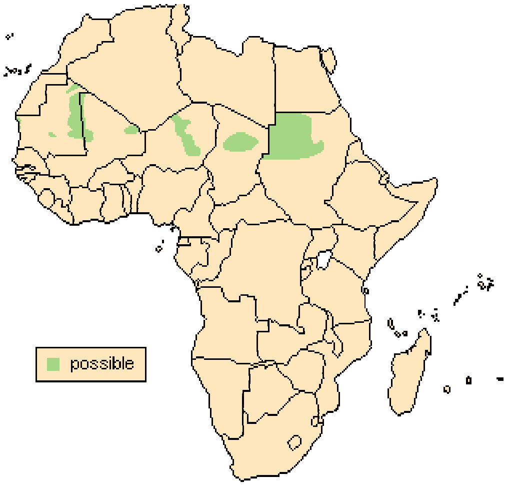
Total Body Length: 200-215

Weight: 200-220 kg

Little is known about the biology and life history of the Roosevelt's Sable as it was only recently recognized as a species separate from *Hippotragus niger*. Thus, most inferences about behavior and ecology are probably similar to the Sable Antelope. It was, however, known as a distinctive subspecies for many years and has many particular characteristics that set in apart from its conspecifics. In particular, Groves and Grubb (2011) points out that this species is noticeably smaller than the other sables with shorter horns, and females are characterized as being reddish in color. The Roosevelt's Sable is isolated from other species of *Hippotragus* by the Kigani River in the south and is thought to be restricted to Tanzania (Ansell 1971).

Addax nasomaculatus (Addax)

http://en.wikipedia.org/wiki



http://www.ultimateungulate.com

Shoulder Height: 100-110 cm

Total Body Length: 150-210 cm

Weight: 80-135 kg

The Addax is the most unique member of the Hippotragini tribe and is characterized by being predominately white in color and the only species in the tribe to have twisted horns. Along with the camels (*Camelus*), the Addax is the most perfectly adapted large mammal on the planet to desert habitats and derives all moisture from the scant vegetation it forages (Eisenberg 1981). It is found in all major Saharan desert habitats. Among its adaptations to desert life, the Addax has broad spatulate hoofs and protruding false hooves which help it to move unencumbered through deep sand dunes, a barrel-shaped body that reduces surfacearea/volume ratio and extremely dry waste production (Nowak 1991; Kingdon and Hoffmann 2013). Herd size is small (<20 members) and contains both sexes of all ages but is lead by a single old male, with an age based dominance hierarchy (Nowak 1991). Reproduction structure is strongly tied to the availability of food. Although nomadic, Addax generally migrate in longitudinal patterns (Nowak 1991). This species is critically endangered in the wild with an estimated 300 individuals left (IUCN 2014).

Oryx beisa **(Beisa Oryx)**

http://photos.safaribookings.com

http://www.scirecordbook.org

Modifications by Holland

Shoulder Height: 110-120 cm

Total Length: 198-220 cm

Weight: 115-210 kg

The Beisa Oryx was, until recently, treated as a subspecies of the Gemsbok (*Oryx gazella*), but numerous morphological (Kingdon 1997; Groves and Grubb 2011; Kingdon and Hoffman 2013), karyotypic (Kumamoto et al. 1999) and molecular (Masembe et al. 2006; Osmers et al. 2012) data have shown it to be one of several unique species formally included within *O. gazella*. Several characteristics that distinguish the Beisa Oryx include a prominent ochraceous wash over the dorsal pelage (Groves and Grubb 2011), no throat or ear tufts, proportionally smaller horns than other species (Lydekker 1908), ears with a small, but prominent black tip (Kingdon and Hoffman 2013), and a proportionally shorter toothrow (Groves and Grubb 2011). This species, like all members of the genus *Oryx,* produces males with incredibly tough shoulder skin to prevent fatal stabbing during duels with other males. The skin is so thick and tough that it is used as a shield cover by native tribes (Sclater and Thomos 1899; Lydekker 1908; Shortridge 1934). Beisa Oryx are found primarily in arid regions of Ethiopia and the Horn of Africa, with some populations occurring in Kenya and southeastern Sudan (Kingdon 1997; Kingdon and

Hoffman 2013). The Beisa Oryx prefers open, semi-arid grasslands and avoids wet ground and heavy cover. Herds are comprised of both males and females, with each sex forming a separate dominance hierarchy determined by ritualized sprints and posturing. Such herds are dominated by a large bull but herd movement is dictated by dominant cows. Young remain within the herd (Kingdon 1997).

Oryx gallarum **(Galla Oryx or Neumann's Oryx)**

https://www.flickr.com

http://www.scirecordbook.org

Modifications by Holland

Shoulder Height: 110-120 cm

Total Body Length: 200-220

Weight: 115-210 kg

The Galla Oryx (*Oryx gallarum*) was originally described as a species (Neumann 1902) but was subsequently relegated to a subspecific rank by other authors (Lydekker 1908; Ansell 1971; Wison and Reeder 2005). However, increased morphological, karyotypic, and molecular data suggests it is a separate species (Groves and Grubb 2011). Little is known about the biology and life history of the Galla Oryx as it was only recently re-recognized as a species separate from *Oryx beisa*. Thus, most inferences about behavior and ecology are probably similar to the Beisa Oryx. Several distinct characteristics set the Galla Oryx apart from its conspecifics including proportionally longer hooves (Lydekker 1908) and a much paler coat and markings (Groves and

Grubb 2011). The Galla Oryx prefers arid scrubland and has a distribution that includes Central Ethiopia, Sudan, and parts of northeastern Uganda and Somalia (Ansell 1971). The Tana River appears to be a natural divide between this species and the Fringe-eared Oryx (*Oryx callotis*) (Lydekker 1908; Ansell 1971; Groves and Grubb 2011; Kingdon and Hoffman 2013).

***Oryx callotis* (Fringe-eared Oryx)**

http://www.burchellgoldenoryx.com

http://www.scirecordbook.org

Modifications by Holland

Shoulder Height: 110-120 cm

Total Length: 200-230 cm

Weight: 116-210 kg

The Fringe-eared Oryx (*Oryx callotis*) is a distinctive looking species formally included within *Oryx beisa*. However, recent studies (Groves and Grubb 2011; Lee et al. 2013) reaffirm the Fringe-eared Oryx is a unique species. The most distinguishable morphological character for this species is the extraordinarily large ears tipped with long hair fringes that give this animal its name. Additional characteristics include a reddish-brown pelt, reduced dorsal stripe, comparatively broad skull, and thicker horns (Groves and Grubb 2011; Lee et al. 2013). The Fringe-eared Oryx is found on arid plains and scrubland in southeastern Kenya and northeastern Tanzania (Estes 1991; Kingdon and Hoffman 2013). The Fringe-eared Oryx is separated from the Galla Oryx in the north by the Tana River and the Aberdare Mountains in southern Kenya (Stewart and Stewart 1963; Ansell 1971). The Fringe-eared Oryx occurs in larger herds than other *Oryx* species, but has a similar social and mating structure as the Beisa Oryx (Lee et al. 2013).

***Oryx gazella* (Gemsbok)**

http://www.safari-guide.co.uk/ http://www.scirecordbook.org

Shoulder Height: 117-138 cm

Total Body Length: 220-240 cm

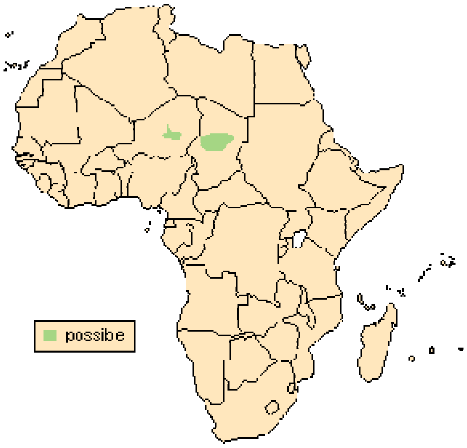
Weight: 180-240 kg

The Gemsbok (*Oryx gazella*) is the largest and most powerfully built of the *Oryx* species and is the only species currently found in southern Africa. Gemsbok are characterized by prominent facial markings, a large black flank stripe that extends from the elbow to the belly, a large dewlap containing a hard kernel of fleshy matter, a long bushy tail, no ear tufts, and extremely long, straight horns (Shortridge 1934; Lydekker 1908; Kingdon and Hoffman 2013). Endemic to southern Africa, this species is distributed from the Great Karoo through the Kalahari Desert south of the Cunene and Zambezi Rivers through southwest Angola (Lydekker 1908; Kingdon and Hoffman 2013). This species occurs primarily in semi-desert plains with scattered woodlands and is among the most heat tolerant of all large mammals (Estes 1991). Gemsbok form large herds comprised of both males and females. Unlike other *Oryx* species, males employ three different social strategies:

some non-territorial males stay with a herd throughout the year; others form territories and fight males/mate with females in mixed herds that pass through their territory; and other males don't establish territory but command harems that migrate within a herd (Estes 1991). Consequently, aggression with Gemsbok is particularly high and fights to the death are not unheard of. Additionally, wounded Gemsbok are dangerous animals and have been known to wound or kill other animals including lions (Lydekker 1908; Estes 1991). Calves are born throughout the year but generally coincide with the peak wet season (Kingdon and Hoffman 2013).

Oryx dammah (Scimitar-horned Oryx or Dammah Oryx)

http://www.takepart.com



http://www.ultimateungulate.com

Shoulder Height: 110-125 cm

Total Body Length: 235-280 cm

Weight: 135-140 kg

The Scimitar-horned Oryx (*Oryx dammah*) is the most unusual member of the genus *Oryx*. They are characterized by having a striking cream body with red neck, black eyes, lips and nostrils, a small preoribital gland, comparatively small teeth, and distinctive curved, ridged horns (Groves and Grubb 2011; Kingdon and Hoffman 2013). This species formally occurred over much of north central Africa including Algeria, Chad, Egypt, Libya, Morocco, Niger, Senegal, Sudan, and Tunisia where it grazed on desert vegetation (Wilson and Reeder 2005). This species was practically hunted to extinction by the 1940s due to poaching and habitat degradation due to overgrazing (Newby 1978). Scattered reports of individuals continued in remote areas until the early 1980s (Kingdon and Hoffman 2013). The ICUN officially declared the species 'Extinct in the Wild' in 2000 (IUCN 2014). Fortunately, the Scimitar-horned Oryx has a healthy captive population and as part of long-term reintroduction programs have been released in protected areas in Morocco, Sengal, and Tunisia (IUCN 2014). Paleontological evidence suggests that the species might have been recovering from a bottleneck due to climatic change since the middle of the Pleistocene (Newby 1978). Historical data suggests that Scimitar-horned Oryx was also more social than other *Oryx* species and followed migration routes along the Sahara in the thousands (Lydekker 1908). Captive observations show this species occurs in mixed herds that are male dominated by size and age (Newby 1974). Caving follows times of favorable climatic and nutritional conditions every 8-10 months (Newby 1978).

***Oryx leucoryx* (Arabian Oryx)**

http://s.radar.oreilly.com

http://www.nhm.org

Shoulder Height: 80-100 cm

Total Body Length:

Weight: 65-75 kg

The Arabian Oryx (*Oryx leucoryx*) is the smallest member of the Hippotragini and the only species that occurs outside of Africa. This species is characterized by having a small build, white body with brown legs, brown facial markings, smaller skull and toothrow, and shorter, more slender horns than other *Oryx* species (Groves and Grubb 2011). The Arabian Oryx was formally found throughout the Middle East in Iraq, Israel, Jordan, Kuwait, Oman, Saudi Arabia, Syria, and Yemen and its western most range included the Sinai Peninsula of Egypt (Wilson and Reeder 2005). The last wild specimens were killed in Oman in the early 1970s (Henderson 1974). Captive breeding populations have reintroduced the Arabian Oryx in parts of Oman and Saudi Arabia in the 1980s where they are now considered Vulnerable due to increased protection and conservation efforts (Khan et al. 2011; Elmeer et al. 2012; IUCN 2014,). Arabian Oryx prefer open rocky country along the edge of deserts where arid plant diversity is highest. This species is highly nomadic and small groups led by dominant males follow rainfall to succulent vegetation. Birthing is dictated by vegetation growth, and most females give birth to only a single young a year (Jungius 1978).

Taxonomic History of Genera and Species Within Hippotragini

In George Gaylord Simpson's paramount work, 'The Principles of Classification and a Classification of Mammals' (1945), he remarked:

"With the possible exception of some rodents, this [Bovidae] is the most difficult of all mammalian families from a taxonomic point of view" (pg 287).

Although recognized as a natural group for over one hundred years, the taxonomy within and among the hippotragin antelopes has certainly lived up to those prophetic words. Hippotragin antelopes (*Addax* and *Oryx* in particular) are some of the earliest animals recorded in written history. The Book of Deuteronomy, written around 1406 B.C., chronicles animals that were considered clean to eat and included the d⍰shon (Addax) and the yáhmûr (Arabian Oryx) among them. Oryx are also considered to be one of the primary contenders (along with the rhinoceros) for the legend of the unicorn, and as such, have appeared in countless beastiaries during the Middle Ages (albeit with some cosmetic changes) (Lavers 2009). Due to the convoluted history of this group, the taxonomic history for hippotragin antelopes will be broken down at the subfamily/tribe level first, followed by the genus and species name histories. See appendix 1 for a primary taxonomic history and breakdown.

Hippotraginae/Hippotragini and Genera:

Linnaeus (1758) erected the order Pecora to describe mammals with cloven hoofs and four stomachs. In this order he included antelopes, camels, cattle, deer, giraffes, goats, musk deer, and sheep. In particular, he placed the Gemsbok in *Capra* as *Capra gazella* and included with it various other species of antelope and goat. Pallas (1777) removed the Gemsbok from *Capra* and placed it in *Antilope* along with reedbucks, gazelles, and several other antelopes that would eventually be part of Hippotraginae including the Roan Antelope and the Scimitar-horned Oryx on the basis of various anatomical differences. Increases in technological and scientific exploration led to an influx of new species in the late 1700s based primarily on morphological differences such as color or horn size and shape. Pallas was at the head of this revolution and named several species of oryx, including *Oryx leucoryx* (1777). As exploration and scientific curiosity pushed across Africa, other species of antelope were discovered and named, including the Roan Antelope (Saint-Hilaire 1803) and the Addax (Rafinesque 1815). At this time, all antelopes belonged to *Antilope (Antelope).* As the number of antelope species increased, the resulting complexity of antelope diversity made it difficult to contain to a single genus.

Perhaps the most important contributions in the mid-1800s were made by Swedish zoologist Carl Jakob Sundevall who erected *Hippotragus* (1845) for the Roan and Sable Antelopes, a name that was given preference over a slew of other, older suppressed names including: *Aegocera* (1827); *Aigererus* (1838); *Aigocerus* (1827); *Egocerus* (1822); *Oegocerus* (1842); and *Ozanna* (1845) (Wilson and Reeder 2005). This was incredibly important for two reasons: first, it provided a framework for differentiating antelope into separate genera based on morphological and behavioral differences; these inferences led other zoologists to do the same and allowed for the re-recognition of *Addax* (de Blainville 1816) and *Oryx* (de Blainville 1816). Second, the recognition of *Addax, Hippotragus,* and *Oryx* resulted in the acknowledgement of a new subfamily or tribe, which was eventually called Hippotraginae or Hippotragini (Sundevall 1845).

While the names Oryginae (Brooke 1876) and *Cerophorus* (de Blainville 1816) for the Addax were briefly proposed and subsequently abandoned, nomenclature at the genus level and above remained mostly stable throughout the 1800s and early 1900s. Flower and Lydekker (1891), Schlater and Thomas (1894-1900), and Pocock (1910; 1919) recognized Hippotraginae as a subfamily and also placed *Addax, Hippotragus,* and *Oryx* within its ranks. Shortridge (1934) rejected the name Hippotraginae and instead used Oryginae, believing Brooke's (1876) name had preference. The next crucial step in understanding hippotragin taxonomy occurred when Schlosser (1904; 1923) reduced the number of subfamilies within Bovidae to two primary clades based upon studies of dentition: Boödontia (with the single subfamily Boviane), and Aegodontia (with all remaining bovid subfamilies). In this new scheme, Hippotraginae was reduced to a tribe in Boödontia and related to cattle and duikers and not to goats, gazelles, or wildebeests (Prothero and Foss 2007). Simpson (1945) presented the most complete synthesis at the time and included numerous fossil genera in his classification. He found Hippotraginae to encompass three tribes that were formally treated as subfamiles: Reduncini (Reduncinae, Alcelaphini (Alcelaphinae), and Hippotragini with *Addax, Hippotragus,* and *Oryx,* but remarked that the relationships within and among these groups was tentative. Simpson's classification remained the standard for hippotragin classification for nearly 50 years with only minor alterations at the tribal level (Ansell 1971; Eisenberg 1981; Honacki et al. 1982; Corbet and Hill 1986; Nowak 1999; Macdonald 2001). Gentry (1992; 2000) provided some of the last comprehensive morphological studies of Bovidae in which he found Hippotraginae to be comprised of Reduncini and Hippotragini and sister to Alcelaphinae.

Since that time, molecular studies have largely replaced morphological classifications, or at the very least, have been syntheses of molecular and morphological data (Gatesy et. al 1997; Groves and Grubb 2011). Current molecular evidence suggests that hippotragin antelopes are best relegated to a tribal level within Antilopinae: one of two subfamilies within the Bovidae (Mathee and Davis 2001; Kuznetsova et al. 2002; Hassanin and Douzery 2003; Ropiquet 2006; Hassanin et al. 2012; but see Rebholz and Harley 1999; Hernández-Fernández and Vrba 2005). Further, the members of this tribe form a clade with Alcelaphini and Caprini (Hassanin and Douzery 2003; Hernández-Fernández and Vrba 2005; Ropiquet 2006; Hassanin et al. 2012; Kopecna et al. 2014). The rejection of Aegodontia and Boödontia was caused by excessive reliance on tooth structure. It has been demonstrated that independent bovid lineages evolved convergent tooth structure to take advantage of new grassland niches as they appeared (Kingdon and Hoffman 2013).

Species within *Addax, Hippotragus,* and Oryx:

During the mid-1700s through the early 1900s, the number of new hippotragin species increased as more expeditions were mounted and more specimens were returned to Europe. Species were described due to arbitrary traits such as differences in pelt color or horn shape and often on just a few specimens. Giving new names to individuals based on morphological variation led to an inflation of species so that by the early 1900s more than twenty kinds of *Hippotragus,* four kinds of *Addax*, and almost thirty kinds of *Oryx* were recognized in some form (Wilson and Reeder 2005).

It soon became clear that a more rigorous classification was required as scientists realized with growing uncertainty that what constituted a species and the limitations it employed on race and variety was not well understood (Lydekker 1908). The emergence of the Biological Species Concept in Mayr (1942) did much to assuage those problems. Under a stricter criterion for species delimitations, many former species were abandoned as phenotypic variations within a single population or species. Individuals that were diagnosable but violated a rule under the Biological Species Concept (such as reproductive compatibility) were relegated to a subspecific status. The result was a drastic reduction in the perceived number of species (Groves and Grubb 2011). Ansell (1971) provided the most in-depth treatment of hippotragin species following the implementation of the Biological Species Concept and recognized the following species: monotypic *Addax nasomaculatus*; monotypic *Hippotragus leucophaeus*; *Hippotragus equinus* with provisional subspecies *H.e. equinus, H.e. cottoni, H.e. langheldi, H.e.bakeri, H.e. charicus,* and *H.e. koba*; *Hippotragus niger* with *H.n. niger, H.n. kirkii, H.n. roosevelti,* and *H.n. variani*; monotypic *Oryx dammah*; monotypic *Oryx leucoryx*; and *Oryx gazella* with *O.g. gazella, O.g. beisa, O.g. gallarum, O.g. annectens,* and *O.g. callotis*. This classification was followed through the 1970s until the use of molecular data became possible (Honacki et al. 1982; Corbet and Hill 1986; Wilson and Reeder 1993; Nowak 1999; Macdonald 2001).

Molecular data led to the resurrection of the Beisa Oryx as a species separate from the Gemsbok (Kumamoto et al. 1999; Masembe et al. 2006; Osmers et al. 2012). Additionally, the emergence of the Phylogenetic Species Concept as an important tool in describing species coupled with increasingly complex molecular and morphometric data has shown that, if anything, species diversity has been underrepresented for the last half century. This has cumulated in the discovery of new cryptic species and the elevation of subspecies to species rank (Groves and Grubb 2011), which is presented in the checklist of Hippotragini with authorities above.

Paleontology and Divergence Times

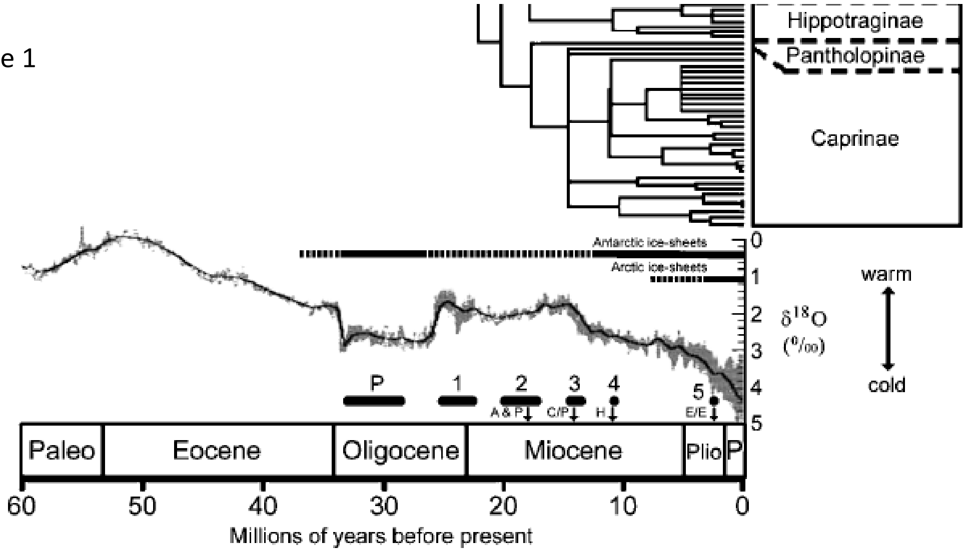
The first ancestors of the Hippotragini, Alcephalini, and Caprini evolved in Eurasia during the early Miocene (Simpson 1945; Turner and Antón 2004; Prothero and Foss 2007; Kingdon and Hoffman 2013, although see Geraads et. al 2008). Fossil genera including *Palaeoryx, Tragoreas, and Damalavus* were intermediates between Hippotragini+Alcephalini and Caprini (Prothero and Foss 2007). Late Miocene crown members of Hippotragini are found in Northern Africa and include *Tchadotragus* and *Saheloryx* (Geraads et al. 2008). It was not until the Pliocene that hippotragin diversity exploded in Eurasia as a response to cooling temperatures and the advancement of grasslands. This was due to continued continental uplift which caused a major expansion of C4 plant diversity (Turner and Antón 2004). Genera found in the lower Pliocene include *Leptotragus, Microtragus, Pachytragus,* and *Pseudotragus* exclusively in Europe; *Olonbulukia, Paraprotoryx, Prosinotragus, Sinoryx,* and *Sinotragus* exclusively in Asia; and *Hippotragus, Paleoryx, Protoryx,* and *Tragoreas* throughout Eurasia (Simpson 1945; Bibi et al. 2009). The late Pliocene marked a dramatic shift in hippotragin evolution as climate continued to cool and aridity increased, marking a major expansion of desert conditions during which *Addax* and *Oryx* first appeared (Turner and Antón 2004; Kingdon and Hoffman 2013).

Although species diversity plunged in Europe and Asia, with only *Hippotragus, Sivatragus,* and *Sivoryx* remaining, groups in Africa continued to evolve and thrive in response to desert conditions and included the genera *Addax, Hippotragus, Oryx* and *Praedamalis* (Simpson 1945; Turner and Antón 2004; Kingston and Harrison 2007; Prothero and Foss 2007) and by the

Pleistocene had expanded throughout northern, eastern, and southwestern Africa; *Oryx* re-entered Asia through the Arabian Peninsula (Turner and Antón 2004; Prothero and Foss 2007). By the end of the Pleistocene, all Asian hippotragin genera had gone extinct with the exception of *Oryx.* Several extinct species for extant genera are known. *Hippotragus* includes *H. gigas* and *Oryx* includes *O. silvalensis*, both of African Pliocene/Pleistocene ages (Mckenna and Bell 1997). No known fossil species are referable to *Addax*.

Molecular data largely corroborates fossil data (Mathee and Davis 2001; Hassanin and Douzery 2003; Hassanin et al. 2012). In all analyses, *Hippotragus* appears sister to an *Addax*+*Oryx* clade. However, molecular data disagrees with paleontological evidence by suggesting that *Hippotragus* began to differentiate into the species we know today during the Mid-Miocene at approximately 8.5 million years ago (Figure 1, Hernández-Fernandez and Vrba 2005) whereas the earliest definitive *Hippotragus* fossils do not appear until about 5 million years ago (Bibi et al.2009).

Figure 1



This is substantial because it suggests that *H. equinus*+ *H.leucophaeus* and *H. niger* diverged soon after Hippotragini was formed, and during the same time as *Addax* and *Oryx* began to diverge (Hernández-Fernández 2005; Kingdon and Hoffman 2013). Additional evidence for this is presented by Pitra et al. (2002) who found that *Hippotragus* species have some of the highest levels of genetic diversity rates known for any mammal. *Addax/Oryx* molecular data also corroborates fossil data. Molecular evidence extrapolated from Baysesian relaxed molecular clocks (Hassanin and Douzery 2003) corroborates the idea that the *Addax/Oryx* clade diversified as the Sahara Desert spread over northern Africa during the late Miocene/early Pliocene approximately 5 million year ago; *Addax* remained in the Sahara while *Oryx* diversified in the late Pliocene and Pleistocene in slightly less extreme desert and desert fringe niches (Kingdon and Hoffman 2013).

Phylogenetics and Comparative Analyses of Hippotragini

Many of the important classifications and criterion for hippotragin antelopes were mentioned above in the section on taxonomic history. However, several works are worthy of future elaboration as they are particularly important to the history of the phylogenetics of the group. One of the first major syntheses of hippotragin phylogenetics is found in the *Catalouge of the Ungulate Mammals in the British Museum* (Lydekker and Blaine 1914). Comprised of three volumes, Lydekker and Blaine’s catalogue developed keys to diagnose various genera of African mammals. In the case of hippotragins, the keys were based on easily diagnosable features such as hoof and horn shape as follows: normal, pointed hooves and straight horns for *Hippotragus* and *Oryx*; flat, rounded hooves and twisted horns for *Addax.* The horn angle was used to determine whether a species belonged to *Hippotragus* (vertically above orbits) or *Oryx* (behind orbits). Ansell (1971) provided the most complete review of Hippotragini phylogeny and morphological analyses in the 1970s but provided little original work.

Little has been published in the use of comparative analyses to explain character evolution. Ansell (1971) noted that morphology of the hoof shape serves as an important diagnostic feature with ecological ramifications: *Hippotragus*, a woodland/savanna species, has long pointed hooves idea for walking through grass, while the *Addax/Oryx* clade has broad, short hooves to help circumnavigate shifting gravel and sand without getting bogged down, with *Addax* being the most specialized among the clade.

When discussing phylogenetic relationships of the Hippotragini it is important to remember than each genus was clearly diagnosable, and has remained practically unchanged since its inception. Thus most of the reviews/works on the phylogenetic history of Hippotragini is rehashed from early works dating back to Flower (1883) and other authors (Lydekker and Blaine

1914; Simpson 1945; Ansell 1971; Wilson and Reeder 1993). Interrelationships among Hippotragini have been largely overlooked and most morphological studies of antelopes have been undertaken at the tribal or subfamily level involving increasing complex character states with mixed results (Janis and Scott 1988; Gatesy et al. 1992; and Hassassin and Douzery 2003). The most complete review of morphological phylogenies and species delimination among hippotragin species is based upon discriminant analyses of cranial characteristics (Groves and Grubb 2011). With the emergence of molecular data, Bovidae relationships have largely stabilized. Studies involving improved morphometrics and paleontological evidence (Mckenna and Bell 1997; Gentry 2003; Prothero and Foss 2007), endocrinology (Vrba and Schaller 2000), total evidence supertrees (Price et al. 2005) and mitochondrial and nuclear DNA markers (Gatesy and O'Leary 2001; Mathee and Davis 2001; Hernández-Fernández and Vrba 2005) have all confirmed that the tribe Hippotragini forms a clade with the wildebeests and goats: (Caprinae(Alcelaphini+Hippotragini))(Figure 2).

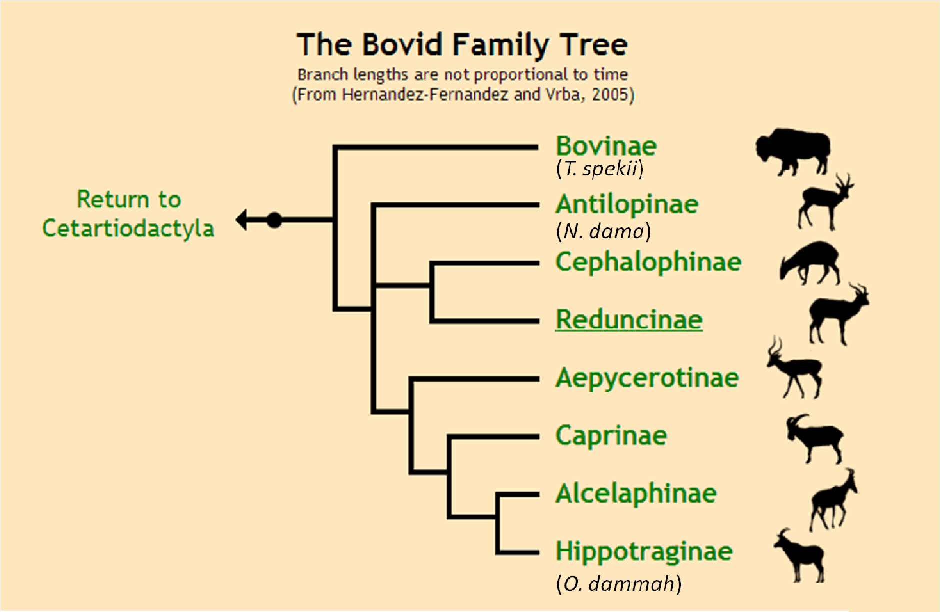


Figure 2 http://www.ultimateungulate.com/

Phylogenetics among Genera

An inclusive species-level phylogenetic hypothesis using supertree methodology consisting of 201 source trees consistently found *Hippotragus* to be sister to an Addax/*Oryx* clade (Price et al. 2005). Later support for this arrangement has been found utilizing complete mitochondrial genomes. Bootstrap percentages of maximum likelihood and Bayesian trees support a monophyletic Hippotragini (100%) with *Hippotragus* (82%) as a sister group to *Addax/Oryx* (100%) (Hassanin et al. 2012). The most recent tests of phylogeny among hippotragin genera provide further support; Bayesian analyses of full mitochondrial genomes with fossil calibration points produce MCC trees with high levels of support (100%) for (*Hippotragus(Addax/Oryx*) (Bibi 2013). A general tree of hippotragin relationships is provided below (Figure 3).

Phylogenetics Among Species

Hippotragus- Since the Blaubok (*H.leucophaeus*) is extinct, relatively little has been published on the relationship between it and the rest of *Hippotragus*. However, cytochrome *b* sequences extracted from mounted specimens suggest that the Blaubok is sister to the extant species (Robinson et al. 1996). For Roan Antelope (*H. equinus*), Groves and Grubb (2011) used discriminant analyses of cranial characteristics to suggest this species may soon be split into 2 species: *Hippotragus equinus* (Eastern Roan Antelope) consisting of populations in eastern, central, and southern Africa and a western species *Hippotragus koba* (Western Roan Antelope). A survey of 52 unique control region haplotypes found high support (100%) among Bayesian analyses of mitochondrial data for a split between eastern and western clades (Robinson and Alpers 2001). A later study utilizing additional mtDNA markers and nuclear DNA found similar results and supports (Alpers et al. 2004). Discriminant analyses of cranial characteristics for the Sable Antelope (*H. niger*) and Roosevelt's Sable Antelope (*H. roosevelti*) form a clade and are sister species to *H. equinus* (Groves and Grubb 2011). This correlated previous results which found strong support (100%) using mtDNA control regions (Matthee and Robinson 1999). Additional molecular support of mtDNA control region using larger and more geographically representative samples corroborated these findings with similar support (Pitra et al. 2002; Pitra et al. 2006). Several recent studies have found evidence for additional unique clades based upon high bootstrap support of mitochondrial DNA control (over 80% at 95% CI) suggesting that the genetic differences underpinning these evolutionary lineages may be more complicated than originally expected (Jansen van Vuuren et al. 2010; Groves and Grubb 2011).

Addax- All morphological and molecular evidence strongly suggests the single species of *Addax* is the sister group to *Oryx*. An inclusive species-level phylogenetic hypothesis using supertree methodology of morphological and molecular data consisting of 201 source trees consistently found *Addax* to be the sister group to *Oryx* (Price et al. 2005). Later support for this arrangement has been found utilizing complete mitochondrial genomes. Bootstrap percentages of maximum likelihood and Bayesian trees support *Addax* as the sister group to *Oryx* (100%) (Hassanin et al. 2012). The most recent tests of phylogeny among the *Addax/Oryx* clade provides further support; Bayesian analyses of full mitochondrial genomes with fossil calibration points produce MCC trees with high levels of support (100%) for *Addax*+*Oryx* (Bibi 2013).

Oryx- Phylogenetics and morphological studies among the six species supports a morphocline based phylogeny starting in Arabia and northern Africa and spreading south (Grubb 2000). Molecular data investigating the entire mitochondrial control region strongly supports (95% bootstrap support) the pairing of both desert species (*O. dammah* and *O. leucoryx*) as sister to the remaining African species (Iyengar et al. 2006). The most complete review of *Oryx* phylogeny investigated cytochrome *b*, 12S RNA, 16S RNA, and control region and found strong support for *O. leucoryx* to be sister to all African species (100% for maximum likelihood and neighbor-joining methods). Under maximum parsimony, there was less support (74%) with the placement of *O. dammah*; and was suggested as being as either grouped with *O. leucoryx* or with the remaining African species (Amer and Shobrak 2011). Among African species, control region and cytochrome *b* sequences suggest *O.gazella* is sister to the remaining three species; which roughly corresponds with morphological tests (Masembe et al. 2006; Groves and Grubb 2011).

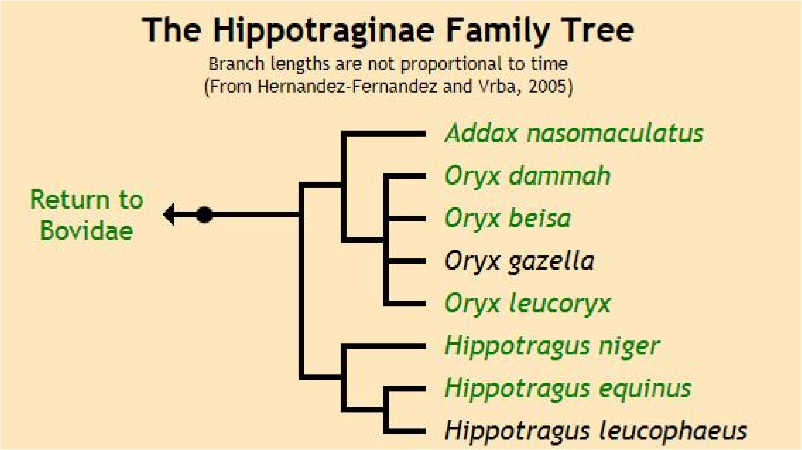


Figure 3 http://www.ultimateungulates.com/

Historical Biogeography

Historical biogeography has been discussed at some length earlier in conjunction with paleontology and divergence time estimates. In summary, it was not until the Pliocene that hippotragin diversity exploded in Eurasia as a response to cooling temperatures and the advancement of grasslands. This was due to continued continental uplift which caused a major expansion of C4 plant diversity and is corroborated with fossil data (Turner and Antón 2004). At the onset of the Early Pliocene *Hippotragus*, the ancestor of *Addax/Oryx,* and many other genera were present throughout Eurasia (Simpson 1945; Bibi et al. 2009). However, by the late Pliocene as climate continued to cool and aridity increased, major expansion of desert conditions began in Africa and the Middle East and as a result, species diversity plunged in Europe and Asia. However, groups in Africa continued to evolve and thrive in response to desert conditions and included the genera *Addax, Hippotragus,* and *Oryx* (Simpson 1945; Turner and Antón 2004; Kingston and Harrison 2007; Prothero and Foss 2007). Molecular data largely corroborates fossil data and geological data (Mathee and Davis 2001; Hassanin and Douzery 2003; Hassanin 2012) with the exception of the timing of when the modern species of *Hippotragus* begun to appear with some suggesting an early split during the Mid-Miocene based on molecular data (Hernández-Fernández and Vrba 2005) and others favoring a later split during the Pliocene based on fossil evidence (Bibi et al. 2009).

Increases in grass diversification and production led to the evolution of narrow muzzles and more selective feeding strategies in the *Hippotragus* species we see today (Turner and Antón 2004). Biogeography of these species is highly dictated by exploiting zones of impoverished fauna and flora (Kingdon and Hoffman 2013). Roan Antelopes are found primarily in grassland and tree savanna especially in association with *Brachystegia*/*Isoberlinia* wooded savannah. They prefer more open areas than other sympatric *Hippotragus* species and selectively graze poor nutrient grasses to prevent competition from other herbivores and avoid predators (Estes 1991). The range of this species reflects this pattern, with distributions occurring throughout central Africa in wooded habitats but not in desert or heavy jungle (Smith 1985). Similarly, Sable and Roosevelt's Antelope are also found in association with certain plant communities, in particular *Brachystegia* woodland. These species prefer light canopy and forest edge over open areas and also browse more than any other species of Hippotragini; in this way they avoid competition with the Roan Antelope where they occur sympatrically (Nowak 1991). A stronger preference for *Brachystegia* woodland restricts these species south of the equatorial rainforests (Smith 1985). Roosevelt's Antelope is restricted to Tanzania by several major river systems and has little overlap with conspecifics (Smith 1985). The Blaubok formally occurred in the south-western coast of Cape Providence (Ansell 1971). It has been suggested that its smaller size was a response to more impoverished areas than either the Roan or Sable Antelope could tolerate (Kingdon and Hoffman 2013).

Molecular evidence extrapolated from Baysesian relaxed molecular clocks (Hassanin and Douzery 2003) corroborates the idea that the *Addax/Oryx* clade diversified as the Sahara Desert spread over northern Africa during the late Miocene/early Pliocene approximately 5 million year ago. Fossil and archaeological evidence suggests that *Addax* occurred across the entirety of Northern Africa west of the Nile River until the end of the 19th century/early 20th century (Kingdon and Hoffman 2013).

Oryx are the most specious members of Hippotragini and diversified in the late Pliocene and Pleistocene in slightly less extreme desert and desert fringe niches than *Addax* but more extreme than habitat preferred by *Hippotragus*. That versatility appears to be a driving component of *Oryx* speciation (Kingdon and Hoffman 2013). By the Pleistocene they had expanded throughout northern, eastern, and southwestern Africa and re-entered Asia through the Arabian Peninsula (Turner and Antón 2004; Prothero and Foss 2007). *O. gazella* occurs exclusively in semi-arid brush/grassland of the Kalahari and Karoo in south-central and southwestern Africa (Kingdon and Hoffman 2013). East Africa is home to the largest number of species: *O. beisa, O. callotis,* and *O. gallarum*. Large river systems appear to play an important role as barriers between many species of *Oryx. O. gazella* is separated from other *Oryx* species by the Zambezi River. Species populations are strongly divided by the Tana River, with *O. gallarum* occurring south of the river and *O. callotis* occurring north of the river (Ansell 1971; Smith 1985; Kingdon and Hoffman 2013). *O. beisa* was historically found throughout Africa east of the Nile River to the Gulf of Aden (Smith 1985; Kingdon and Hoffman 2013). Not all species of *Oryx* were found in the eastern and southern parts of the continent. Two species were desert fringe specialists (Estes 1981). Although both species were declared "Extinct in the Wild" at one point, historical evidence suggests they once had much larger ranges (Kingdon and Hoffman 2013). *O. dammah* historically inhabited desert fringe habitat surrounding the Sahara Desert and bordered by the Nile River (Smith 1985; Kingdon and Hall 2013). *O. leucoryx* is the only species of hippotragin to recolonize Asia and was formally found through the Arabian Peninsula north to Jordan. There is no evidence to suggest this species was ever found in Africa (Groves and Grubb 2011; Kingdon and Hoffman 2013).

Biodiversity and Conservation

As a group, hippotragin antelopes are threatened primarily by habitat destruction. While populations of some species has stabilized due to intense management practices the problems associated with hybridization, small effective population size, and taxonomic uncertainty among populations formally considered as single species has put conservation efforts for many species in danger (IUCN 2014).

Hippotragus equinus- Status: Least Concern but with population trending downwards. There are an estimated 76,000 individuals in the wild with most occurring in protected areas. Habitat destruction and poaching are primary threats to the survival of this species. It should be noted that genetic studies suggest this species might soon be split into two species. If this happens, conservation efforts for these populations will alter (IUCN 2014).

Hippotragus leucophaeus- Status: Extinct. This species went extinct in 1800.

Hippotragus niger- Status: Least Concern with population trend stable. There are an estimated 75,000 individuals in the wild although the majority of them occur in protected areas or private property. Habitat destruction and poaching are primary threats to the survival of this species. Taxonomic changes have divided this species into two species but may be split into more as more genetic data emerges. If this happens, conservation efforts for these populations will alter. A distinctive form, the Giant Sable Antelope (*H.n. variani*) is particularly vulnerable to poaching and armed conflict (IUCN 2014).

Hippotragus roosevelti- Status: Unknown. The IUCN is currently working on management plans to reflect changes in the taxonomy of *Hippotragus* (IUCN 2014). This species has a limited distribution and is probably more sensitive to changes in its habitat than other species of *Hippotragus* which have much larger distributions.

Addax nasomaculatus- Status: Critically endangered with population trend decreasing. There are an estimated 300 individuals in the wild due to hunting and habitat loss. Increases in inbreeding is a major concern in highly fragmented populations. Habitat destruction is caused primarily by the addition of wells to water cattle which alter plant community and structure. Addax are keystone Saharan herbivores; it is unknown what impact this has on desert plant communities. More than 1600 Addax occur in zoos and breeding facilities and reintroduction efforts are ongoing (IUCN 2014).

Oryx beisa- Status: Near Threatened with population trend decreasing. There are an estimated 50,000 individuals in the wild. Major threats include poaching and habitat degradation. This species is considered to be more susceptible to threats because the majority of the individuals (83%) occur in unprotected areas. There are some populations in captivity (IUCN 2014).

Oryx callotis- Status: Vulnerable with population trend decreasing. There are an estimated 17,000 individuals in the wild. There are not any major threats for this species, as the majority of populations live in protected areas. Those that occur outside these sanctuaries are threatened by poaching and habitat destruction but to a lesser degree than other species of *Oryx* (IUCN 2014).

Oryx dammah- Status: Extinct in the wild. This species went extinct in the 1940s with the IUCN officially declaring the species 'Extinct in the Wild' in 2000. Fortunately, the Scimitar-horned Oryx has a healthy captive population and as part of long-term reintroduction programs has been released in protected areas in Morocco, Sengal, and Tunisia (IUCN 2014).

Oryx gallarum- Status: The IUCN is currently working on management plans to reflect changes in the taxonomy of *Oryx* (IUCN 2014). This species has a larger distribution and is probably less sensitive to changes in its habitat than other species of *Oryx* which have more restricted distributions.

Oryx gazella- Status: Least Concern with population trend stable or even increasing in some areas. There are an estimated 325,000 individuals in the wild although that number might be higher. There are not any major threats for this species. Its value as a trophy animal is cited as a major reason why this species is carefully managed to maintain high numbers (IUCN 2014).

Oryx leucoryx- Status: Vulnerable with population trend stable. There are an estimated 1000 individuals in the wild and approximately 6000-7000 individuals on managed game preserves throughout the Arabian Peninsula. This species was formally considered endangered but intense management practices and increased protection has allowed this species to enjoy a successful comeback. Major threats to wild populations include the live capture and reselling to private collectors. In some areas such as Oman, this has rendered the population virtually ineffective (IUCN 2014).

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Appendix 1

Primary taxonomic history/literature provided by Simpson (1945), Novak (1991), Reeder and Wilson (2005), Groves and Grubb (2011), and Kingdon and Hoffman (2013); species supplementation from Lydekker (1908), Shortridge (1934), Meester and Setzer (1971), Smith (1985), Alpers et al. (2004), Jansen van Vuuren et al. (2010), (Pitra et al. 2006), and Lee et al. (2013). Specific epithets in bold are subspecies currently recognized by Reeder and Wilson (2007) or Groves and Grubb (2011).

Hippotraginae Sundevall, 1845 or Hippotragini Sundevall, 1845

Oryginae Brooke, 1876

Adacina Pigrim, 1939

Hippotragus

Hippotragus Sundevall, 1845

Aegocera Berthold 1827 [suppressed]

Aegocerus Gervais 1859 [suppressed]

Aigereus Harris 1838 [*nomen oblitum*]

Aigocerus C.H. Smith 1827 [suppressed]

Egocerus Desmarest 1822 [suppressed]

Oegocerus Lesson 1842 [suppressed]

Ozanna Reichenbach 1845 [suppressed]

Hippotragus equinus (È. Geofroy Saint-Hilaire 1803)

aethiopica (Schinz 1821)

aurita (C.H. Smith 1827)

bakeri Heughlin 1863

barbata (C.H. Smith 1827)

cottoni Dollman and Burlace 1928

docoi (Gray 1872)

dogetti de Beaux 1921

gambianus Sclater and Thomas 1899

jubata (Goldfuss 1842)

koba (Gray 1872)

langheldi Matschie 1898

rufopallidus Neumann 1899

sharicus (Schwarz 1899)

truteri (J.B. Fischer 1829)

typicus Sclater and Thomas 1899

Hippotragus leucophaeus (Pallas 1776)

capensis (Müller 1776)

glauca (Oken 1816) [unavailable]

Hippotragus niger (Harris 1838)

anselli Groves 1983

harrisi (Harris 1839)

kaufmanni Matschie 1912

kirkii (Gray 1872)

roosevelti (Heller 1910)*

variani Thomas 1916

<u>*Hippotragus roosevelti* (Heller 1910)*</u>

Addax

Addax Rafinesque, 1815 [*nomen nudum]*

Cerophorus nasomaculatus de Blainville 1816

Antelope suturosa Otto, 1825

<u>*Addax nasomaculatus* (de Blainville 1816)</u>

addax (Cretzschmar 1826)

gibbosa (Savi 1828)

mytilopes (C.H. Smith 1827)

suturosa (Otto, 1825)

Oryx

Oryx de Blainville 1816

Capra gazella Linnaeus 1758

Antilope oryx Pallas 1777

Oryx beisa (Rüppell 1835)*

- *annectins* Hollister 1910*
- ***gallarum*** Neumann 1902*
- *subcallotis* W. Rothschild 1921*
- ***callotis*** Thomas 1892*

Oryx callotis Thomas 1892*

Oryx dammah (Cretzschmar 1872)

- *algazel* (Oken 1816) [unavailable]
- *bezoastica* C.H. Smith 1827
- *ensicornis* (Wagner 1844)
- *nubica* (Wagner 1855)
- *senegalensis* (Wagner 1855)
- *tao* (C.H. Smith 1827)

Oryx gallarum Neuman 1902*

- *annectins* Hollister 1910*
- *subcallotis* W. Rothschild 1921*

Oryx gazella (Linnaeus 1758)

- *annectins* Hollister 1910*
- *aschenborni* Strand 1924)
- ***beisa*** (Rüppell 1835)*

- *bezoartica* (Pallas 1766)
- *blainei* W. Rothschild 1921
- ***callotis*** Thomas 1892*
- *capensis* Ogilby 1837
- ***gallarum*** Neumann 1902*
- *onyx* Gray 1821
- *oryx* (Pallas 1777)
- *pasan* (Daudin 1802)
- *reticornis* (Erxleben 1777)
- *subcallotis* W. Rothschild 1921*

<u>*Oryx leucoryx* (Pallas 1777)</u>

- *asiatica* (Wagner 1855)
- *beatrix* Gray 1857
- *latipes* Pocock 1934
- *leucorix* Link 1795
- *oryx* (Oken 1816) [unavailable]
- *pallasii* Fitzinger 1869