A GENUS-LEVEL PHYLOGENETIC ANALYSIS OF ANTILOCAPRIDAE AND IMPLICATIONS FOR THE EVOLUTION OF HEADGEAR MORPHOLOGY AND PALEOECOLOGY

by

HOLLEY MAY FLORA

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Student: Holley May Flora

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This Thesis has been accepted and approved in partial fulfillment of the requirements for the Master of Science degree in the Department of Earth Sciences by:

Edward Byrd Davis	Advisor
Samantha S. B. Hopkins	Core Member
Matthew Polizzotto	Core Member
Stephen Frost	Institutional Representative

and

Janet Woodruff-Borden	Dean of the Graduate School

Original approval signatures are on file with the University of Oregon Graduate School

Degree awarded September 2019.

THESIS ABSTRACT

Holley May Flora

Master of Science

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Title: A Genus-level Phylogenetic Analysis of Antilocapridae and Implications for the Evolution of Headgear Morphology and Paleoecology

The shapes of artiodactyl headgear play key roles in interactions with their environment and each other. Consequently, headgear morphology can be used to predict behavior. For example, larger, recurved horns are typical of gregarious, large-bodied animals fighting for mates. Smaller spike-like horns are more characteristic of small-bodied, paired mates from closed environments. Here, I report a genus-level cladistic analysis of the extinct family, Antilocapridae, testing prior hypotheses of evolutionary history and headgear evolution. I included 53 post-cranial, cranial, and headgear characters, expanding on previous analyses by developing 14 novel character traits. This phylogenetic analysis not only establishes ancestral headgear morphology of Antilocapridae but allows inferences of major social structure changes. These results confirm previous works inferred through comparison with artiodactyl families that antilocaprids evolved from small-bodied monogamous pairs to large-bodied gregarious herds. Our findings show multiple originations of herding social behavior.

CURRICULUM VITAE

NAME OF AUTHOR: Holley May Flora

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon, Eugene

Montana State University, Bozeman

Boise State University, Boise, Idaho

DEGREES AWARDED:

Master of Science, Earth Sciences, 2019, University of Oregon

Bachelor's of Science, Earth Sciences, 2015, Montana State University

AREAS OF SPECIAL INTEREST:

Functional Morphology

Evolutionary Processes

PROFESSIONAL EXPERIENCE:

Paleontological Assistant, Geocorps, Manti-La Sal National Forest, 2019

Graduate Employee, University of Oregon, Department of Earth Sciences, 2017-2019

Preparing and teaching labs for introductory courses (GEOL 101 & 103), teaching assistant (GEOL 304), and assisting the collections manager (Museum of Natural and Cultural History)

Graduate Employee, University of Oregon, 2017-2019

- Museum of Natural and Cultural History
    - Coordinating volunteers, undergraduates, and supplies for collections.
- GEOL 304 "Fossil Record"
    - Grading exams and running the online assignments.
- GEOL 101 "Introductory Geology" and GEOL 203 "History of Life"

- Teaching multiple lab sections on mineral and fossil identification and geological processes.

Fossil Preparator, Geoscientists in the Parks, Badlands National Park, 2018

Lab Technician, Horner Paleohistology Laboratory, Museum of the Rockies, 2014-2015

GRANTS, AWARDS, HONORS:

David S Easly Memorial Award ($5,000) Spring 2019

University of Oregon, Special "Opps" Travel & Research Award ($1,000) Spring 2019

University of Oregon, Department of Earth Sciences ($310) Winter 2018

University of Oregon Department of Earth Sciences Grant ($1,500) Spring 2018

Undergraduate Scholars Program Travel Grant ($500) Fall 2015

Society of Vertebrate Paleontology Jackson Student Travel Grant ($500) Fall 2015

Undergraduate Scholars Program Research Grant
- Developing a Microfossil Identification Guide for Lab and Field Use ($1,200) Summer 2014
- Causes and Effects of Landslides in Rural Morocco ($900) Spring 2015

Western Undergraduate Exchange Scholarship. 2012-2015

Montana State University Dean's List. 2012

PUBLICATIONS:

John P. Wilson; D. Cary Woodruff, Jacob D. Gardner; Holley M. Flora; John R. Horner; Chris Organ. (2016) *Vertebral Adaptations to Large Body Size in Theropod Dinosaurs*. PLoS ONE 11(7): e0158962. doi:10.1371/journal.pone.0158962

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INTRODUCTION

Headgear are an important feature shared by almost every member of the Ruminantia (Davis et al., 2011). Bony ossicones and other protuberances are found in many ruminant families, although the evolution of the different forms of headgear remains enigmatic. Within a phylogenetic framework the ruminant history may be uncovered.

Past work on Bovidae and Cervidae, families within Ruminantia, have examined correlation between headgear shape and behavior (Caro et al, 2003; Jarman, 1974; Geist,1966; O'Gara,1990; Bubenik & Bubenik, 1990). There are five established categories from Jarman (1974) that illustrate bovid behavior in relation to horn shape and curvature. Here, I merge these five categories into three because there are fewer genera in Antilocapridae and less body size diversity than in the African bovids (Fig.). Jarman's (1974) category A, animals with shorter simple horns, includes species displaying sexual dimorphism in closed environments. An example of this category in extant bovid antelope would be the dik-dik. Dik-diks are small-bodied (< 20kg) antelope living in the African underbrush feeding and living in pairs. The males have short, spiked horns and do not use them for fighting, but display (Scheibe, 1999). In categories B and C, more curved and complex horns are found on animals that use them to fight and wrestle each other to the ground. This is typical of slightly larger (< 50kg) animals that live on the border of forested areas with feeding options of both grass from the plains and higher energy leaves from the forest. This category (previously B and C) can be sexually dimorphic in headgear, but most members of this category use their headgear in competition for resources, so females sport equivalent structures to males. The headgear for these taxa is complex, branching in multiple places or curving medially. In categories D and E, large bodied (> 100kg) taxa with posteriorly recurved headgear, herds have a social structure where both males and females use headgear to ram each other in competition for resources and mates.

For this analysis, fossil taxa (as referred to in Appendix A) are categorized into three behavioral categories (shown in Table 1): small-bodied with small, simple headgear living a closed forest environment (previously Jarman's group A); medium sized with complex and branching headgear, living on the fringe of high nutrient localities and competing for resources (Jarman's B/C); and large-bodied taxa with large, recurved headgear living in social groups in open environments (Jarman's D/E).

Table 1. Behavior Category Breakdown

Antilocaprid Behavior Categories	Category 1	Category 2	Category 3
African Antelope Categories (Jarman, 1974)	A	B, C	D, E
Average Weight	< 20 kg	< 50 kg	>100 kg
Headgear Morphology	Small and simple.	Complex. Medially pointed tines.	Large and recurved. Dorsally directed.
Feeding Style	Closed, forested environments. High nutrient leaves.	Outskirts of forests. High nutrient leaves and grasses.	Open plains environments. Low nutrient grasses.
Social Structure	Sexually dimorphic headgear for display. Living in pairs.	Competing for resources. Living in small groups.	Both males and females have headgear. Socially competing for mates. Living in large herds.

TABLE 1. The categories of social structures for Antilocaprid behavior comparisons with their Bovid counterparts.

Caro et al. (2003) defined the shape and social factors that determine these categories and mapped them onto a bovid phylogeny derived from parsimony. This study found selection for particular shapes in headgear, supporting a pattern in fighting and grouping behaviors. Other families within Artiodactyla with fewer extant taxa have yet to be analyzed similarly. With a single living species, Antilocapridae is one of those families, but it will make an optimal test case because of its rich fossil record.

The family Antilocapridae originated in the Miocene of North America. While it had a peak diversity of six genera during the middle Miocene, only one species, *Antilocapra americana*, remains today (Jannis & Manning, 1998; Davis, 2007). The driving pressure for antilocaprids to diversify in headgear morphology, and for their recent decline, is unknown, but in this study I will address some hypotheses for the drivers of antilocaprid diversification.

Antilocaprids have historically been diagnosed by their headgear morphology (Davis, 2007). Headgear morphology as a main source for diagnostic characters leads to several problems. For identifying taxa, headgear in many families vary within species and for individuals over time. The origination of headgear is not well understood and antilocaprid headgear less so, even as new genetic work begins to illuminate their development and deep homology in cervids and bovids (Wang et al. 2019). Artiodactyl headgear can be ossicones that are part of the skull's bony structure, horns that are covered in keratin, or antlers that are shed annually. These structures also vary in shape and curvature. Artiodactyls use their headgear to interact with their environment and each other. Antilocaprid headgear are a unique structure that are neither ossicone nor horn nor antler as they have a bony horn core, but are covered by a sheath that is shed annually

(O'Gara, 1990). Today's extant antilocaprid, *Antilocapra americana*, has a short blade-like horn core with a pronged sheath. Extinct members of Antilocapridae have even more complex structures to their headgear with multiple horn cores and branching nodes. As I noted above, observations from living ruminants show that the shape and structure of headgear changes animals' interactions with one another and their environment, so it is possible to infer how extinct fauna used them (Caro et al, 2003). However, a modern analogue is needed to determine past behavior of extinct antilocaprids and likely uses of these distinctive headgear morphologies to infer interspecies and environmental relationships. The Bovidae are a family closely related to Antilocapridae (Marcot, 2007) and will provide a good modern analog. As horned ruminants, bovids live in similar ecosystems to those reconstructed for ancient North America: both open and closed environments (Caro et al, 2003).

The Antilocapridae are an ideal family for testing the evolutionary hypotheses developed from studies of bovids and cervids (Caro et al. 2003; Janis & Scott, 1987). Because it is an independent evolutionary lineage with similar starting conditions and a rich fossil record, I can build a phylogeny of the group that allows me to test how antilocaprid behavior has been related to headgear morphology through time and how the gregarious socializing and high-speed displays related to sexual selection seen in today's species evolved. To answer these broader behavioral questions, I must also reconstruct the morphology and preferred environment of the ancestral antilocaprid so that I can properly analyze the direction of character changes on the phylogeny. In the past, relationships between antilocaprid taxa have only been hypothesized using an informal process and never tested with a phylogenetic analysis (See Janis & Manning, 1998; Davis, 2007).

Social behavior in the fossil record is often a mystery. Social systems, when observed, illuminate the functional and environmental adaptations of fauna. In the fossil record, we cannot observe these interactions, but must rely on trace fossils and modern analogues. However, with information about paleoecology many inferences can be made about behavior of extinct organisms. Extinct and extant fauna are limited by their skeletal morphology in how they can interact with each other and their environments (Benton, 2010).

The objective of this study is to look at the evolutionary history of headgear in Antilocapridae and use that headgear to infer behavior. With a phylogeny, it should be possible to answer whether *Antilocapra americana* survived because its headgear have a successful shape for intra- and inter-species interactions that took advantage of North America's transition to open plains. I hypothesize that gregarious behavior like that seen in the extant *Antilocapra* evolved more than once in the family. I also hypothesize that this gregarious adaptation reflected in their headgear arose in answer to North America becoming an open plains environment and a herding social structure being more advantageous, as has been suggested for African antelope living in similar environments (Caro et al. 2003).

This analysis is the first objective phylogenetic analysis of extinct antilocaprid genera. This will also be the first phylogenetic analysis of antilocaprids to focus on morphological character traits other than headgear diagnoses. Previous studies have hypothesized two subfamilies within Antilocapridae: "Merycodontinae" and

Antilocaprinae. With a phylogenetic framework I can begin to test evolutionary questions within Antilocapridae, like those concerning the conditions under which their headgear shapes diversified and the main evolutionary drivers of diversification.

Institutional Abbreviations-AMNH, the American Museum of Natural History, New York; UCMP, University of California Museum of Paleontology, Berkeley; LACM, Natural History Museum of Los Angeles County, Los Angeles; CIT, California Institute of Technology; UNSM, the University of Nebraska State Museum, Lincoln; UOMNCH, the University of Oregon Museum of Natural and Cultural History.

METHODS

To create a phylogenetic framework without an existing phylogeny of Antilocapridae, I visited specimens at the AMNH, UCMP, LACM (including vertebrate paleontology collections from CIT), UNSM, and the UOMNCH. With pictures of fossil specimens to compare existing morphological traits of the family Antilocapridae, I scored antilocaprid genera as composites for each trait (listed in Appendix B). These trait scores (shown in Appendix C) were used to generate a phylogeny.

I generated the Bayesian phylogeny with Beast2.0 (Bouckaert et al, 2014) using morph models 1.1.1 and sample ancestor 2.0.1. The evolutionary history of morphology is reconstructed within the family through reference to fossilized morphological features. The Bayesian method utilizes the preferred evolutionary model and is informed by the stratigraphic record as appearance data. These tip dates, or FADs, from Davis (2007) and Janis and Manning (1998) are prior bound limits for the origination of the family Antilocapridae and each genus.

Other parameters used include: the Gamma 4 shape parameter, the relaxed log normal clock for rate variation, the fossilized birth-death model for rate of speciation, a tree parameter of Rho 1.0 to estimate missing taxa, and the author (Goswami et al., 2007) recommendations of diversification and evolutionary parameters. The Gamma parameter assumes different evolutionary rates for portioned characters. Here, I assumed headgear traits would evolve at a different rate than non-headgear traits and partitioned them to allow this in the analysis. A Rho of 1.0 indicates that all living taxa are included in the analysis. Because there is only one extant antilocaprid to include, there are no missing extant taxa.

The Bayesian analysis ran twice with 10,000 generations, sampling every 1,000 generations. To confirm analyses, I combined them with Tracer as .log files. A burn-in of 10% split the frequencies of these analyses.

Posterior probability is the support metric for Bayesian analyses because the preferred evolutionary model depends on the likelihood of a tree displaying the character traits. Posterior probability is the percentage of the trees produced that share each branch node. These probabilities range from 0 to 1 for each node.

To root a phylogeny of Antilocapridae, non-antilocaprid taxa were also included in this analysis (refer to taxon list in Appendix A or specimen list in Appendix D). The ingroup taxa include all nineteen extinct genera from the family Antilocapridae and the only extant genus, *Antilocapra*. The outgroup is made up of basal, exemplar genera from close artiodactyl families: Giraffidae, Cervidae, Bovidae, and Camelidae. The outgroup taxa were constrained to fall outside of Antilocapridae with the assumption that Antilocapridae is a monophyletic group.

To maintain consistency and avoid species-level complications, this phylogenetic analysis uses genus-level taxonomy as the species of Antilocapridae are in need of extensive systematic revision (Davis 2007).

In the fossil record, taxa are determined by their morphological features (Benton and Pearson, 2001). Features that that vary across specimens without ontogenetic degrees of change are informative traits. The character criteria here use explicit character states with parsimony-informative features. To inform evolutionary history of headgear traits, a comprehensive suite of non-headgear traits were also necessary for this phylogenetic analysis. 53 characters of headgear, cranial, dental, and postcranial features are included to create a robust phylogeny. These characters were chosen from existing diagnoses of antilocaprid genera and outgroup taxa (Davis, 2007 & Lister et al., 2005). Pre-existing diagnoses primarily relied on headgear morphology and 18 of the 53 characters refer to headgear (see Fig. 1). To add to the non-headgear traits, I developed 14 novel characters from observation while scoring material.

Different explicit character states are scored from photographs taken of antilocaprid type specimens and identified material during my visits to collections at the AMNH, UCMP, LACM, UNSM, and the UOMNCH. The uninformative traits, those that apply to all the genera, do not say anything about the evolutionary relatedness within Antilocapridae and were left out of the analysis.

FIGURE 1. *Ottoceros* skull LACM 1372 A-6235.51-1 showcasing headgear and cranial characters: 1(1), 2(2), 3(0), 4(1), 5(0), 6(1), 7(0), 9(1), 10(0), 11(0), 12(1), 13(0), 14(1), 16(1), 17(2), 18(0), 23(0), 24(1), 41(1), 42(1), 43(1).

To test hypotheses about the ways the environment shaped the evolution of behavior in Antilocapridae, I have used the Bayesian phylogenetic framework of the taxa to reconstruct the evolution of behavioral groups. These groups, simplified from those defined by Jarman (1974) are: small-bodied with simple headgear, larger-bodied with complex headgear, and large-bodied with large recurved headgear. By tracing the character history in Mesquite (W. Maddison and D. Maddison, 2018) the most parsimonious state for each node is listed, showing the ancestral state for each character at the branch. Ancestral characters for hypothetical ancestral antilocaprids can be accessed in this way, allowing for inferences of morphological features of basal antilocaprids. In the same way, tracing character states allows for the traits that make up specific headgear morphologies to be highlighted and sorted into social categories. The characters that exemplify headgear morphology for these categories include: length of shaft, number of nodes, and the shape of tines. Categories are designated by the majority of characters and likely body weight. The determined category is matched with the feeding style and social behavior of modern African bovids for an analogous comparison.

RESULTS

The results of this phylogenetic analysis (see Fig. 2) clarify pre-existing hypotheses about antilocaprid relationships. For the diagnoses in this systematic paleontology, I refer to the phylogenetic characters that are unambiguous synapomorphies of the clade or taxon.

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Antilocapridae Gray, 1866

Definition: The clade including the common ancestor of *Merriamoceros* and *Antilocapra* and all of its descendants.

Revised Diagnosis: These taxa are diagnosed by fused metapodials, complete distal metapodial keels, parallel-sided astragali, and smaller horns that are round in cross section and covered by skin or hair at the base of the horn core with exposed bony tines.

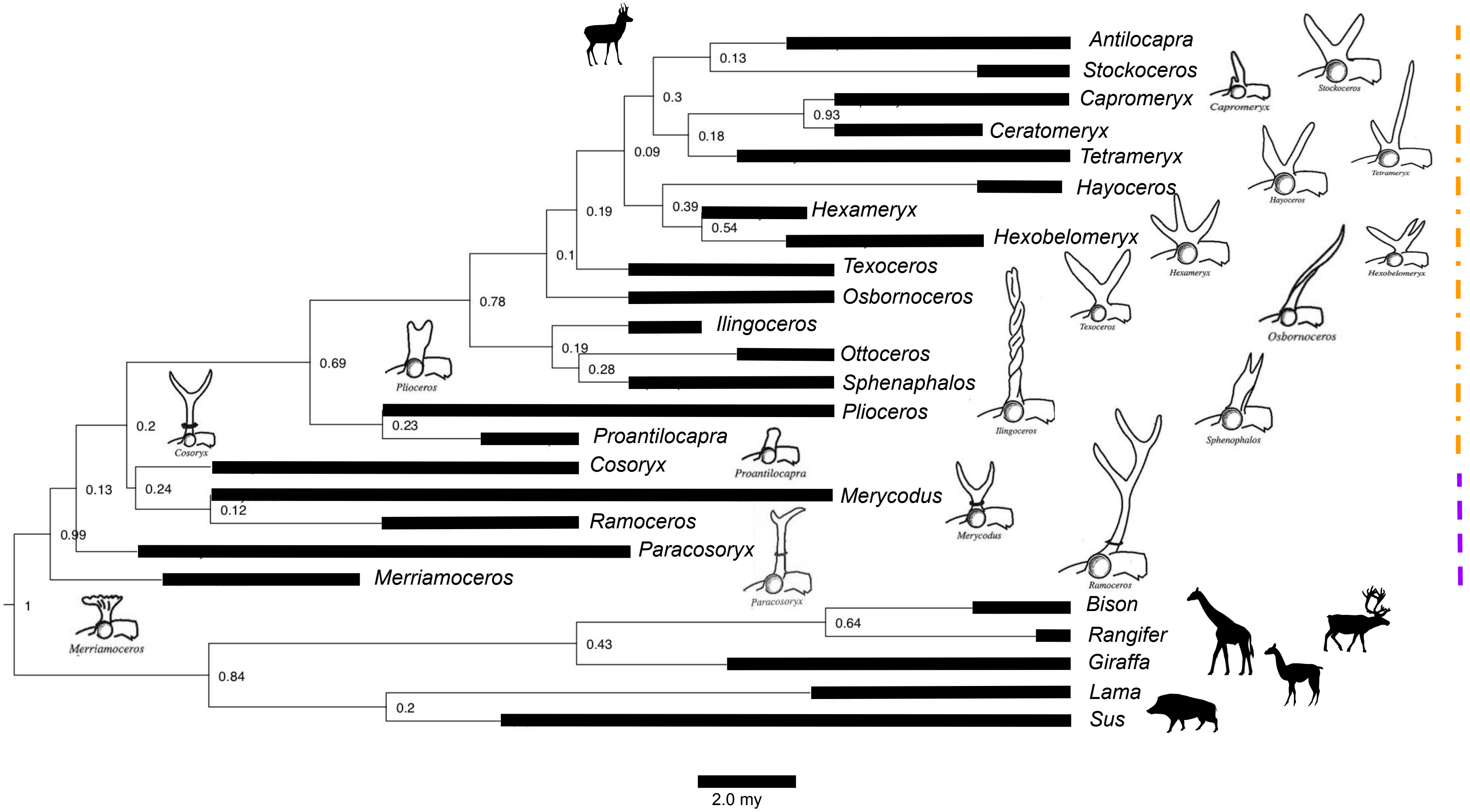

FIGURE 2. The maximum clade credibility phylogeny constructed with two runs of 10,000 trees had a 10% burn in. The 10% burn in estimate gives a stable start for the tree. The node labels of posterior support range from 0.1 to 1. This phylogeny has been timescaled so that the thick bars represent appearance in the fossil record. Subfamilies Antilocaprinae and “Merycodontinae” are differentiated along the right edge by a dashed-dotted line and dashed line, respectively. Skull outlines from Davis, 2007 and PhyloPic silhouettes.

Discussion: Previously, Antilocapridae was split into two subfamilies, “Merycodontinae” and Antilocaprinae (Matthew, 1909). Here, “merycodontine” genera (*Merriamoceros, Paracosoryx, Cosoryx, Merycodus,* and *Ramoceros*) do fall basally in Antilocapridae although not as one clade. Of these “merycodontine” taxa, *Ramoceros*, *Merycodus* and *Cosoryx* resolve as a monotypic clade where their tines are medially pointed. This could be redefined as tribe Ramocerotini, but for this phylogeny the “merycodontines” are considered enigmatic taxa and are unranked and the group “Merycodontinae” is considered paraphyletic. The second subfamily, Antilocaprinae, is strongly resolved (0.69 posterior support) as a monophyletic clade of the remaining genera. Within the subfamily only one previously defined tribe remains. The highest support value, 1, is found at the base of the tree confirming the prior assumption that the ingroup Antilocapridae is a monophyletic clade.

Genus *Merriamoceros* Frick, 1937

Revised Diagnosis: *Merriamoceros* has dorsally directed headgear and a reduced trichotomy on its headgear with a wedge shaped horn core. The posterior tine is smaller than the anterior and both are shortened into the flared portion of the horn core in a palmate shape.

Discussion: The most basal genus of Antilocapridae in this analysis is *Merriamoceros*. This is the first of the “Merycodontine” group.

Genus *Paracosoryx* Frick, 1937

Revised Diagnosis: Elongate shaft directed posteriodorsally. The anterior tine is smaller than the posterior and recurved. The premolars of *Paracosoryx* are basal with a small entosyle.

Discussion: *Paracosoryx* is the earliest antilocaprid to appear, but it is not the most basal in this phylogeny.

Genus *Merycodus* Leidy, 1854

Revised Diagnosis: *Merycodus* has equally sized tines that are equal in length relative to the core shaft.

Genus *Ramoceros* Frick, 1937

Revised Diagnosis: *Ramoceros* has hypsodont cheek teeth and an obtusely angled dentary relative the coronoid process.

Discussion: A monophyletic node, *Merycodus* and *Ramoceros* differ from each other in directionality of core shaft, the ratio of the core shaft to tine length, and *Ramoceros* having tricotomously branching tines.

Genus *Cosoryx* Leidy, 1869

Revised Diagnosis: *Cosoryx* has posteriorly-directed headgear originating more postoribitally than supraobritally and slightly depressed into the skull. *Cosoryx* has reduced premolars, an anterior cingulid present, but no ectostylid on the cheek teeth. *Cosoryx* also has a longer diastema and a widely flared scapula.

Discussion: *Cosoryx* diverges from *Ramoceros* and *Merycodus* by having fewer nodes than *Ramoceros* and equal-sized tines like *Merycodus*. This genus has been suggested as indeterminate (Frick, 1937) but has a support of 0.24 here.

Subfamily Antilocaprinae Gray, 1866

Definition: The clade including the common ancestor of *Proantilocapra* and *Antilocapra* and all of its descendants.

Revised Diagnosis: Branched, permanent keratinous pronghorns are the headgear of Antilocaprines. Blade-like headgear cross sections originating in the supraorbital with reduced tine tips, hypsodont teeth, an absent lacrimal fossa, a hollow auditory bulla and long, gracile limbs with elongated metapodials and a closed metatarsal gully characterize this subfamily.

Discussion: Antilocaprinae have a distinctly different form to their headgear than the earlier antilocaprids (the paraphyletic group "Merycodontinae"). Beginning with *Plioceros* and *Proantilocapra*, antilocaprines have evidence that their headgear was covered with keratinous sheathes in life (Davis, 2007).

Genus *Plioceros* Frick, 1937

Revised Diagnosis: *Plioceros* has elongate pronghorn core shafts with blade-like tines and cross section. The anterior tine is smaller than the posterior and is angled outward.

Genus *Proantilocapra* Barbour and Schultz, 1934

Revised Diagnosis: *Pronantilocapra* has an ectostylid present but not a metastylid. The diastema of *Proantilocara* is short and the coronoid process angled more obtusely relative the dentary. Compared to its shortened and reduced tines, the pronghorn core shaft of *Proantilocapra* is elongate.

Discussion: Within Antilocaprinae, a monophyletic clade containing *Plioceros* and *Proantilocapra* is the first to diverge. This clade is diagnosed from the other Antilocaprinae with the anterior-most tine smaller than the posterior tine and recurved. Their cheek teeth also have a small entostyle present.

Tribe Ilingocerotini Frick, 1937

Definition: The common ancestor of *Ilingoceros* and *Sphenophalos* and all of its descendants.

Revised Diagnosis: Large headgear with elongate pronghorn core shafts with reduced tines. The cross section of pronghorn cores is narrow and rectangular. The metastylid is present on cheek teeth.

Discussion: This tribe includes *Ilingoceros, Sphenophalos,* and *Ottoceros,* all known from the Hemphillian of California, Oregon, and Nevada, suggesting its members were specialists for the opening, drying habitats of that region at that time. This tribe splits from the remaining Antilocaprines with 0.78 posterior support.

Genus *Ilingoceros* Merriam, 1909

Revised Diagnosis: The ratio of pronghorn core shaft to tine length in Ilingoceros is the longest for any antilocaprid. Tine tips directed outwardly from shaft. The horn core shaft is also twisted, resulting in a more rectangular to wedge shaped cross section.

Genus *Sphenophalos* Merriam, 1909

Revised Diagnosis: Pronghorn cores of *Sphenophalos* laterally compressed in cross section and outwardly directed.

Genus *Ottoceros* Miller and Downs, 1974

Revised Diagnosis: Compressed pronghorn core cross sections are wedge shaped and headgear originates on the skull surface. Premolars are not reduced in *Ottoceros*.

Genus *Osbornoceros* Frick, 1937

Revised Diagnosis: *Osbornoceros* has wedge-shaped pronghorn cores originating in the supraorbital as well as unreduced premolars and cheek teeth without a metastylid.

Discussion: *Osbornoceros* has the least supported node (0.1), suggesting caution about interpreting its position in the tree.

Genus *Texoceros* Frick, 1937

Revised Diagnosis: *Texoceros* has a partially fused metapodial gully and lacks parallel-sided astragali. Short pronghorn core shafts, but not as reduced as seen in *Stockoceros*, and circular cross sections.

Genus *Hexameryx* White, 1941

Revised Diagnosis: Significantly shortened shaft in *Hexameryx* leaves the tines as the predominant morphology. The headgear has circular cross sections and tines covered with keratinous sheaths.

Discussion: *Hayoceros*, *Hexameryx*, and *Hexobelomeryx* form a clade with 0.39 posterior probability support. The lack of support for this node is unsurprising because postcranial material is lacking from many identified specimens, leaving uncoded characters. *Hexameryx* and *Hexobelmeryx* couple with better posterior probability support (0.54), but all three genera are grouped by their large tines with anterior and posterior directionality.

Genus *Hexobelomeryx* Furlong, 1941

Revised Diagnosis: The anterior most tine is larger than the remaining two with little differentiation between tine directionality. Similar to *Hexameryx*, the core shafts are very short leaving the predominant morphology the three tines.

Genus *Hayoceros* Frick, 1937

Revised Diagnosis: *Hayoceros* has a short-shafted pronghorn core with elongate tines and a wedge-shaped cross section. These headgear structures are covered in a keratinous sheath similar to that of *Antilocapra* with a recurved tine produced anteriorly with the sheath.

Discussion: *Hayoceros* is one of the last antilocaprid genera to evolve, along with *Stockoceros*.

Genus *Tetrameryx* Lull, 1921

Revised Diagnosis: *Tetrameryx* has some of the longest tines in Antilocapridae. The asymmetry of a small anterior tine and larger posterior is exaggerated in *Tetrameryx*.

Genus *Ceratomeryx* Gazin, 1935

Revised Diagnosis: In *Ceratomeryx*, the posterior tine is smaller than the anterior. The posteriorly directed shaft originates in the supraorbital.

Discussion: *Ceratomeryx* and *Capromeryx* are sister taxa with 0.93 posterior probability support for the node uniting them. *Ceratomeryx* was previously suggested to be closely related to *Tetrameryx* (Gazin, 1935), and here *Tetrameryx* is sister to the *Ceratomeryx* and *Capromeryx* node with a low (0.18) posterior probability support.

Genus *Capromeryx* Matthew, 1902

Revised Diagnosis: *Capromeryx* has a small, circular cross section and a smaller anterior tine than posterior. These tines are dorsally pointed.

Genus *Stockoceros* Frick, 1937

Revised Diagnosis: The headgear of *Stockoceros* has a short pronghorn core shaft with two distinct, elongate and narrow tines. Also covered in a keratinous sheath, these tines are equal in size and the pronghorn core is reduced at the tine tip.

Discussion: Previous workers have recognized tribes Stockoceratini and Antilocaprini, but my analysis brings together genera previously placed in both tribes. In this phylogeny, *Antilocapra* and *Stockoceros* are sister to each other, so I am not recognizing any tribes within Antilocaprinae except the Ilingocerotini.

Genus *Antilocapra* Ord, 1818

Revised Diagnosis: The headgear cross section of *Antilocapra* is bladelike, and because it is extant, it is known to have recurved tines of keratin. The anterior tine is smaller and the more recurved. An anterior cingulid is present on *Antilocapra* cheek teeth.

Discussion: *Antilocapra* and *Stockoceros* have equant horn core shafts and tines. With more postcranial material catalogued for both of these taxa, they are also grouped by large, flared atlas vertebrae.

Phylogenetic Trait Mapping

With tip dates and first appearance data included in the phylogeny, timing can be attributed to these characteristics. “Merycodontines”, with the majority of the basal plesiomorphic characters, originate 19 m.y.a. (Fig. 2). Multiple nodes, like those seen in *Ramoceros*, appear in the Barstovian (14 m.y.a.). Antilocaprinae and reduced tines covered by a keratinous sheath evolve at the same time. The more complex shapes exhibited in antilocaprids (twisted horn cores, larger headgear with elongate shafts) evolve at 9 m.y.a..

“Merycodontine” taxa survive as long as the earliest Antilocaprine taxa persist (Fig. 2) with a diversity of four genera alive at one time. Antilocaprinae had a greater peak diversity but not until after most “merycodontines” had gone extinct in the Clarendonian. The end of the Clarendonian is also one of the first of three stages where antilocaprid diversity dramatically decreases (Fig. 2). Losing the majority of “merycodontines” at one time left basal antilocaprines and *Merycodus* the only taxa representing Antilocapridae. The Hemphillian and Rancholabrean are the other two NALMAs with extinction events for Antilocapride. The Hemphillian marks the end of the "merycodontine" taxa and the majority of antilocaprine diversity (Fig. 3). The loss of taxa in the Rancholabrean leaves only the extant *Antilocapra* in Antilocapridae.

When all headgear characters are compared and sorted into behavioral categories (Fig. 3), most "merycodontine" taxa are category 1 with small, simple headgear and outwardly directed shafts. The exceptions, *Ramoceros* and *Merycodus,* are in category 2 for their medially pointed tines. Antilocaprinae has a greater diversity of social categories. Antilocaprinae originates in category 3 with the reduced tines and elongated shafts of *Plioceros* (Fig. 4). The later antilocaprines, appearing 9 m.y.a., exhibit category 2 characters of complex headgear. Category 1 antilocaprines do appear in the Blancan (4.8 m.y.a.) after the "merycodontines" are extinct. These category 1 taxa and the category 3 *Antilocapra* and *Stockoceros* survive closest to the present.

Ancestral headgear characters determined by parsimony on this phylogeny are: 1(1), 2(?), 3(0), 4(2), 5(?), 6(1), 7(?), 8(0), 9(2), 10(1), 11(0), 12(0), 13(0), 14(0), 15(?), 16(?), 17(?), 18(?). An ancestral hypothetical ancestral antilocaprid would be reconstructed with headgear. This headgear would have a round cross-section, likely with a burr, and one unbranching tine dorsally directed.

DISCUSSION

This phylogeny illustrates a distinct change in headgear through time (Fig. 2). Ancestral headgear characteristics (small, simple branching headgear with a short shaft) place a hypothetical ancestral antilocaprid in the small-bodied, closed environment category (Fig. 2 & Fig. 3). Basal antilocaprids, "merycodontines", have short-shafted, small headgear. Their headgear branches at one to three nodes into small, curving tines. The variability in “merycodontines”, other than number of nodes, is the directionality of the tines. The majority of this group fit in the small-bodied, closed environment category (Fig. 3). For the most derived of “merycodontines”, *Ramoceros*, tines are medially pointed, forming a cage-like space in between horn cores. The most basal of “merycodontines”, *Merriamoceros*, has a flared and palmate horn core supporting small tines directed dorsally. The more derived group, Antilocaprines, present more character states. Most headgear in this group have an equal, or larger-than-equal ratio of shaft-to-tine length with reduced tine tips. *Plioceros*, one of the basal most Antilocaprines, has headgear very similar to the extant genus, *Antilocapra*. These genera have short, narrow shafts and reduced tines. *Antilocapra* then sports a keratinous sheath with one node and recurved tine tips. *Plioceros* has one node on its core, also covered by a keratinous sheath. Both these genera fit into the large-bodied, open plains environment category (Table 1 & Fig. 3). More complex structures are also present in antilocaprines, *Ilingoceros* and *Osbornoceros* show longer, twisted shafts. These shapes and numerous nodes on other Antilocaprine taxa place half of the taxa in the complex, forest outskirts category (Table 1 & Fig. 3). These major changes could imply the environment of the time would pressure headgear evolution, contrary to findings by Caro (2003) weakly linking headgear shape to environment.

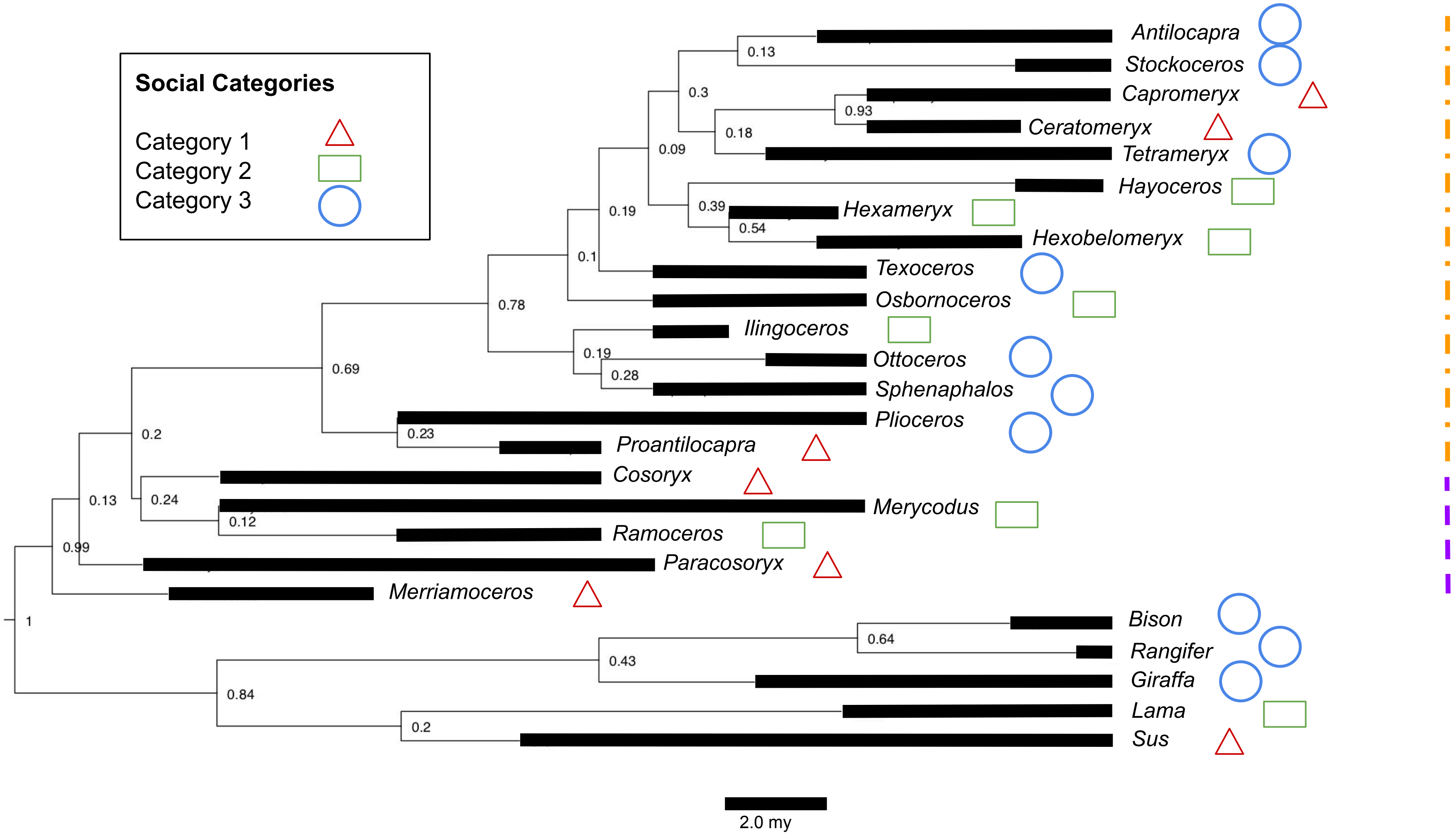

FIGURE 3. Phylogeny of Antilocapridae genera and outgroups from Artiodactyla with social/behavioral categories mapped. Subfamilies Antilocaprinae and Merycodontinae are differentiated by the dashed lines alongside the present edge. Social categories shown here represent:1) small-bodied with simple dimorphic headgear, 2) mid-sized with complex headgear for resource competition, and 3) large with recurved headgear for social competition within herds.

Evolutionarily, this phylogeny confirms the paraphyletic group of "merycodontines" are basal to Antilocaprine taxa (Fig. 2), as has been suggested by previous workers (Janis & Manning, 1998; Davis, 2007). The "merycodontines" fall closer to the root of the phylogeny with staggered originations of genera between 19 and 14 m.y.a.. "Merycodontines" are the longer lived of antilocaprids, surviving until 4.8 m.y.a.. But overall, the subfamily Antilocaprinae makes up the majority of the phylogeny, and after 14 m.y.a., the entire diversity. Antilocaprines are also the more derived genera, splitting from the node shared with *Cosoryx* and *Merycodus* sometime before 17.5 m.y.a.. Antilocaprines *Ceratomeryx* and *Capromeryx* were the latest node in Antilocapridae to diverge, but other antilocaprines also evolved as sister taxa more recently.

My results suggest gregarious behavior evolved in multiple branches in Antilocapridae (Fig. 4). *Plioceros* is the first to appear in this category 14 m.y.a.. *Plioceros* was followed into this category by *Sphenaphalos* and *Texoceros,* and then *Ottoceros* and Tetrameryx 9 and 6.8 m.y.a., respectively. Finally, *Antilocapra* and *Stockoceros* are labeled gregarious 5.8 and 1.9 m.y.a.. *Tetrameryx* and *Stockoceros* persisted through the Rancholabrean before leaving Antilocapra the only gregarious genus. These taxa are all large-bodied with large reduced tines and posteriorly directed shafts.

The spread of grasslands in the Oligocene (Stromberg, 2005) likely contributed to the sharp decline in diversity and overall extinction of genera as closed-habitat ecosystems disappeared. Forest islands within North America allowed smaller taxa with less social herding tendencies to persist into the Hemphillian. These forested areas were mosaics of shrubs and woodlands. Forested mosaics remained in North America through the late Miocene even though most ungulate faunas had adapted to grasses by the early Miocene. Open habitats began spreading at the end of the Oligocene, but did not make up the majority of environments until the early Miocene. Forests gave way to C_3 grasses and then C_4 grasses dominated the open ecosystems by invading floodplains 3 m.y.a. (Stömberg & McInerny, 2011). *Plioceros*, the earliest antilocaprid to display gregarious characteristics (Fig. 3), appeared 14 m.y.a., during the middle Miocene. *Plioceros* arose alongside grassland expansion. *Stockoceros* and *Antilocapra* originated during the takeover of C_4 grasses. During this time, antilocaprids displayed all social categories (Fig. 3), but forested mosaics had not disappeared. When C_3 plants expanded into open environments they did not overtake existing forest areas, and when C_4 grasses replaced C_3, they did not replace remaining forests (Edwards et al., 2010). More open grassland environments allowed for the gregarious antilocaprids to be more successful than those living in or alongside decreasing forest areas. Similar environmental hypotheses could be tested by comparing the evolutionary trends of other artiodactyl families' headgear morphology during ecosystem change and determining the abiotic and biotic pressures for these trends.

With the loss of "merycodontine" taxa, we see a some early antilocaprines filling the behavioral categories of early habitats (Fig. 3). These reversals from the initial taxa in behavioral category 2 back to category 1 may be showing niche replacement or habitat competition as genera turn over. Evolutionary change in antilocaprids might be driven by the abiotic factors of environmental change or biotic competition for habitat, resources, and social status. These potential driving factors could be used to test the category reversals of early antilocaprines or to better choose analogues.

Future Work

Future analyses resolving species level antilocaprid relationships can better resolve the place of Antilocapridae within Artiodactyla and antilocaprid headgear within artiodactyl history. With more intensive character analysis and a closer inspection of specimens, a well-supported tree with further resolution could be brought to Antilocapridae at a species level. Future research includes rerunning this analysis omitting headgear characters to observe any differences in support. Omitting the 18 headgear characters will develop a phylogeny whose relationships are determined by independently of the evolution of headgear, allowing an independent analysis of the evolution of headgear traits. Any differences in posterior support could highlight which headgear characters are morphologically important and suggest some drivers of evolutionary change. Comparing the inferred behavior of extinct taxa with modern African antelope diversity and niche use can further test this method. Similar analyses on ruminant families with more extant species will allow confirmation of social structures determined by the method. Modern African antelope have diverse extant species and a fossil record to test both morphologically and behaviorally where previously these antelope were only compared to modern cervids (Caro, 2003).

If future work continues to place Antilocapridae as a basal member of Artiodactyla it would suggest an Asian origin for antilocaprids. As a family, Antilocapridae is already present in North America by the Miocene. A recorded split in the late Oligocene has yet to be recovered from the fossils of Asia (Davis, 2007). More fossil antilocaprid collection can continue to fill in the evolutionary gap for the origins of Antilocapridae.

Conclusions

My analysis of the evolutionary history of Antilocapridae confirms prior hypotheses. The subfamilies within Antilocapridae are the small-bodied “merycodontines” with small, branching headgear and the larger-bodied antilocaprines with reduced tines and larger headgear. An ancestral antilocaprid is likely to have “merycodontine”-like headgear and be small-bodied.

Morphologically, antilocaprid ancestral headgear traits included small, simple headgear and developed into larger, stockier and more complex structures before reducing and simplifying to today’s morphology. This simple ancestral antilocaprid headgear that is neither ossicone nor antler is potentially rooted in early Artiodactyla. Both bovid horns and cervid antlers share gene expression profiles, and ruminant headgear has most recently been shown to have a single origin within Pecora, a group originating in the Eocene (Wang et al, 2019). When considered in the light of my cladistic analysis, the first to include fossil antilocaprids, similar basal structures to those I propose for antilocapridae could be hypothesized in other early artiodactyls. Regenerative antlers appear in Cervidae during the Miocene, so an earlier intermediate structures comparable to that of antilocaprids is a likely ancestral headgear for Ruminantia.

APPENDICES

APPENDIX A: LIST OF SPECIES

Taxa:	*Paracosoryx wilsoni*	Frick, 1937
	Ramoceros ramosus	Cope, 1874
	Merriamoceros coronathus	Merriam, 1913
	Merycodus necatus	Leidy, 1854
	Cosoryx furcatus	Webb, 1969
	Proantilocapra platyocornea	Barbour and Schultz, 1934
	Osbornoceros osborni	Frick, 1937
	Plioceros blicki	Frick, 1937
	Ottoceros peacevalleyensis	Miller and Downs, 1974
	Sphenophalos nevadanus	Merriam, 1909
	Ilingoceros alexandrae	Merriam, 1909
	Texoceros guymonensis	Frick, 1937
	Antilocapra Americana	Ord, 1818
	Hayoceros barbouri	Skinner, 1942
	Stockoceros conklingi	Stock, 1930
	Hexameryx simpsoni	White, 1941
	Hexobelomeryx fricki	Furlong, 1941
	Capromeryx furcifer	Matthew, 1902
	Ceratomeryx prenticei	Gazin, 1935
	Tetrameryx shuleri	Lull, 1921
	Giraffa camelopardalis	Linnaeus, 1758
	Rangifer tarandus	Linnaeus, 1758
	Bison bison	Linnaeus, 1758
	Lama glama	Linnaeus, 1758
	*Sus scrofa**	Linnaeus, 1758

Ingroup: Exemplar species from each genus of extinct antilocaprid and the extant pronghorn, *Antilocapra Americana* that typify the genera.
Ourgoup: Representative and basal genera from the next closest families in Artiodactyla
*The *Sus scrofa* used here is *S. scrofa domesticus* which exhibits reduced dental morphologies from the wild examples. Members of the subspecies *S. scrofa domesticus* have a shortened tooth row with multiple cusps on each tooth more densely associated than in the wild subspecies of *S. scrofa*.

APPENDIX B: CHARACTER LIST

The following are character descriptions:

Headgear Characters

1. 0- Headgear absent, 1- Headgear present

   It is determined by the presence or absence of headgear. Type of headgear, size, and shape do not change how this character is scored. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

2. 0- Exposed bony headgear, 1- Skin- or hair-covered headgear, 2- Keratinous-sheath-covered headgear

   This character is unordered. In fossils, a keratinous sheath is inferred from the grooves of past veins. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

3. 0- Permanent headgear, 1- Headgear shed

   This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007). In Antilocapridae, horn cores have been collected at varying stages of completeness, but, horn cores are not found cleanly separated from the skull cap as seen in cervid antler falls. With horn cores permanent in the extant *Antilocapra*, this character mostly shows differences between extant genera and is likely state 0 for fossil antilocaprids.

4. 0- Horn cores bladelike with a narrow cross section, 1- Horn cores wedge-shaped in cross section, 2- Horn cores round in cross section

   The character is unordered. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

5. 0- Headgear originates in the postorbital bone, 1- Headgear originates in the supraorbital bone

   This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

6. 0- Headgear origination depressed into the skull, 1- Headgear origination above the skull surface

   Depressed originations are subtle but show a slight buckle at the base. In cross section, state 0 is concavely dimpled at the skull surface surrounding the horn core. State 1 has a smooth slope from the skull surface to the horn core shaft. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

7. 0- No burr present on headgear, 1- Burr distinct from the horn shaft at the surface of the skull, 2- Burr high on the horn shaft

   This character is unordered. This character is drawn from the diagnoses of artiodactyl clades, but may no longer be significant morphologically (Davis, 2007).

8. 0- One burr present, 1- Two burrs present, 2- Many burrs present

This character is unordered. Number of burrs present can change over a lifetime with animal growth especially in structures that are regenerated annually (Bubenik and Bubenik, 1990). Injuries to the headgear can also add burrs. As such, this character can lend ontogentic distinction to specimens. This is a novel character adopted for this analysis.

9. 0- Outwardly-directed shaft from skull, 1- Posteriorly-directed/tilted shaft, 2- Dorsally-directed shaft, 3- Anterolaterally-directed shaft

This character is unordered. The directionality of the shaft is considered independently of the directionality of the tines. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

10. 0- Short-shafted horns, 1- Ratio of base of the shaft length to shaft length above the tines is equal, 2- Slender horns with an elongated shaft length

This character is ordered. This ratio is the comparison of the headgear shaft length to tine length and where on the shaft tines originate. In specimens with only one tine, I draw the shaft-tine boundary at the point of any change in curvature. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

11. 0- “secondary” shaft or branch splitting posteriorly to form third tine not present on headgear, 1- reduced “secondary” shaft present forming trichotomy horns, 2-

long “secondary” shaft present, 3- two to three tines present on “secondary” shaft (Cervid-like)

This character is unordered. Secondary shafts are differently proportioned from trichotomy horns but are similarly shaped (see Fig. 4). This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

Ramoceros AMNH FM 51303 trichotomy core, state 1; and an *Alces* AMNH 21832 antler, state 3.

FIGURE 4. Examples of different character states for trait #11 on *Ramoceros* and *Alces.*

12. 0- Palmate horn absent, the headgear has clearly defined tines or tips; 1- Palmate horn present, the horn material is broadened and tine tips obscured, usually scoop- or shovel-shaped

The palmate horn can originate at the shaft of the headgear or the tine. The palmate state is also shown in AMNH 21832 above. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

13. 0- Horizontal platform or bar not protruding from shaft, 1- Horizontal platform present extending from shaft, 2- Horizontal platform present with many small tines extending perpendicularly

This character is ordered. This character differs from #11 by being an independent shaft to support multiple tines. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

14. 0- No nodes on headgear resulting in one unbranching tine, 1- One node per horn giving a prong shape, 2- Two nodes resulting in a tiered prong and branch, 3- Three nodes giving two tiers with two branches each and four tines
This character is ordered. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

15. 0- Anterior tine smaller than the posterior tine, 1- Anterior tine equal to the posterior, 2- Posterior tine smaller than anterior
This character is unordered. Tine length is considered independently of curvature. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

16. 0- Tines pronounced with a short shaft; 1- Ratio of shaft length to tine length equal; 2- Tines elongated, longer than shaft length
This character is ordered. These ratios are describing the tine length in relation to the headgear structure rather than the shaft descriptions of character 10. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

17. 0- Tines dorsolaterally pointed or extended, 1- Tines anteriorly pointed, 2- Tines posteriorly pointed, 3- Anterior tines point medially

This character is unordered. Tine directionality is independent of shaft direction. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

18. 0- Tine tips reduced, 1- Tine tips widely flared at the ends, 2- Tine tips recurved

This character is unordered. Reduced tine tips are blunt and can be circular in cross section. Widely flared tine tips thin as they expand at the edges, typically bladelike. Recurved tine tips come to a point but also curve away from the headgear shaft. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

Dental Characters

For all dental character descriptions, refer to Fig. 5.

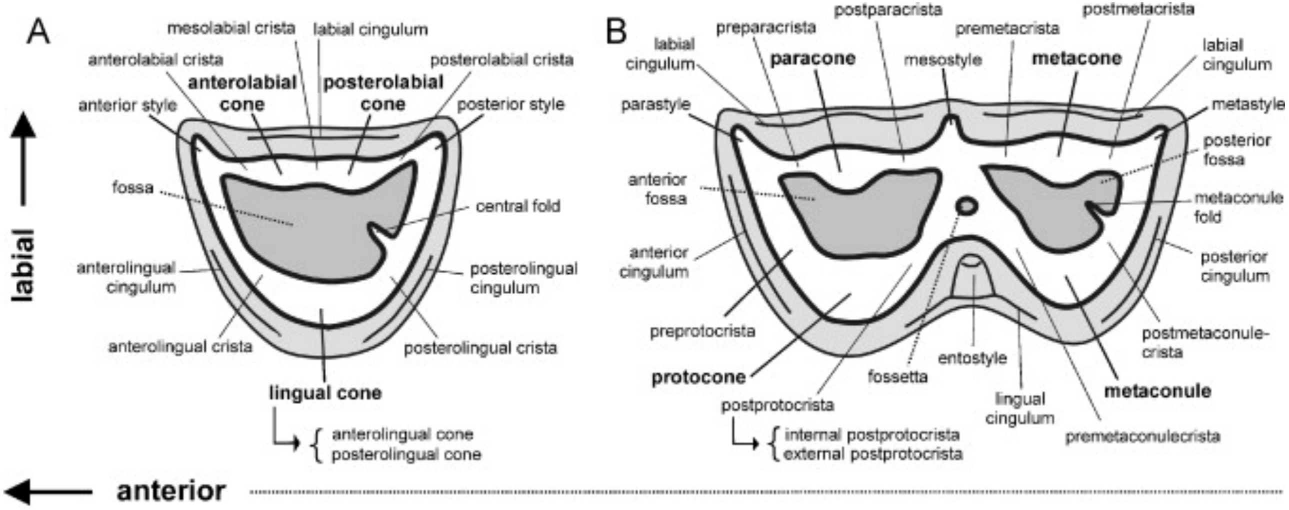

FIGURE 5. Dental nomenclature used for morphological traits, all dental characters refer to the dental nomenclature utilized by Bärmann & Rösner (2011). Figure 2 from Bärmann and Rösner (2011) used here with permission from the authors.

19. 0- Upper incisors absent, 1- Upper incisors present

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

20. 0- Lower canine not incisiform, 1- Lower canine incisiform

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

21. 0- Lower canine separated from incisors by a diastema, 1- Lower canine not separated from incisors by a diastema

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

22. 0- Upper canine absent, 1- Upper canine present

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

23. 0- Premolars not reduced, 1- Premolars reduced

Reduced premolars are smaller in crown height. The difference in crown height from the molars seen in lateral view is the greatest distinction. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

24. 0- Brachydont cheek teeth, 1- Hypsodont cheek teeth

Hypsodonty is defined as having high crowned teeth with extended enamel. Most specimens observed were hypsodont, with few being difficult to distinguish from their placement within the skull. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

25. 0- Entostyle not present on check teeth, 1- Entostyle present

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

26. 0- Tiny loph (metaconule fold) present on m3, 1- Intermediate loph present on m3, 2- Dentin lake present on m3

This character is ordered. The intermediate loph is more elongate. This is a novel character adopted for this analysis.

27. 0- Ectostylid not present on cheek teeth, 1- Ectostylid present on check teeth

The ectostylid is the ridge the possible entostyle originates from. This character is separate from #25 because the ectostylid can be present without the entostyle. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

28. 0- Metastylid not present on cheek teeth, 1- Metastylid present on cheek teeth

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

29. 0-Anterior cingulid absent, 1- Anterior cingulid present within the occlusal surface, 2- Anterior cingulid present on labial side of cheek teeth

This character is unordered. These features are likely homologuous and originiate from the same point, but it is unclear if state 1 would precede state 2 or vice versa. This is a novel character adopted for this analysis.

30. 0- Lingual cuspules in upper premolars absent, 1- Lingual cuspules in upper premolars present

This character is drawn from the diagnoses of artiodactyl clades (Lister et al., 2005).

31. 0- Buccal cingulum in upper molars absent, 1- Buccal cingulum in upper molars present

This character is drawn from the diagnoses of artiodactyl clades (Lister et al., 2005).

32. 0- Outer cuspule ridge on M3 profile absent, 1- Outer cuspule ridge on M3 profile with a raised ridge present

This is a novel character adopted for this analysis.

33. 0- p4 not laterally angled/splayed, 1- p4 laterally angled/splayed

The angling of the p4 is typically from the base of the tooth and displays a wide occlusal surface. This is a novel character adopted for this analysis.

34. 0- Diastema absent, 1- Short diastema present, 2- Long diastema present

This character is ordered. Here, a short diastema is one that is shorter than the tooth row. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

35. 0- Ratio of length M3 compared to postcanine tooth row smaller than 1:2, 1- Ratio of length of M3 compared to postcanine tooth row equal 1:1, 2- Ratio of length of M3 compared to postcanine tooth row larger than 2:1

This character is ordered. Length of M3 is measured along the same axis as the tooth row. Both are measured along the dentary, where the crown of the teeth meets the gumline. This is a novel character adopted for this analysis.

36. 0- Angle of tooth row in dentary parallel to dentary in occlusal view, 1- Angle of tooth row labially tilted in dentary, 2- Angle of tooth row lingually tilted in occlusal view

This is an unordered character. This is a novel character adopted for this analysis.

Cranial Characters

37. 0- Coronoid at a right angle relative to the dentary, 1- Coronoid at an obtuse angle relative to the dentary

The angle for this character should be measured along the center of the coronoid and dentary as viewed laterally. This is a novel character adopted for this analysis.

38. 0- Articular surface of coronoid D-shaped, 1- Articular surface of coronoid triangular, 2- Articular surface of coronoid rectangular

This character is unordered. The articulated surface shape is similar to the cross section of the coronoid viewed occlusally. This is a novel character adopted for this analysis.

39. 0- Coronoid and condyloid processes close together, 1- Coronoid and condyloid processes separated

This character describes the coronoid and condyloid processes as viewed laterally. When separated, the coronoid process extends posteriorly and leaves a distance between the more proximal, shorter condyloid process (see Fig. 6). When close together, the condyloid process is extended and originates higher up the dentary, placing the coronoid and condyloid adjacent to each other. This is a novel character adopted for this analysis.

FIGURE 6. *Merycodus* UNSM 83618 dentary displaying character state 1, separated processes.

40. 0- Fossa leading to the mental foramen absent from dentary, 1- Small fossa leading to the mental foramen present in dentary

This fossa, when present, is in the dentary directly ventral to the postcanine tooth row and dips laterally into the dentary. This is a novel character adopted for this analysis.

41. 0- Lacrimal fossa absent, 1- Lacrimal fossa present

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

42. 0- Large auditory bullae absent, 1- Large auditory bullae present

The bullae, if present, are ovate in shape and formed with thin bone. Smaller auditory structures are far refined in size and barely extend away from the skull. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

43. 0- Postorbital bar absent, 1- Postorbital bar present

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

44. 0- Expanded/protruding nasals absent, 1- Expanded/protruding nasals present

The delicate nasals protrude anteriorly to the end of the skull in some artiodactyls. In fossils, the scoring of this character can be dependent upon the degree of preparation and preservation for a specimen. If the nasals are not visible to score this character, the state is recorded as ?. When present, the thin nasals are visible in cross section at the anterior most view of the nasal passage.

This character is drawn from the diagnoses of artiodactyl clades (Lister et al., 2005).

Post-Cranial Characters

45. 0- Elongated metapodials absent, 1- Elongated metapodials present

Elongate, gracile metapodials are slender and lightweight. Elongate metapodials are gracile and disproportionately lengthened along the ventral-dorsal axis. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

46. 0- No metapodial fusion, 1– Partial metapodial fusion, 2- Complete metapodial fusion with a closed metatarsal gully

This character is ordered. Partial fusion here leaves only the gully unfused. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

47. 0- Parallel-sided astragali absent, 1- Parallel-sided astragali present

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

48. 0- Ulna not reduced, 1- Ulna reduced

A reduced ulna is disproportionately slender on the distal end, tapering to a point. The ulna is also slightly convexly curved from the olecranon process to the radial head. This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

49. 0- Side toes (digits II and IV) absent, 1- Side toes present

This character is drawn from the diagnoses of artiodactyl clades (Davis, 2007).

50. 0- Atlas narrow and bowtie-shaped, 1- Atlas wide and rectangular

The shape of the atlas is as viewed dorso-ventrally. This is a novel character adopted for this analysis.

51. 0- Atlas without transverse foramen, 1- Atlas splayed with fossa present in the transverse processes

The splayed transverse processes of the atlas display a foramen within the process itself near the posterior arch. The foramen is oriented dorso-ventrally. This is a novel character adapted for this analysis.

52. 0- Scapula narrow, 1- Scapula widely flared in a wedge shape

This is a novel character adopted for this analysis.

53. 0- Scapula without medial ridge, 1- Medial ridge protruding to proximal edge of scapula

This ridge originates at the glenoid and radiates to the border (see Fig. 7). This is a novel character adopted for this analysis.

FIGURE 7. Scapula UNSM 6677-39 displaying character state 1.

*Scoring material over multiple specimens, if uncertainty from variability is present a ? is the representative score. If two potential states are clear both are represented by ½.

Characters 1-7, 9-25, 27-28, 34, 41-43, 45-49 described in Davis, 2007.
Characters 30-31, 44 described in Lister et al., 2005.
Other characters utilized for these studies that are not listed here either were not included for lack of character state diversity or because fossil antilocaprids do not allow for scoring.
Characters 8, 26, 29, 32-33, 35-40, 50-53 are novel characters produced for this study.

APPENDIX C: CHARACTER MATRIX

Character #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Antilocapra	1	2	0	0	1	0	0	?	2	0	0	0	0	1	1	1	2	2	0	1	1	0	1	1	0	2	0	1	1	?	0	1	0	2	0	0	1	?	?	?	?	1	1	1	1	2	1	1	0	?	1	0	0
Capromeryx	1	2	0	2	1	1	0	?	2	0	0	0	0	1	1	0	0	0	0	1	1	0	2	1	0	1	0	1	0	1	?	1	1	1	0	0	?	?	?	1	1	?	?	?	?	?	?	?	?	?	0	0	0
Ceratomeryx	1	2	0	2	1	0	0	?	2	0	0	0	0	1	1	0	0	0	0	1	1	0	?	1	?	1	0	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?
Cosoryx	1	1	?	2	1	1	1	0	2	1	0	2	0	1	2	1	3	2	0	1	1	0	1	1	0	2	0	1	1	1	1	1	1	2	0	2	0	0	0	0	?	?	1	?	1	2	?	1	0	1	1	1	0
Hayoceros	1	2	0	1	0	1	?	?	1	0	0	0	0	2	2	0	1	0	0	1	1	0	1	1	1	2	0	1	0	?	1	1	1	1	1	0	?	?	?	0	?	?	?	?	1	?	1	?	?	?	?	?	?
Hexameryx	1	2	0	2	0	1	?	?	1	0	1	0	0	2	1	0	0	0	0	1	1	0	?	1	?	2	0	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hexobelomeryx	1	2	0	2	0	1	?	?	1	0	1	0	0	2	1	0	0	0	0	1	1	0	1	1	0	2	0	1	1	?	?	1	0	1	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ilingoceros	1	2	0	1	0	1	0	?	1	2	0	0	0	1	1	2	2	0	0	1	1	0	0/1	1	0	?	?	1	0	?	?	1	1	2	0	0	1	?	?	0	1	1	?	?	?	?	?	?	?	?	?	0	?
Merriamoceros	1	2	0	1	1	1	2	0	2	1	1	1	0	0	?	?	?	1	0	1	1	0	0	1	?	?	?	?	?	?	?	1	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Merycodus	1	1	?	2	1	1	?	0	2	1	0	0	0	2	3	1	3	2	0	1	1	0	0	0	0	2	1	1	0	?	?	1	?	1	0	1	0	0	1	0	?	?	?	?	?	?	?	?	?	?	1	0	0
Osbornoceros	1	2	0	1	1	1	1	0	1	0	0	0	0	2	?	?	0	0	0	1	1	0	0	1	0	1	0	0	0	1	1	1	0	2	0	0	0	0	0	0	?	?	?	?	1	2	1	?	0	1	?	?	?
Ottoceros	1	2	0	1	0	1	0	?	1	0	0	1	0	1	?	1	2	0	0	1	1	0	0	1	?	?	?	1	0	?	1	1	?	?	?	?	?	?	?	?	0	1	1	?	?	?	?	?	?	?	?	?	?

Coded character matrix of 53 equally weighted morphological traits scored from specimens and photographs of 25 genera.

Appendix C. Continued

Character #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
Paracosoryx	1	1	?	2	0	0	2	0	1	1	0	0	0	1	1	2	2	2	0	1	1	0	2	?	1	2	1	1	2	1	1	1	0	2	0	0	?	?	?	0	?	0	1	?	?	?	?	0	?	?	1	0	0
Plioceros	1	2	0	1	1	0	0	?	2	1	0	0	0	1	0	1	2	2	0	1	1	0	0	1	1	2	0	1	0	?	1	1	0	2	0	0	0	0	0	0	0	1	1	?	1	2	1	1	0	0	1	0	?
Proantilocapra	1	2	0	1	1	0	0	?	2	2	0	0	0	1	0	?	2	2	0	1	1	0	0	1	1	2	1	0	0	?	1	?	0	1	0	?	1	?	?	0	?	?	1	?	?	?	?	?	?	?	?	?	?
Ramoceros	1	1	?	2	1	1	1	0	1	2	2	0	1	3	3	2	3	2	0	1	1	0	0	1	1	2	1	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	?	?	?	?	?	0	?	?	?	0	?
Sphenaphalos	1	2	0	1	0	1	0	?	1	2	0	1	0	1	1	1	0	1	0	1	1	0	0	1	0	1	0	1	0	?	?	0/1	0	2	0	0	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	0	?
Stockoceros	1	2	0	2	0	1	0	?	2	0	0	0	0	1	1	1	0	0	0	1	1	0	0	1	0	2	1	1	1	1	1	1	1	2	0	2	1	0	0	1	?	?	?	?	1	2	1	?	0	0	1	1	0
Tetrameryx	1	2	0	2	0	1	0	?	2	0	0	0	0	1	0	?	0	0	0	1	1	0	1	1	0	0	0	1	1	?	1	?	1	1	0	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Texoceros	1	2	0	2	0	1	1	0	1	0	0	0	0	1	1	1	0	0	0	1	1	0	1	1	0	2	0	1	0	?	?	1	0	2	0	0	?	?	?	?	?	?	?	?	1	1	0	?	0	1	1	?	?
Giraffa	1	1	0	2	0	1	1	0	1	0	0	0	0	0	?	?	?	0	0	1	1	0	2	0	0	1	?	0	0	?	1	1	0	2	0	2	?	0	?	?	?	?	1	?	?	?	?	1	?	?	?	0	0
Lama	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	1	0	1	?	2	1	0	0	?	?	1	0	1	?	0	1	0	?	1	1	1	1	?	1	1	0	0	0	0	0	0	1
Bison	1	2	0	2	0	1	0	?	0 1	2	0	0	0	0	?	?	?	2	0	1	1	0	0	1	1	1	1	1	2	0	1	1	0	2	0	0	1	0	1	0	?	0	1	0	?	?	1	0	?	?	?	1	0
Rangifer	1	0	1	2	0	1	1	1	2	2	0	1	1	3	0	2	3	1	0	1	1	0	0	1	1	2	1	?	?	?	?	?	?	1	?	?	1	?	?	?	?	?	1	?	?	?	?	0	?	?	?	0	0
Sus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	1	1	0	0	0	0	0	0	?	?	0	0	1	?	2	?	1	?	0	1	0	0	0	0	0	0	1	1	0	0	1	0

Coded character matrix of 53 equally weighted morphological traits scored from specimens and photographs of 25 genera.

APPENDIX D: SPECIMEN LIST

Museum Abbreviation	Specimen Number	Genus	Element
AMNH	FM 11094	*Antilocapra*	Dentary
AMNH	FM 130201	*Antilocapra*	Dentary
AMNH	FM 11094	*Antilocapra*	Skull
AMNH	FM 5036	*Antilocapra*	Limbs
AMNH	FM 2776	*Antilocapra*	Post Crania
UCMP	131828	*Antilocapra*	Horn core
UCMP	45196	*Antilocapra*	Skull
UNSM	50820	*Antilocapra*	Skull
UNSM	46612	*Antilocapra*	Ramus
AMNH	Mamm 98229	*Bison*	Skull
AMNH	Mamm 16309	*Bison*	Skull
AMNH	Mamm 16312	*Bison*	Skull
AMNH	Mamm 16340	*Bison*	Dentary
AMNH	Mamm 16378	*Bison*	Calcanea
AMNH	Mamm 16377	*Bison*	Phalanges
AMNH	Mamm 19380	*Bison*	Dentary
AMNH	FM 2771*	*Capromeryx*	Dentary
AMNH	FM 141303	*Capromeryx*	Dentary
UCMP	30337*	*Capromeryx*	Left dentary
UCMP	26648	*Capromeryx*	Skeleton
UCMP	13046	*Capromeryx*	Ramus
UNSM	5438*	*Capromeryx*	Partial skull
UNSM	5439	*Capromeryx*	Horn core
UNSM	88627	*Capromeryx*	Ramus
UNSM	21468	*Capromeryx*	Lft M1
UNSM	21450	*Capromeryx*	Lft M3
UNSM	21473	*Capromeryx*	Ramus
UNSM	88632	*Capromeryx*	Astragalus
UNSM	88634	*Capromeryx*	Ungual
AMNH	FM 51483	*Cosoryx*	Post crania
AMNH	FM 51055	*Cosoryx*	Post crania
AMNH	FM 31154*	*Cosoryx*	Horn core
AMNH	FM 9475	*Cosoryx*	Limb bones
AMNH	FM 30991	*Cosoryx*	Dentary
AMNH	FM 137179	*Cosoryx*	Horn core
AMNH	FM 51488	*Cosoryx*	Dentary
AMNH	FM 51398	*Cosoryx*	Dentary
AMNH	FM 32450	*Cosoryx*	Limb bones
AMNH	*FM 32900	*Cosoryx*	Horn core
AMNH	FM 32904	*Cosoryx*	Partial skull
AMNH	FM 32902	*Cosoryx*	Skull
AMNH	FM 32326	*Cosoryx*	Skull
AMNH	FM 31511*	*Cosoryx*	Skull
AMNH	FM 31435*	*Cosoryx*	Horn core
AMNH	FM 51055	*Cosoryx*	Skeleton
UCMP	16463	*Cosoryx*	Rt M1
AMNH	Mamm 81821	*Giraffa*	Skull

All catalogued specimens observed in collections throughout the study. Type specimens are designated by *.

Appendix D. Continued

Museum Abbreviation	Specimen Number	Genus	Element
AMNH	Mamm 81820	*Giraffa*	Skull
AMNH	FM 95264*	*Hayoceros*	Horn core
AMNH	FM 25526*	*Hayoceros*	Horn core
AMNH	FM 2772	*Hayoceros*	Dentary
AMNH	FM 25681	*Hayoceros*	Dentary
AMNH	FM 25680	*Hayoceros*	Dentary
AMNH	FM 25680	*Hayoceros*	Dentary
UNSM	2661	*Hayoceros*	Horn core
UNSM	88635	*Hayoceros*	Lft M3
UNSM	21445	*Hayoceros*	Ramus
UNSM	21458	*Hayoceros*	Ramus
UNSM	21447	*Hayoceros*	Ramus
UNSM	21453	*Hayoceros*	Lft M3
UNSM	21456	*Hayoceros*	Rt M2
UNSM	21452	*Hayoceros*	Lft M2
UNSM	88657	*Hayoceros*	Metacarpus
UNSM	88687	*Hayoceros*	Calcaneum
UNSM	88672	*Hayoceros*	Astragalus
UNSM	88692	*Hayoceros*	Cubonavicular
UNSM	88686	*Hayoceros*	Phalanx
UNSM	88679	*Hayoceros*	Phalanx
UNSM	88647	*Hayoceros*	Humerus
UNSM	88664	*Hayoceros*	Tibia
UNSM	88660	*Hayoceros*	Acetabulum
UNSM	88655	*Hayoceros*	Ulna
UNSM	88646	*Hayoceros*	Scapula
UNSM	88662	*Hayoceros*	Tibia
AMNH	FM 103347	*Hexameryx*	Horn core cast
CIT	2791	*Hexobelomeryx*	Dentary
CIT	2784	*Hexobelomeryx*	Ramus
CIT	2792	*Hexobelomeryx*	Dentary
CIT	277	*Hexobelomeryx*	Radii
LACM	78604	*Hexobelomeryx*	Metapodials
LACM	78602	*Hexobelomeryx*	Astragalus
LACM	78572	*Hexobelomeryx*	Rt p3
LACM	78608	*Hexobelomeryx*	Phalanges
AMNH	FM 32203	*Ilingoceros*	Horn core
UCMP	11893*	*Ilingoceros*	Horn core
UCMP	11880*	*Ilingoceros*	Horn core
UCMP	11882	*Ilingoceros*	Frontal
UCMP	11894	*Ilingoceros*	Horn core
UCMP	11892	*Ilingoceros*	Scapula/horn core
UCMP	13039	*Ilingoceros*	Dentary cast
LACM	14748	*Ilingoceros*	Humerus
LACM	147485	*Ilingoceros*	Acetabulum
LACM	147493	*Ilingoceros*	Dentary
LACM	147487	*Ilingoceros*	Metapodial

All catalogued specimens observed in collections throughout the study. Type specimens are designated by *.

Appendix D. Continued

Museum Abbreviation	Specimen Number	Genus	Element
LACM	147490	*Ilingoceros*	Calcaneum
LACM	147495	*Ilingoceros*	Tibia
LACM	147494	*Ilingoceros*	Humerus
LACM	147488	*Ilingoceros*	Phalanx
LACM	147479	*Ilingoceros*	Ulna
LACM	147480	*Ilingoceros*	Tibia
LACM	147492	*Ilinigoceros*	Tibia
UCMP	31365	*Illingoceros*	Horn core
AMNH	Mamm 80036	*Lama*	Skull/post-crania
AMNH	Mamm 147879	*Lama*	Skeleton
AMNH	Mamm 173571	*Lama*	Skull
AMNH	Mamm 126571	*Lama*	Skull
UOMNCH	2015-1-3	*Lama*	Skeleton
AMNH	FM 31177	*Merriamoceros*	Horn core
AMNH	FM 51338	*Merriamoceros*	Horn core
AMNH	FM 31025	*Merriamoceros*	Partial skull
AMNH	FM 51915	*Merriamoceros*	Ramus
AMNH	FM 31019	*Merriamoceros*	Dentary
UCMP	20052*	*Merriamoceros*	Horn core
CIT	3002	*Merriamoceros*	Horn core
CIT	3003	*Merriamoceros*	Horn core
AMNH	FM 51638	*Merycodus*	Rt dentary
AMNH	FM 51108	*Merycodus*	Partial skull
AMNH	FM 17339*	*Merycodus*	Skull
AMNH	FM 14102	*Merycodus*	Lft dentary
AMNH	FM 51790*	*Merycodus*	Dentary
AMNH	FM 31179	*Merycodus*	Horn cores
AMNH	FM 33121	*Merycodus*	Horn Core
UCMP	26795	*Merycodus*	Post crania
UCMP	12608*	*Merycodus*	Ramus
UCMP	13197	*Merycodus*	Cheek teeth
UCMP	13178	*Merycodus*	Rt m3
UCMP	13136	*Merycodus*	Horn core
UCMP	13062	*Merycodus*	Ramus
UCMP	13255	*Merycodus*	Limbs
UCMP	32110	*Merycodus*	Horn core
UCMP	32109	*Merycodus*	Dentary
UCMP	31137	*Merycodus*	Dentary
UCMP	63900	*Merycodus*	Dentary
UCMP	29927	*Merycodus*	Dentary
UCMP	33139	*Merycodus*	Metatarsal/carpal
UCMP	29233	*Merycodus*	Horn cores
UCMP	29334	*Merycodus*	Calcanea
UCMP	57855	*Merycodus*	Ramus
UCMP	19805	*Merycodus*	Dentary
UCMP	31157	*Merycodus*	Horn core
UCMP	31150	*Merycodus*	Tibia

All catalogued specimens observed in collections throughout the study. Type specimens are designated by *.

Appendix D. Continued

Museum Abbreviation	Specimen Number	Genus	Element
LACM	34825	*Merycodus*	Horn core
LACM	34827	*Merycodus*	Horn core
LACM	34830	*Merycodus*	Horn cores
LACM	34631	*Merycodus*	Molar
LACM	33385	*Merycodus*	Tibia
LACM	34220	*Merycodus*	Cheek tooth
LACM	34211	*Merycodus*	Dentary
LACM	34732	*Merycodus*	Horn cores
LACM	34784	*Merycodus*	Tibia
LACM	34772	*Merycodus*	Calcaneum
LACM	16390	*Merycodus*	Dentary
CIT	1264	*Merycodus*	Ramus
CIT	699	*Merycodus*	Horn cores
CIT	1259	*Merycodus*	Dentary
CIT	712	*Merycodus*	Dentary
UNSM	5036*	*Merycodus*	Skull
UNSM	83618	*Merycodus*	Dentary
UNSM	83631	*Merycodus*	Ramus
UNSM	83632	*Merycodus*	Dentary
UNSM	83653	*Merycodus*	M2
UNSM	83851	*Merycodus*	Horn core
UNSM	83648	*Merycodus*	p4
UNSM	83660	*Merycodus*	M3
UNSM	83656	*Merycodus*	Ramus
UNSM	93417	*Merycodus*	Skull
UNSM	93402	*Merycodus*	Dentary
UNSM	87972	*Merycodus*	Dentary
UNSM	87918	*Merycodus*	Skull
UNSM	87899	*Merycodus*	Skull
AMNH	FM 32985	*Osbornoceros*	Dentary
AMNH	FM 32980*	*Osbornoceros*	Horn core
AMNH	FM 32983	*Osbornoceros*	Ramus
AMNH	FM 32984	*Osbornoceros*	Ramus
AMNH	FM 32991	*Osbornoceros*	Tibia
AMNH	FM 53347	*Osbornoceros*	Horn core
LACM	1372*	*Ottoceros*	Skull
AMNH	FM 30991*	*Paracosoryx*	Rt ramus
AMNH	FM 137179	*Paracosoryx*	Horn core cast
AMNH	FM 51018	*Paracosoryx*	Ramus/post-crania
AMNH	FM 30988*	*Paracosoryx*	Left ramus
AMNH	FM 51013	*Paracosoryx*	Skull
AMNH	FM 31577*	*Paracosoryx*	Right dentary
AMNH	FM 51012	*Paracosoryx*	Skull
AMNH	FM 32856*	*Paracosoryx*	Horn core
AMNH	FM 33789	*Paracosoryx*	Skeleton
AMNH	FM 32470*	*Paracosoryx*	Skull
AMNH	FM 32474	*Paracosoryx*	Skull

All catalogued specimens observed in collections throughout the study. Type specimens are designated by *.

Appendix D. Continued

Museum Abbreviation	Specimen Number	Genus	Element
AMNH	FM 31682*	*Plioceros*	Horn core
AMNH	FM 95547	*Plioceros*	Horn core cast
AMNH	FM 52095	*Plioceros*	Dentary
AMNH	FM 52147	*Plioceros*	Skull
AMNH	FM 31570	*Plioceros*	Ramus
AMNH	FM 32101*	*Plioceros*	Skull/post crania
AMNH	FM 31570*	*Plioceros*	Ramus
UCMP	14489	*Plioceros*	Dentary
AMNH	F:AM 99252	*Proantilocapra*	Horn core cast
AMNH	FM 52147	*Proantilocapra*	Skull
UNSM	1095*	*Proantilocapra*	Partial skeleton
AMNH	FM 31348*	*Ramoceros*	Horn post
AMNH	FM 51303	*Ramoceros*	Horn core
AMNH	FM 51342	*Ramoceros*	Skull
AMNH	FM 31271*	*Ramoceros*	Horn post
AMNH	FM 51265	*Ramoceros*	Skull
AMNH	FM 51278	*Ramoceros*	Skull
UNSM	83574	*Ramoceros*	M3
UNSM	83576	*Ramoceros*	M2
UNSM	83608	*Ramoceros*	Astragali
UNSM	54890	*Ramoceros*	Tibae
UNSM	83544	*Ramoceros*	Horn core
UNSM	83543	*Ramoceros*	Horn core
UNSM	54016	*Ramoceros*	m2
UNSM	83586	*Ramoceros*	p4
UNSM	83553	*Ramoceros*	Ramus
UNSM	83545	*Ramoceros*	Metatarsals
UNSM	83564	*Ramoceros*	Cheek teeth
UNSM	83560	*Ramoceros*	m3
AMNH	Mamm 37408	*Rangifer*	Skull
AMNH	Mamm 122669	*Rangifer*	Skull
AMNH	Mamm 98151	*Rangifer*	Skull
AMNH	Mamm 12047	*Rangifer*	Dentary
AMNH	Mamm 122389	*Rangifer*	Skull
AMNH	Mamm 14240	*Rangifer*	Skull
AMNH	Mamm 14240	*Rangifer*	Dentary
AMNH	Mamm 17585	*Rangifer*	Skull
AMNH	FM 52046	*Sphenophalos*	Dentary
UCMP	11887*	*Sphenophalos*	Horn core
UCMP	35624	*Sphenophalos*	Tibia/astragalus
UCMP	12537	*Sphenophalos*	Horn core
UCMP	12611	*Sphenophalos*	Molar
UCMP	35625	*Sphenophalos*	Cheek teeth
UCMP	70308	*Sphenophalos*	Metatarsal
CIT	399	*Sphenophalos*	Skull cap
LACM	6655	*Sphenophalos*	Astragali
LACM	6664	*Sphenophalos*	Basioccipital

All catalogued specimens observed in collections throughout the study. Type specimens are designated by *.

Museum Abbreviation	Specimen Number	Genus	Element
LACM	6666	*Sphenophalos*	Calcaneum
LACM	90723	*Sphenophalos*	Phalanx
LACM	90716	*Sphenophalos*	Calcaneum
LACM	90715	*Sphenophalos*	Rt calcaneum
LACM	90712	*Sphenophalos*	Astragali
UNSM	2605*	*Sphenophalos*	Horn core
UNSM	2605*	*Sphenophalos*	Horn core
AMNH	FM 11094	*Stockoceros*	Limb bones
AMNH	FM 27018*	*Stockoceros*	Horn core/crania
AMNH	FM 22484	*Stockoceros*	Skull
AMNH	FM 22490*	*Stockoceros*	Dentary
AMNH	FM 22488*	*Stockoceros*	Skull
AMNH	FM 11094	*Stockoceros*	Crania
AMNH	FM 42523	*Stockoceros*	Right metatarsals
AMNH	FM 42524	*Stockoceros*	Left metatarsals
AMNH	FM 42745	*Stockoceros*	Phalanges
AMNH	FM 42747	*Stockoceros*	Unguals
AMNH	FM 42751	*Stockoceros*	Calcanea/astragali
AMNH	FM 42778	*Stockoceros*	Sacrum
AMNH	FM 42827	*Stockoceros*	Caudals
AMNH	FM 42753	*Stockoceros*	Axis
AMNH	FM 42752	*Stockoceros*	Atlas
LACM	154507	*Stockoceros*	Limbs
UNSM	39269*	*Stockoceros*	Horn core
UOMNCH	2015-1-7	*Sus*	Skeleton
AMNH	FM 13220*	*Tetrameryx*	Horn core cast
UCMP	32872*	*Tetrameryx*	Horn core
UCMP	38334	*Tetrameryx*	Skull
UCMP	38520	*Tetrameryx*	Dentary
LACM	174*	*Tetrameryx*	Horn core
LACM	1010	*Tetrameryx*	Pubis
LACM	209	*Tetrameryx*	Horn core
UNSM	05435	*Tetrameryx*	Dentary
UNSM	05436	*Tetrameryx*	Dentary
AMNH	FM 31312	*Texoceros*	Dentary
AMNH	FM 31645	*Texoceros*	Dentary
AMNH	FM 31765	*Texoceros*	Dentary
AMNH	FM 31645	*Texoceros*	Dentary

All catalogued specimens observed in collections throughout the study. Type specimens are designated by *.

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