

A cranium of *Navahoceros* and its phylogenetic place among New World Cervidae

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Received 9 June 1990, accepted 10 October 1990

The cranium of the Pleistocene deer *Navahoceros fricki* (Schultz & Howard) from Mexico is described and compared with other New World Cervidae. The sister group of *Navahoceros* is *Rangifer*, and these two genera together with *Blastoceros* and *Hippocamelus* form a distinct clade within the subfamily Odocoileinae.

1. Introduction

In 1975, Björn Kurtén based a new cervid genus, *Navahoceros*, on *Rangifer fricki* Schultz & Howard, 1935 from Pleistocene deposits in western United States and Mexico. Besides its formal generic name, he proposed the vernacular name “mountain deer”, as suggested by a combination of its geographic distribution and its short stocky limbs.

Although Kurtén (1975) diagnosed *Navahoceros* as a distinct genus, he deferred discussion of its broader relationships, making explicit comparisons only with two other North American genera, *Odocoileus* and *Sangamona*. In a later paper, primarily concerned with the stilt-legged *Sangamona*, Kurtén (1979:313) stated that *Navahoceros* “... may be related to the living South American *Hippocamelus*, from which it differs by the presence of three (rather than two) tines on the antlers.” Clearly *Navahoceros* shares with *Hippocamelus* very short cannon bones. In the case of the living Andean deer at least, correlation of its skeletal proportions with mountainous habitats is certain. In his excellent sum-

mary of North American Pleistocene Cervidae (Kurtén & Anderson 1980:115); Kurtén reiterates the probable relationship of *Navahoceros* and *Hippocamelus*, but also suggests an affiliation with *Rangifer*.

The purposes of the present contribution are first to describe the cranium of *Navahoceros*, and secondly, by comparing its cranial characters with those of other New World Cervidae, to further assess its phylogenetic relationships.

I am pleased to offer this contribution about Kurtén’s mountain deer to the memory of its discoverer.

2. Material and methods

The cranium of *Navahoceros* is best represented by LACM (CIT) 2351 from San Josecito Cave in southern Nuevo Leon, in the Sierra Madre Oriental of Mexico (Figs. 1–2). Although both sides of the ear region were in excellent condition, the left bulla was partly broken; it was therefore possible to remove the left petrosal for more detailed study (Fig. 3). I have made extensive



Fig. 1. Right lateral and dorsal view of cranium of *Navahoceros fricki*, LACM (CIT) 2351. 57% natural size.

comparisons between this cranium and those of the following living genera of New World Cervidae: *Blastoceras*, *Hippocamelus*, *Ozotoceros*, *Odocoileus*, *Mazama*, *Pudu* and *Rangifer*. All measurements are given in mm.

3. Description of cranium

The specimen LACM (CIT) 2351 is a nearly complete braincase of an adult female. It lacks the palate, the rostrum anterior to the cribriform

plate, much of the orbits and the zygomatic arches. The braincase measures 87.4 mm wide at its broadest point; among Odocoileinae, this width is exceeded only by that of *Blastoceras* and *Alces*.

Frontal

The frontals form a saddle-shaped surface with a broad shallow concavity anteriorly and a strong median convexity posteriorly. The fronto-parietal suture trends laterally and slightly posterior from the midline, with a strong posterior extension

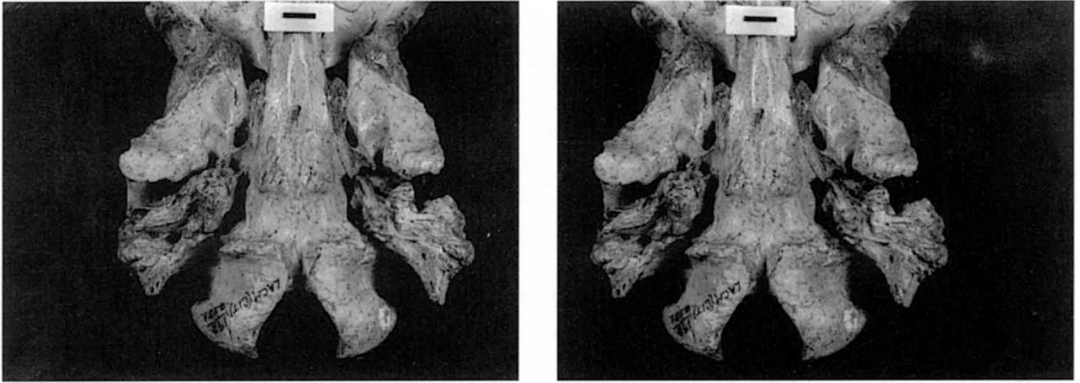


Fig. 2. Stereo view of basicranium of *Navahoceros fricki*, LACM (CIT) 2351. Scale bar 1 cm.

in the region where the antler pedicel would arise in a male skull. The frontal reaches a point about 40 mm behind the postorbital bar. The postorbital bar is about 13.5 mm wide at its upper end. It extends 25 mm from its origin, but is broken just at the point where it turns ventrad toward the jugal. The supraorbital foramen is about 5.5 mm in diameter and is set in a distinct longitudinal furrow; posterior to it are two smaller foramina for vessels which evidently drain the diploic bone of the frontal. Anterior to the principal supraorbital foramen are three more small foramina, only one of which transits ventrad from the dorsal surface of the frontal bone into the roof of the orbit.

Parietal

The dorsal exposure of the parietal is gently convex, and about 60 mm long. Its anterior width is about 74 mm, but it narrows posteriorly to 62 mm. Most of the dorsal surface is furrowed with minute foramina and relatively porous bone. This area is sharply delineated from the shinier, denser surface of temporal muscle origin by a pair of lyrate parasagittal crests. The narrowest gap between these crests, at the parieto-occipital suture, is 40 mm. In lateral aspect, the parietal contributes only the upper 1/4 of the temporal surface as in all of the larger *Odocoileinae*. In *Hippocamelus*, *Mazama* and *Pudu*, on the other hand, the parietal contributes the upper 1/3 of the temporal surface. The parieto-squamosal suture runs anteriorly horizontally about 67 mm; then it plunges

sharply ventrad to meet the alisphenoid, thereby separating the orbitosphenoid from the squamosal. The parietal deeply excavates the posterior face of the postorbital bar.

Occipital

The occipital contributes considerably to the dorsal surface of the braincase and is broadly continuous with the parietal. The parieto-occipital suture curves posteriad, terminating at the posterodorsal corner of the squamosal. The mastoid crest of the occipital extends ventrolaterally another 11 mm along the posterior edge of the squamosal to its junction with the upper end of the mastoid bone. The surface exposure of the mastoid extends as a narrow vertical plate compressed between the posterior face of the squamosal and the anterolateral edge of the occipital. A small mastoid foramen pierces the posterior face of the supraoccipital, marking the upper edge of the mastoid exposure.

The posterior face of the occiput is gently convex in both dorsoventral and mediolateral planes. It measures about 52 mm above the foramen magnum and about 112 mm across the broadest dimension of the mastoid exposures. The paroccipital processes of the exoccipitals just below the mastoids are robust, but in LACM (CIT) 2351 their tips are missing.

In its basicranial aspect (Fig. 2) the occipital is dominated by the very large, heavily buttressed condyles. Their greatest transverse diameter is 66.5 mm; while their maximum ventral width is

49 mm. These buttresses are much wider and thicker than in *Rangifer* which in turn are heavier than those in *Hippocamelus*. If the function of these ventral occipital buttresses is to prevent overflexing of the head, then their size in a genus with only three-tine antlers, especially in this female skull, is surprisingly large. The ventral condylar buttresses show no sign of bridging laterally toward the paroccipital processes as they do strongly in *Rangifer*.

In *Navahoceros* the condyloid and hypoglossal foramina exit the cranium close to one another in a common depression within the broader condyloid fossa in the same manner as in *Rangifer*. In *Blastoceras*, *Hippocamelus*, *Mazama* and *Pudu*, on the other hand, these two foramina are widely separated, the condyloid nerve exiting near the extreme dorsolateral position adjacent to the condyle.

Basioccipital

The width of the anterior part of the basioccipital is exaggerated by the presence of lateral crests extending partly across the very large median lacerate foramina. The widest diameter is 33.5 mm. A groove above the lateral crest represents the route of the inferior petrosal venous sinus as it drains into the jugular system. In *Navahoceros*, as in *Blastoceras*, this lateral crest of the basioccipital is better developed than that in *Rangifer* or *Hippocamelus*. In smaller forms such as *Odocoileus*, *Ozotoceros* and *Mazama*, the lateral wall has a flat or even concave profile and no crest is developed. Farther posterolaterally the posterior lacerate foramen is marked by a small semicircular notch on the anterior face of the basioccipital, presumably for passage of the internal jugular vein and cranial nerves IX and X. The posterior lacerate foramen appears to be similarly developed in all odocoileine crania except that in *Hippocamelus* there is an opposing groove that traces down the posteromedial face of the bulla.

The basilar tubercles for *M. rectus capitis ventralis* are large as in other large Cervidae. They are separated by a median groove as in *Rangifer* and *Blastoceras*, but unlike *Hippocamelus*, *Odocoileus* and smaller New World cervids where there is a distinct sagittal carina. A

carina does arise more anteriorly, however, on the basisphenoid. As it extends anteriorly it is perforated by a small, rough-edged fossa, closely resembling that in *Rangifer* and *Hippocamelus*, which lodges the posterodorsal corner of the elongated posterior ossification of the vomer, characteristic of Odocoileinae. Similar fossae are smaller and less consistently developed in *Odocoileus* and smaller members of the New World Cervidae.

Alisphenoid

In *Navahoceros* the foramen ovale is covered ventromedially by a broad flange of the basisphenoid, and this flange extends anteriorly to form a canal that evidently shielded the course of the mandibular nerve and vessels. A similar, albeit weaker, flange occurs in *Rangifer*, but is not evident in other Odocoileinae. The foramen ovale is only about 40 mm long; whereas in *Rangifer* for example it is nearly twice as long. Immediately anterior to that foramen, sharing a common depression, is a pterygoid foramen; the same arrangement (smaller foramen ovale and separate pterygoid foramen) occurs in *Hippocamelus*. Possibly the larger size of the foramen ovale in other taxa represents the addition within the same opening of the pterygoid foramen. The foramen orbitotundum is 7.5 mm wide and 12.1 mm deep. Its ovate outline is broken by an anterolateral cleft where the orbitosphenoid meets the alisphenoid. This strong cleft is characteristic of cervoids, but may become less obvious in older than in younger individuals.

The lateral wall of the alisphenoid is overlapped by a ventral projection of the squamosal just anterior to the foramen ovale; this feature does not appear in other Odocoileinae. The dorsal edge of the alisphenoid contributes to a large oblique tuberosity, the posterior third of which is completed by the squamosal; this tuberosity is 14 mm long by 5 mm thick and gives origin to the major tendon of *M. pterygoideus*.

Orbitosphenoid

The orbitosphenoid forms a subtriangular plate surrounding the optic foramen and covering much of the orbital wall of the braincase. Its base abuts

the pterygoid from the foramen orbitotundum to a point about 15 mm anterior to the optic foramen. Its dorsal apex extends about 30 mm anterodorsal to that foramen. The upper part of the orbitosphenoid is narrower anteroposteriorly than in *Hippocamelus*. The dorsal part of the orbitosphenoid lies 14 mm below the lower edge of the postorbital bar in *Navahoceros*, and at similar heights in *Blastoceras*, *Hippocamelus* and *Rangifer*; whereas in *Mazama*, *Ozotoceros* and *Odocoileus* it reaches up to about the same level as the postorbital bar.

Squamosal

The squamosal, as noted above, makes up about 3/4 of the lateral aspect of the braincase as in other large cervids. The area on the lateral wall dorsal to the glenoid fossa includes two small suprasquamosal foramina and a large, anteriorly-facing pocket for an anteroventral part of *M. temporalis*. The suprameatal fissure looms like an enormous cavern measuring 11 mm along its long posterodorsal axis. It includes the area that would ordinarily be called the postglenoid foramen. In *Blastoceras*, *Hippocamelus* and *Rangifer* this fossa is about half as large; the postglenoid foramen is separated from it by a bony constriction.

The glenoid fossa is broad and gently convex. The postglenoid process of the squamosal is strongly developed and is nearly 30 mm wide, although it is partly broken at its lateral edge. It is subdivided by a low middle area into a medial and a lateral postglenoid process. The medial postglenoid process weakly contacts the anterior edge of the bulla over a distance of about 10 mm. Its medial edge defines a distinct groove for an entoglenoid vein that passes laterally across the anterior face of the bulla to join other units of the venous sinus system in the postglenoid area.

Bulla

The auditory bulla generally resembles that of *Rangifer* and *Hippocamelus*. The anterior end bears a broad and prominent styloid process as in other Odocoileinae. The main, swollen portion of the bulla is 16 mm wide, and although it thus equals the bulla of *Rangifer* in size, it is not so

smoothly swollen as in that genus. The stylohyoid bone is 5 to 6 mm in diameter and forms a conspicuous channel extending posteriorly from the central apex of the bulla to its posterior edge. The raised edges of this channel are as prominent as in *Hippocamelus*. The large stylomastoid foramen lies immediately posterolateral to the stylohyoid bone and is almost entirely enclosed within the mastoid. It opens directly above the anteromedial edge of the paroccipital process, contrary to the more lateral position in many Old World Cervidae. In cross section the external auditory meatus is almost twice as tall (14.5 mm) as it is wide (8 mm); it bears a strong ventral keel as in *Rangifer* and *Blastoceras* but not *Hippocamelus*.

Petrosal (ventral surface) (Fig. 3)

The ventral surface is dominated by the long, narrow promontorium. In comparison with other Cervidae, *Navahoceros* is quite remarkable for the length of its promontorium which extends anteriorly as an unbroken convexity to the anterior tip of the petrosal. Although an anterior extension of similar length and position occurs in *Hippocamelus*, *Rangifer* and *Blastoceras*, it is much less prominent toward its anterior end. In *Mazama* and *Pudu* the anterior ridge is shorter, lower and blunt ended, and finally in *Odocoileus* and *Ozotoceros* it is not only shorter, lower and blunt, but it also turns medially forming an angle of about 45 degrees with the long axis of the promontorium.

A groove runs anteriorly along the medial edge of the promontorium from the medial side of the fenestra cochleae toward the median lacerate foramen. A similar feature is weakly developed in *Rangifer*. In *Hippocamelus*, *Blastoceras* and *Ozotoceros*, this groove continues medially and then gives rise to another that loops anteriorly along the middle of the promontorium.

The lateral side of the promontorium falls off abruptly as a nearly vertical face for the origin of *M. tensor tympani*, described more fully below. The only other Cervidae with comparably deep *M. tensor tympani* fossae are *Hippocamelus* and *Blastoceras*.

Near the posterior end of the promontorium, the osseous spiral lamina of the first (and largest)



Fig. 3. Stereo views of left petrosal of *Navahoceros fricki*. Upper pair in ventral view, lower pair in endocranial view. Natural size.

cochlear whorl produces a prominent convexity. This transversely-oriented convexity of the promontorium continues the whole distance to the medial edge of the promontorium. In this respect the promontorium resembles *Blastoceras* more closely than *Hippocamelus* or *Rangifer*.

The New World Cervidae appear to be divided into two quite distinct groups on the basis of the width and thickness of the medial edge of the petrosal. The larger taxa, including *Navahoceros*, *Blastoceras*, *Hippocamelus*, *Rangifer* and *Sangamona*, are distinguished by the great mass of dense, corrugated bone, the tegmen tympani, which extends horizontally adjacent to the promontorium and then, opposite the fenestra cochleae, rises vertically into a great pillar of bone joining the mastoid posteriorly. A ventral

part of this massive posteromedial wall of the petrosal braces against the basioccipital and farther posteriorly a concavity along its medial edge helps define the jugular notch. In the smaller New World genera, *Odocoileus*, *Ozotoceros*, *Mazama* and *Pudu*, the medial edge of the petrosal bone is relatively thin and extends no more than about 1 mm medial to the fenestra cochleae. In none of these Cervidae does the bulla contact the medial edge of the petrosal. This dichotomy in bone development along the medial edge of the petrosal may be size-related; presumably its more massive form in the larger genera simply fills a larger volume and adds structural support. Whether it also has some phylogenetic significance must be judged in the light of other, more elaborate characters.

The fossa for *M. stapedius* has a nearly circular outline centered posterior to the lateral wall of the fenestra cochleae. It closely resembles that of *Blastoceras* and differs from that of *Hippocamelus*, *Rangifer* and *Mazama*; in each of these latter genera the fossa is lozenge-shaped with its tapered end reaching the medial edge of the petrosal. In *Odocoileus* and *Ozotoceros* the fossa is much more transversely elongate, with an elliptical outline.

The ventral exit of the facial canal opens just anterolateral to the stapedial muscle chamber. Its oblique passage toward the stylomastoid foramen can be traced by a groove above the stapedial fossa from which it is separated by a wide ridge. A distinct terrace on that ridge represents the attachment of the stylohyoid bone which also crosses the posterior edge of the stapedial fossa; it is embryonically connected with the stapes as an adjacent part of the second branchial arch. This terrace, representing a well ossified connection of the stylohyoid into the medial side of the middle ear, is also well-developed in *Blastoceras*, *Hippocamelus* and *Rangifer*, but is only moderately so in *Ozotoceros*, *Odocoileus* and *Mazama*.

The largest fossa in the middle ear is that for *M. tensor tympani*. In *Navahoceros* the tensor tympani fossa is kidney-shaped, with its flat, medial side deeply excavated into the lateral wall of the promontorium and its dorsal rim very deeply incised. The size and shape of this fossa are almost identical in *Blastoceras* and *Hippocamelus* to that in *Navahoceros*; nonetheless in the former genera its encroachment into the promontorium is not so flat nor so vertical, and its dorsal rim is not so deeply incised. In *Rangifer* this fossa is subtriangular in outline and encroaches even less deeply into the promontorium than in the other large genera. Furthermore, in *Navahoceros* and the other two genera noted above, the posteromedial corner of the fossa reaches lateral to the fenestra vestibuli, whereas in *Rangifer* that corner of the fossa lies directly anterior to that fenestra. In *Odocoileus* and *Ozotoceros* the tensor tympani fossa is subcircular; and in *Mazama* it is long and narrow. In all of these smaller genera the fossa encroaches only moderately on the promontorium.

The fallopian aqueduct, through which the major petrosal nerve passes rostrally, opens

through the anterolateral edge of the petrosal near or on its ventral surface. There are remarkable differences in size and exact position among the various New World genera. In *Navahoceros* the aqueduct is a very small, horizontal slit just on the ventral surface of the petrosal immediately anterior to the marked deepening of the tegmen tympani. The aqueduct occupies the same position in *Blastomeryx*, *Hippocamelus* and *Rangifer*, but in *Rangifer* the opening is almost invisibly small, and may have been functionless; whereas in the two large South American genera the opening is many times larger than in *Navahoceros*. In *Odocoileus*, *Ozotoceros* and *Mazama* the aqueduct is small and lies on the extreme lateral edge of the petrosal.

Petrosal (endocranial surface)

On the endocranial surface of the petrosal the central feature is the large complex internal acoustic meatus. It is deeply pocketed in all of the New World Cervidae and is divided by a low ridge which runs sagittally to a point near its posterior end, then turns mediad. The ridge separates one large medial fossa from two smaller lateral ones. Near the anterolateral corner a large shallow groove representing the course of the facial nerve crosses posteromedially down the anterolateral surface of the meatus and plunges ventrad through the anterolateral fossa. A low angle view into the anterior wall of the facial canal reveals a small foramen which transmits the major petrosal nerve as it branches anteriorly from the facial nerve. There is also a posterolateral fossa of moderate size.

The medial half of the internal acoustic meatus consists predominantly of a large ovate fossa, the internal acoustic pore, which provides access to two small foramina. The anterior one is for the endolymphatic duct which follows a spiral course as it enters the chamber of the cochlea. The small posterior foramen transmits the auditory nerve through a small foramen into the vestibule.

With respect to the endocranial side of the petrosal, *Navahoceros* compares closely with both *Rangifer* and *Blastoceras*. In *Rangifer* as in *Navahoceros* the facial canal can be seen in dorsal view, as there is no overhanging bony lip, and the exit for the major petrosal nerve is small and

similarly placed in both genera. In contrast *Blastoceras* has a strong overhanging lateral lip and also a very large opening for the major petrosal nerve. *Hippocamelus* also has a large process overhanging the facial canal and hiding it from dorsal view. *Rangifer*, along with *Odocoileus*, *Ozotoceros* and *Mazama*, has the posterolateral fossa relatively much smaller and more medially placed relative to the facial canal than in *Navahoceros*.

In contrast with the very open contours of the internal acoustic meatus in *Navahoceros* and *Blastoceras*, four genera, namely *Rangifer*, *Hippocamelus*, *Mazama* and *Pudu* have the posterior wall closed in sharply by a broad posterior bony lip. This strikingly different configuration evidently represents encroachment by the anterior semicircular canal beneath the bone surface. In *Ozotoceros* the canal crosses the endocranial surface of the petrosal more obliquely, thus producing a limited overhang on the medial side only. In *Odocoileus* there is no overhang, for the canal is set back a short distance from the meatus, and it crosses the surface transversely.

The curious anterior encroachment of the anterior semicircular canal, noted above in *Mazama* and other taxa, also alters the relationship of the subarcuate fossa. In primitive ruminants the subarcuate fossa is usually pocketed deeply into the area enclosed by the posterior semicircular canal. In various more advanced ruminants it tends to be reduced in various manners. *Navahoceros* retains a small but deep subarcuate fossa in the far posterolateral corner of the petrosal

about as in *Ozotoceros*. In *Blastoceras* there is a broad shallow concavity in the same general area. *Odocoileus* has a moderately deep subarcuate fossa placed almost equidistant between the medial and lateral sides of the petrosal. In *Rangifer*, *Hippocamelus* and *Mazama* the area overlying the posterior semicircular canal forms a broad flat plateau. On the other hand, they do have a distinct subcircular fossa posterolateral to that plateau. Even though it has a different relationship to the semicircular canals, if it houses the flocculus of the cerebellum, it may be homologous to the subarcuate fossa.

4. Phylogenetic relationships

This discussion is based entirely on cranial characters derived from the foregoing description. The principal characters selected here are indicated in Table 1. The condition stated is presumed in each instance to be the derived character state. Genera that share the condition described in *Navahoceros* are listed. These characters require further comparisons and testing to more fully establish their polarities as well as their utility. This discussion of relationships among New World Cervidae is preliminary and in many respects incomplete. Phylogenetic hypotheses generated by the cranial characters considered here must be corroborated by dental and postcranial comparisons among fossil and recent taxa, and also by molecular and genetic techniques among living taxa.

Table 1. Character states (derived) in *Navahoceros*, and genera sharing the same state.

Character	<i>Navahoceros</i>			
1 Keel on anterior end basioccipital	absent	<i>Rangifer</i>		
2 Condylloid foramen next to hypoglossal	present	<i>Rangifer</i>		
3 Medial flange covers foramen ovale	strong	<i>Rangifer</i>		
4 Foramen ovale confluent with pterygoid foramen	absent			<i>Hippocamelus</i>
5 Orbitosphenoid apex well below postorbital bar	present	<i>Rangifer</i>	<i>Blastoceras</i>	<i>Hippocamelus</i>
6 Deep stylohyoid channel	present	<i>Rangifer</i>		<i>Hippocamelus</i>
7 Ext. aud. meatus with strong ventral keel	strong	<i>Rangifer</i>	<i>Blastoceras</i>	
8 Short, bent promontorium	absent	<i>Rangifer</i>	<i>Blastoceras</i>	<i>Hippocamelus</i>
9 Strong crest between fen. vestibuli and staped. fossa	strong	<i>Rangifer</i>	<i>Blastoceras</i>	<i>Hippocamelus</i>
10 Tensor tymp. fossa deeply excavated medially	present	<i>Rangifer</i>	<i>Blastoceras</i>	<i>Hippocamelus</i>
11 Fallopian aqueduct small	present	<i>Rangifer</i>		
12 Posterior rim of int. acous. meatus blocked	absent		<i>Blastoceras</i>	

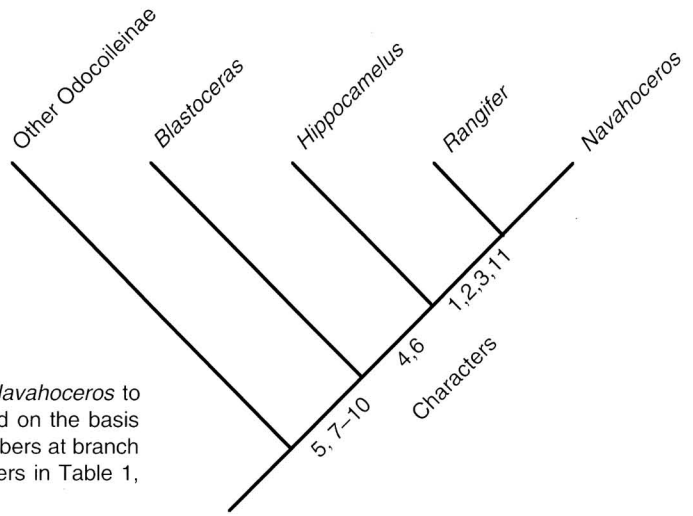


Fig. 4. Phylogenetic relationships of *Navahoceros* to other large Odocoileinae, hypothesized on the basis of cranial comparisons. Character numbers at branch nodes refer to shared derived characters in Table 1, see text.

A number of characters suggest a broad alliance between the two largest South American genera, *Blastoceras* and *Hippocamelus*, on the one hand and the North American genera *Navahoceros* and *Rangifer* on the other. These taxa separate repeatedly from the middle-sized genera, *Odocoileus* and *Ozotoceros*. For example, the latter have a short, "bent" promontorium instead of the long high promontorium (character 7) that is possibly the primitive condition in *Navahoceros*. The diminutive genera, *Mazama* and *Pudu* are even more frequently distinct from the others; for example they have thin-edged petrosals and narrow styloid processes on their bullae.

The problem thus narrows down to the detailed arrangement among the four larger genera noted above. The largest number of *Navahoceros* characters (1, 2, 3 and 11) are shared solely with *Rangifer*. A critical question concerns the polarities of these characters. For example, the first of these, the absence of keel on anterior end of basioccipital, may well be the primitive condition within Odocoileinae. (For that reason, Table 1 states it as the presence of a keel, the presumed derived condition within New World Cervidae). Characters 2 and 11, however, closely placed condyloid and hypoglossal foramina, and reduced Fallopian aqueduct, are almost surely synapomorphies of *Rangifer* and *Navahoceros*.

Once *Rangifer* is selected as the sister genus of *Navahoceros*, then *Hippocamelus* appears to

be their sister group. Character 6, deep stylohyoid channel on the bulla, diagnoses this phylogenetic group. It may be debated whether *Blastoceras* should replace *Hippocamelus* as the sister group of *Navahoceros* and *Rangifer*, as indeed character 12 suggests. The weight of the evidence, however, seems to rule out that alternative phylogenetic hypothesis. In any event the four larger Odocoileinae represent a fundamental clade within the New World radiation as indicated by a constellation of shared, derived characters (i.e. 5, 8, 9 and 10). This phylogenetic hypothesis is also supported by several dental characters that are beyond the scope of this study. The phylogenetic arrangement derived from this cranial analysis is presented as Fig. 4.

This leaves a number of historical questions unanswered, notably the questions of when and where these diverse genera originated. The northern genera, *Navahoceros* and *Rangifer*, do not appear to be the most primitive members of this clade; indeed the reverse may prove to be the case. The fossil record of Odocoileinae in North America and South America probably holds the answer. The question of how such South American genera as *Antifer* and *Morenelaphus* are related to *Navahoceros* and its three living relatives has not been explored on the basis of cranial remains, although the antlers suggest possible relationships to *Blastoceras* and *Rangifer* (Ubilla 1985). Clearly the cranium of *Navahoceros* will

provide an important datum point for future phylogenetic studies of New World Cervidae.

Acknowledgements. I thank Dr. David Whistler of the Los Angeles County Museum for loaning me the cranium of *Navahoceros* and for other advice concerning this study. Matt Joeckel prepared the photographs and provided valuable assistance on many aspects of ruminant cranial morphology. This research has been supported by National Science Foundation Grant no. BSR 8918065. This is contribution no. 371 from the Paleobiology Laboratory of the Florida Museum of Natural History.

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