THE OCCURRENCE AND PHYLOGENETIC STATUS OF MERYCODUS FROM THE MOHAVE DESERT TERTIARY

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CONTENTS

INTRODUCTION

The collections of the University of California Museum of Paleontology contain a fairly representative assemblage of *Merycodus* skeletal elements from the Great Basin province. During the collecting seasons of 1925 and 1926, Miss Annie M. Alexander and Miss Louise Kellogg discovered in the Barstow and the Ricardo deposits of the Mohave Desert unusually complete series of limb bones associated with *Merycodus* skulls. The associated skeletal remains, with the numerous dissociated limb bones, cranial bones, and teeth from these and other localities, afford opportunity to observe the constancy of osteological characters within this group as well as a sound basis for morphological comparison with other genera of the Antilocapridae and Cervidae.

The concensus of opinion among American paleontologists, who have described and discussed the genetic relationships of *Merycodus,* places the genus in the Antilocapridae. The following account may serve to emphasize the soundness of the view.

The earlier collections from the Mohave Tertiary beds described by Merriam[1] include a cranium from the Barstow, broken antlers, rami, teeth, and fragmental limb elements. These remains were referred to *Merycodus necatus* Leidy and to *M. furcatus* Leidy. Two species are now recognized from these deposits based upon characters established by Matthew[2] and earlier writers.

ACKNOWLEDGMENTS

In addition to the *Merycodus* specimens in the University of California Museum of Paleontology, largely collected through the field work supported by Miss Annie M. Alexander, it has been my privilege to examine many specimens in other museums.

For the use of specimens in the American Museum of Natural History, New York, and for valuable suggestions, I am indebted to Dr. W. D. Matthew. Mr. Childs Frick of the same institution kindly allowed me the privilege of examining merycodont material recently secured by him from the Santa Fé deposits. For like courtesies I wish to express my thanks to the following gentlemen and institutions: C. W. Gilmore, Curator, Division of Vertebrate Paleontology, United States National Museum; Dr. W. J. Sinclair, Princeton University; Professor Richard S. Lull, Peabody Museum, Yale University; and Professor F. B. Loomis, Amherst College, New Haven. Dr. William Alanson Bryan, Director of the Los Angeles Museum, kindly loaned *Capromeryx* material, and Dr. J. Grinnell, University of California Museum of Vertebrate Zoology, granted the use of recent antilocaprid and cervid specimens.

For criticism of the paper in manuscript and for kindly interest throughout this study, I am indebted to Dr. Chester Stock, California Institute of Technology, Pasadena, California.

The wash and line drawings were made by Mr. John L. Ridgeway of the Carnegie Institution, Washington.

[1] Merriam, J. C., Tertiary mammalian faunas of the Mohave Desert. Univ. Calif. Publ. Bull. Dept. Geol., vol. 11, no. 5, 1919.

[2] Matthew, W. D., Third contribution to the Snake Creek fauna. Bull. Am. Mus. Nat. Hist., vol. 50, pp. 198–206, 1924.

DESCRIPTION OF MATERIAL

MERYCODUS NECATUS Leidy

U. C. Mus Pal. Vert. Coll. no. 26781; U. C. loc. A288, Barstow, California.

No. 26781 comprises a relatively complete cranium with antlers, detached right maxillary with cheek dentition, right and left rami with cheek dentition, a number of cervical vertebrae, sacrum, hip bones, and fore and hind limb bones. From the same deposits are many antlers, series of superior cheek teeth, detached teeth, lower jaws with teeth, and also limb elements.

The cranium, no. 26781 (pls. 24, 25), bears right and left antlers with burrs partly broken away. The right antler shows a multiplicity of rings, a condition quite commonly occurring in specimens from the Mohave Tertiary (pl. 24, fig. 1). The burrs occur on the beam midway between the superior orbital rim and the fork. The beam is relatively short compared with the tines, of which the anterior is the longer by 12 mm. The beams above the burrs flatten laterally and broaden anteroposteriorly to the fork, where the tines arise with a slight forward curvature. The tines are not widely spread at the base, and from the fork, distally, form a deep, rather narrow V (pl. 25).

In no. 26781 the rami are broken away immediately behind the symphysis, the right just posterior to $M_{\overline{3}}$, and the left, a short distance farther (pl. 25). The premolar-molar tooth series is complete in the right jaw and the molar series in the left jaw.

Limb bones.—The limb elements, of which there is a relatively complete series, are like those in *M.* cf. *furcatus*, no. 26795, and will be discussed later.

MERYCODUS cf. FURCATUS Leidy

U. C. Mus. Pal. Vert. Coll. no. 26795; U. C. loc. A289, Ricardo, California.

The skull in no. 26795 (pls. 24, 26, 27) is more complete than no. 26781 from the Barstow in that it has both maxilli with teeth. Associated rami and appendicular skeletal elements are present. As in the case of the Barstow collection, Ricardo beds have furnished many fragmental jaws with teeth, antlers, and limb bones.

The cranium, no. 26795, supports a perfect pair of antlers. The antlers differ from those in *M. necatus*, no. 26781, in the length of beam and absence of burrs. The tines are relatively short, compared with the length of beam. The beam is 101.4 mm. long, whereas in *M. necatus,* no. 26781, it measures 45.5 mm. The anterior tine extends 80.8 mm. and the posterior, 47.0 mm. above the fork, while in *M. necatus,* no. 26781, they are respectively 82.9 mm. and 72.8 mm. Hence it will be seen that the tines are shorter in relation to beam in *M.* cf. *furcatus* than they are in *M. necatus,* but are actually longer in the latter genus.

In *M.* cf. *furcatus* the anterior tine curves to the rear and the posterior tine curves forward, the space between is wider than that in no. 26781 and is U-shaped (pl. 26).

The beam commences to flatten laterally, with the distal third of the shaft, to the point of forking. The flattened area and the posterior tine is rotated outward and causes an oblique alignment with the longitudinal axis of the skull for the distal two-thirds of the antler (pl. 27). From base to tip the antlers are slightly divergent. In *M. necatus,* no. 26781, the antlers from base to tip are parallel with the longitudinal axis of the skull and converge distally.

In no. 26795 the right ramus lacks the top of the coronoid process, the condyle, and the emarginate part of the angular (pl. 26). It is otherwise complete, with full incisor and premolar-molar dentition. The left ramus is broken away anterior to P_4 and just back of M_3.

Limb bones.—The limb elements are well represented and will be discussed with those of no. 26781.

STRUCTURAL CHARACTERS OF MERYCODUS

Skull

Basicranial region (pls. 24, 27).—The basioccipital is transversely convex between the tympanic bullae as in *Capromeryx mexicana.* This region in *Antilocapra americana* and *Odocoileus columbianus* is broad and relatively flat. The tympanic bullae are relatively low and elongate, not pyramidal as in the compared genera. The styliform process, conspicuous in the deer, is vestigial or absent in nos. 26648 and 26795. In *O. columbianus* the bulla is relatively short anteroposteriorly and rises medially in a sharp apex; in *A. americana* the anteroposterior diamater is greater but the bulla rises to a median apex and in *C. mexicana* the bulla is high and broadly inflated.

The paroccipital processes are broken but the basal part indicates that they were more closely appressed to the bullae than in *A. americana* or *O. columbianus.*

The tympanohyal pit, as in the Antilocapridae, is situated laterally at the confluence of the bulla and auditory meatus, not at the outer posterior border of the bulla as in the deer.

The auditory meatus is similar to that in the Antilocapridae in its posterodorsal plane. This element in *O. columbianus* is directed more at right angles to the long axis of the skull and opens distally on an horizontal plane.

The basicranial elements are more closely compacted in the Antilocapridae than in the deer. The foramina preserved in no. 26781 exhibit characters closer to *A. americana* than to *O. columbianus.*

The postglenoid process is not so pronounced as in the deer, and the postglenoid border, as in the Antilocapridae, is produced in an unbroken line dorsoposteriorly to the lateral margin. In *O. columbianus* the postglenoid line is rather deeply concave medially at the postglenoid foramen and toward the outer margin is depressed ventrally.

Basi-facial region (pl. 24).—The premaxillae and the maxillae anterior to Pm^2 and midpalatine part of the skull are broken away. This is true also of the pterygoid region. There is an indication of the posterior palatine foramen in no. 26795 between M^2 and M^3. This foramen is present in *C. mexicana* opposite M^2. It is large in *A. americana,* between M^2 and M^3, while in *O. columbianus* it is very small and opposite the protoconal pillar of M^2.

The postpalatine maxillar notch extends forward to a line even with the posterior face of the hypoconal pillar of M^3, as in *A. americana.* In *O. columbianus* the notch extends forward to a point opposite the protoconal pillar of M^3.

The postnarial notch is U-shaped. It is the same in *A. americana* and in *O. columbianus.* The notch is V-shaped in *Capromeryx mexicana* and in Grants gazelle. In *Merycodus* and *A. americana* the *notch* terminates at a line drawn between the posterior margins of the third molars. The postnarial notch in *C. mexicana, Tetrameryx schuleri,*[8] and Grants gazelle extends to a point between the posterior lobes of the third molars. In *O. columbianus* the notch does not approach the palatine surface, nor is it deeply incised, also it terminates back of the extreme posterior margin of the maxillae.

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[8] Lull, R. S., Fauna of the Dallas sand pits. Am. Jour. Sci., vol. 11, 1921.

Facial region. (pls. 25, 26).—The premaxillary and nasal bones are not present in *Merycodus,* nos. 21551, 26795, 26781, nor in *Capromeryx,* no. 26648. In nos. 26781 and 26795 the maxillaries are complete back of Pm^2 with the full cheek dentition. The molar and lachrymal bones and the anterior margins of the frontals are crushed so that the suture lines are somewhat obscured. However, the lachrymal maxillary suture is distinct enough to show that the vacuity terminates posterior to the posterosuperior border of the maxillary and does not extend into the maxillary as in *O. columbianus.* The lower and anterior margin of the vacuity is well defined and shows the opening to be much like that in *A. americana,* though apparently directed closer to the longitudinal axis of the skull, and, as in *A. americana,* the vacuity extends along the dorsal face of the frontals, while that in the deer examined is confined to and terminates along the anterolateral border of the frontal.

The lachrymal, though crushed, shows no evidence of a pit, and if reconstructed would closely approximate the full preorbital contour of *A. americana.*

The frontal, lachrymal, and jugal form a tubular orbit as in *A. americana.* The preorbital rim projects laterally and is not appressed as in the deer.

Cranial region (pls. 24–27).—In no. 26795 the cranium is crushed dorsoventrally. The cranii in nos. 26781 and 21551, while fractured in places, have not lost their normal symmetry.

The frontoparietal suture in all the specimens extends from the inner posterior base of the horn cores and curves posteriorly to meet in the sagittal line 17 mm. (no. 26781) back of the base of the horns.

In *A. americana* the frontoparietal suture is transverse to the long axis of the skull and curves medially near the sagittal line to form a >, the apex pointing forward.

In *O. columbianus* this suture passes from the posterior base of the antler anteriorly to a point in a transverse line drawn between the anterior margins of the base of the antlers, and from thence it turns medially to the sagittal line.

In the *Merycodus* skulls the frontals are abruptly depressed just anterior to the antlers and flatten out anteriorly to the frontonasal suture. The depression in *A. americana* occurs more posteriorly, between the middle axis of the horn cores and about in line with the posterodorsal rim of the orbits. In *O. columbianus* the frontals arch down out from beneath the posterior third of the orbits.

The dorsal surface of the parietal has a decided, transverse convexity, not broad and relatively flat as in *A. americana* and *O. columbianus.* The temporal ridges are distinct and abruptly converge to form a sagittal ridge anterior to the supraoccipital. The squamosal and parietal bones are inflated laterally, considerably more so than in *A. americana.* The corresponding bones in *O. columbianus* are very slightly arched and the squamosal presents an almost flat, vertical lateral face.

The parietal and squamosal elements are depressed anterior to and above the auditory meatus along the mastoid and supraoccipital suture lines. This gives rise to pronounced lambdoidal and supraoccipital crests.

The supraoccipital is narrow and high. In posterodorsal aspect it is broadly >-shaped, the apex forward, and depressed medially. The lateral margins form sharp ridges that pass forward to meet the temporal ridges near the sagittal line. Posteriorly the lateral margins curve laterally and ventrally to form, with the mastoid and exoccipitals, the lambdoidal crest.

The supraoccipital in *A. americana* is relatively broad with no crest; the interparietal area is slightly depressed and the temporal ridges are widely separated. The lambdoidal crests are appressed.

In *O. columbianus* the supraoccipital is very broad, the lateral sutures meeting the posterodorsal extremity of the squamosal. It is flat with a greater dorsal surface than in *A. americana.*

In nos. 21551 and 26781, the exoccipitals join posteriorly in the middle line to form a broad dorsoventral, concave ridge, on both sides of which the exoccipitals are concave. Dorsally, the median ridge contracts and the supraoccipital forms an inyon that overhangs the exoccipitals.

The median ridge formed by the exoccipitals in *A. americana* is relatively sharp and narrow and describes a straight line dorsoventrally. The exoccipitals are concave from the median line to the lambdoidal crests and supraoccipital processes. Posteriorly the supraoccipital is in a dorsoventral plane with the exoccipitals.

The median ridge in *O. columbianus* is most pronounced near the supra- and exoccipital suture. The exoccipitals form a slightly concave-convex surface across their transverse diameter and flatten laterally to their outer margins.

Horns

It will not be necessary in this paper to enter fully into the classification of *Merycodus* with Cervidae made by Winge[4] and Hilzheimer,[5] for Matthew[6] has specifically replied to their contention for so doing.

Characters heretofore not illustrated are figured with reference to their description. This applies particularly to the carpal and tarsal elements and the metatarsus; also to antlers and sections of antlers. However, Cope[7] early recognized the character of *Merycodus* (*Dicrocerus*) antlers, and accordingly separated them from the deciduous type of antlers characteristic of the deer and placed the genus in the *Antilocapridae*.

Merycodus horns.—In a discussion of the Mohave Tertiary merycodont horns we at once meet (as has also been the case with specimens from other localities) a skull element that in some ungulates is subject to change through disturbed physiological conditions. Sports and lack of symmetry in horn growth are in general readily recognizable as caused by physiological disturbances.

Merycodus horns are peculiar in that they may or may not have burrs in the same species.

As in the Cervidae, their branching and the relative length of beam to tine may show a considerable degree of variation between individuals of the same species. The most constant characters exhibited by *Merycodus* horns are their outgrowth from the frontal bone above the supraorbital rim, and their vertical or anteriorly inclined position, from base to tip, in relation to the basicranial axis of the skull.

The variability in *Merycodus* horns is apparently not due to the same physiological causes that effect the abnormal growths in individuals of the Cervidae and members of the Bovidae. If in *Merycodus* the cause can be attributed to a physiological condition it must have been effective throughout the whole group and would be indicative of a decided change going on in the horn structure during late Miocene and Pliocene time. It is possible that this group of indi-

[4] Winge, Jordfundne og nulevende Hovdyr (Ungulata) fra Lagoa Santa etc., E. Museo Lundi, 111, part 1, p. 221, 1906.

[5] Hilzhilmer, Centralblatt f. Min. Geol. u. Pal., p. 745, 1922.

[6] Matthew, W. D., Contributions to the Snake Creek fauna. Bull. Am. Mus. Nat. Hist., vol. 38, art. 7, 1918.

[7] Cope, Am. Nat., March, 1889.

viduals, of wide geographic range in North America, was being transformed, through changing conditions of habitat and environment, to a type better fitted for continuance; hence such Pleistocene and recent animals as *Capromeryx californicus, C. mexicanus, Tetrameryx schuleri,* and *Antilocapra americana.*

No specimens or records examined show the horn shed from above or at the burr. The horns preserved commonly occur with part of the frontlet, and the majority of specimens are usually broken off some distance above the burr, or have one tine broken, or both tines broken at or just above the point of forking. If these animals annually shed their horns it appears reasonable to suppose that, among so many specimens occurring in the fossil record, some would show the separation of the beam carrying the tines at the point of normal separation in the region of the burr, as in the deer.

The texture of the bone, studied in longitudinal and transverse sections, shows the bone tissue to be of relatively uniform character from base to tip. In the Cervidae, Macewen[8] has shown that preceding and immediately following the shedding of the antlers (in other words, accompanying the phenomenon of the loss of the old, and growth of the new antler), there is a stimulation of the growth of the bone tissue. This is expressed in the enlargement of the bone tissue sinuses in the frontal bone just above the orbit, in the basal part, and in the pedicle of the antler.

The uniform structure (pls. 25, 26) in *Merycodus* horns indicates that no changes of the type above cited occur in the bone tissue. The burrs are not ankylosed to the beam nor does this tissue form any part of the beam as in *Odocoileus.* The burrs are readily detached from the beam, and the underlying surface shows very little or, in many cases, no scar to mark the place where the burr has been. The shallow, longitudinal surface grooves extend along the length of the beam from the base upward and pass in an unbroken course under the burr (pl. 25, fig. 2). A transverse section through the burr and underlying beam shows a distinct line of demarcation between the two (pl. 26, fig. 5). This dividing line is also apparent in the longitudinal section (pl. 26, figs. 3, 4).

When burrs encircle a tine (pl. 25, fig. 6) or occur high up on the beam (pl. 27, figs. 5, 6) the burr may correspond to the callus of a healed, broken bone. The frequent occurrence of apposable rings

[8] Macewen, Sir William, The growth and shedding of the antlers of the deer, Glasgow, 1920.

or burrs, sometimes three or four, in the majority of cases not far above the frontal bone (pl. 25, figs. 1–5) though in some instances not far below or at the bifurcation (pl. 25, fig. 6; pl. 27, figs. 5, 6), negatives this view.

It is not probable that a horn would break or be injured in the same place three or four times. It necessarily follows that the multiplicity of burr rings is due to some other cause than the breaking of beam or tine, particularly when the bone tissue of beam or tine shows no coalescence with the encircling burr.

The numerous nutrient sinuses (pl. 25, figs. 1, 2) show that the antlers had a covering integument of sheath or velvet. It is very probable that the horn covering was rubbed off or shed seasonally.[9] At the time of seasonal change, the nutrient vessels became constricted above the cranial integument which reaches, normally, midway or for a lesser distance toward the fork, although in some exceptional cases much higher. At the point of division between cranial and antler integument, the burrs were formed from mesodermic tissue accompanying the integumental growth. The burrs, then, may be regarded as the terminal point of the heavier skin covering of the head, and the initial point of growth of the lighter covering of the antlers.

The variability in the same species, expressed by the possession or lack of burrs, indicates a change through adaptation by atrophy, or possibly a sex difference.

The variability in size, proportion, and shape (pl. 28, figs. 1–3) of antlers may be of specific or subspecific value. This can best be determined, however, when the extreme forms are found with the parent skull and dentition; otherwise, a number of species might well be erected on the basis of the Barstow Ricardo merycodont antlers. At the present time the numerous teeth and jaw fragments from the same localities show no characters upon which a separation can be made.

Although antlers have been considered as not yielding essential characters pointing to the relationships of types, they may furnish us with important data of phylogenetic value, particularly when more complete skeletons of *Merycodus* are discovered.

In further study, no. 26795 may be found to exhibit certain characters of antler, for example, size and proportion, as well as

[9] In no. 26781 the point of one front and of one rear tine on opposite sides are beveled medially as though from abrasion.

relationship of antler to cranium, of sufficient value to warrant the recognition of this form as specifically distinct from *M. furcatus*. For the present, however, no. 26795 is referred to *M. furcatus*.

A question may be raised as to the possibility that the morphological characters of the antlers studied above result from the fact that the *Merycodus* specimens found in the Barstow and Ricardo deposits were all laid down during seasons prior to the time of antler shedding. This position seems hardly tenable in view of the many specimens of antlers, which have been found in widely separated regions in North American Tertiary formations. Also, their discovery in deposits containing plant remains and silicified wood, suggestive of a semi-arid plains environment, would tend to negative such an assumption. Certainly more information is needed concerning the conditions under which merycodont remains have been entombed and preserved, the probable habit of the animals, and their seasonal changes. For the present the view is held by the writer that the habit of these mammals was adjusted in large measure to a plains type of environment, but the forms probably frequented stream courses and lake banks. If this view be correct, remains of *Merycodus* present under these conditions and representing different stages in the growth of the animal and its seasonal changes, would furnish a relatively complete dental and osteological record for this mammal.

Mandible

The right ramus (pl. 26, fig. 1), *M.* cf. *furcatus* no. 26795 and (pl. 25, fig. 1) *M. necatus* no. 26781, of the *Merycodus* jaws available show the characters most completely.

Two dental foramina are present. The anterior foramen is large, situated 30 mm. in advance of $P_{\overline{2}}$. The small foramen is 10.3 mm. in advance of $P_{\overline{2}}$. In *A. americana*, University of California Museum of Vertebrate Zoology (hereafter mentioned as U. C. M. V. Z.) no. 8299, the foramina are relatively smaller and correspond in position to those in *Merycodus*. In *Capromeryx* the large foramen is midway of the diastema, the small one between $P_{\overline{2}}$ and $P_{\overline{3}}$. The small foramen is not present in specimen U. C. M. V. Z. no. 20597 and the anterior foramen is relatively larger. The mental foramen is situated like those in the compared genera of the Antilocapridae and is not so high in the ascending ramus as in *O. columbianus*, no. 20597.

The ramus is 146.2 mm. long and 22.7 mm. wide back of M_3, with a relatively long diastema. The ascending ramus rises gradually from the alveolar border, posteriorly inclined as in *A. americana,* rather than abruptly, as in *O. columbianus.* The ascending ramus in *C. minor* Taylor,[10] no. 20036,[11] rises less abruptly than in *O. columbianus* but more so than in either *M.* cf. *furcatus* or *A. americana.*

In *Merycodus* cf. *furcatus* the angle is like that in *A. americana,* not produced in a prominent descending process as in *O. columbianus.* The angle in *M.* cf. *furcatus* gradually ascends with no posterior extension of margin to the margin of the ascending ramus.

The prominent angular process is a cervid character not seen in any of the bovid genera examined.

Dentition

Plates 24, 25, 26

The upper and lower dentition of *M. necatus,* no. 26781, shows a stage of wear comparable to that presumably occurring in middle adult age, while *M.* cf. *furcatus,* no. 26795, shows a stage of wear indicative of early adult age. In other specimens various stages of wear, from milk teeth to old adult teeth, give a wide age range of tooth pattern for comparison, particularly of the inferior teeth.

The development of artiodactyl teeth has been discussed by Loomis[12] and on the basis of premolar tooth pattern he has grouped *Merycodus* teeth with dentitions of typical deer. In this grouping no account is taken of the hypsodont character of the *Merycodus* molars; the paper deals principally with the evolution of tooth pattern. *Antilocapra,* on the basis of the dentition, is grouped with the goats and sheep, or Bovidae. On the hypothesis of premolar tooth pattern alone, *Merycodus* is removed from the hollow-horned ruminants and separated from the Antilocapridae, and, by inference, placed in the Cervidae.

The taxonomic position of *Merycodus* should not be confused on the basis of the premolar tooth development alone. As Loomis has pointed out we will probably have to look to the Eocene and early Oligocene for the original branching of the different groups of the Artiodactyla.

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[10] Taylor, W. P., Univ. Calif. Publ. Bull. Dept. Geol., vol. 6, pp. 191–197, 1911.
[11] Chandler, A. C., Univ. Calif. Publ. Bull. Dept. Geol., vol. 9, pp. 111–120, 1916.
[12] Loomis, F. B., Bull. Geol. Soc. Am., vol. 36, 1925.

It is not improbable that the Cervidae and Antilocapridae converge to a common ancestry in the early Tertiary, and it is not strange that they have many characters in common. However, in *Merycodus*, the highly specialized characters, expressed in the supraorbital position of antlers, skull and limb characters, and hypsodont molar teeth (characters that closely approximate those in the Antilocapridae and are unique as compared with the typical American deer *Odocoileus* or *Cervus*) evidence their closer relationship to the Antilocapridae.

In *M. necatus*, no. 26781, the right maxillary has all the cheek teeth from P^2 to M^3 inclusive (pl. 24, fig. 2). The right ramus of the same individual has the full cheek tooth dentition (pl. 25, fig. 1).

Superior dentition.—P^4 is a single-pillared, crescentic tooth with one inner and two outer roots. The buccal surface is characterized by three distinct styles, the intermediate style relatively close to the anterior style as in *A. americana*, U. C. M. V. Z., nos. 8299 and 19231, although in the latter genus all the premolars are hypsodont. The lingual surface is continuous with the posterior face of the tooth and is shaped like the inner anterior crescent of the molar tooth. It is similar in this character to *A. americana* though in the latter, due to increased size, the crescent is less angular than in *M. necatus*. In P^4 of *O. columbianus*, of the outer styles, the innermost primary crest is more medial than in *M. necatus*. However, it converges proximally to the cingulum, to the anterior style as in *M. necatus*. The lingual surface in the deer, from the unworn to the much worn stage, forms a broad crescent with the anterior and posterior walls of the tooth. In *M. necatus* the crescent is narrow anteroposteriorly and the end walls are practically straight from the crescent to the outer styles. The tooth is not quadrate as in *Tetrameryx schuleri* Lull.[13] The crescent in P^4 of *A. americana* is similar to that in the deer, and in the worn tooth it is intermediate between those in *M. necatus* and in *O. columbianus*. The front horn in the basin in *M. necatus* extends to the anterior style or crest in the unworn tooth and recedes toward the center of the basin with wear. The posterior horn in the unworn teeth remains within the anterior two-thirds of the crown; thus the whole basin is anteriorly placed, but not to the same extent as in P^3 and P^2.

M. necatus P^3 (pl. 24, fig. 2) in anteroposterior diameter is relatively longer, as compared with the transverse diameter, than is P^4. The crests and basin, except for the fact that the latter is

[13] Lull, R. S., Fauna of the Dallas sand pits. Am. Jour. Sci., vol. 11, 1921.

confined to the anterior half of the crown, are quite similar to P^4. The crescent is broadly rounded, not narrowed anteroposteriorly as in P^4.

The superior molars are high-crowned and short-rooted and not so hypsodont as in *A. americana.* They occupy, in this character, a position midway between the long-rooted and short-crowned molars of *O. columbianus* and the hypsodont molars of *A. americana.* M^1 in *M. necatus,* no. 26781, shows the greatest amount of wear of the premolar-molar series, the anterior lake being obliterated. It is a much smaller tooth than M^2 and M^3. These teeth exhibit no anterior or posterior intermediate crests as do the slightly worn teeth of *O. columbianus,* no. 20597. M^3 in *M. necatus,* nos. 26781, 26884, 26885, has well developed postero-external styles, which are absent in *O. columbianus,* and which probably foreshadow the broad, posterior lobe of M^3 in *Capromeryx mexicana,* no. 26648, and in *A. americana,* U. C. M. V. Z. nos. 19231 and 20597.

The premolar-molar teeth in *M.* cf. *furcatus,* no. 26795, are less worn and less robust than those in *M. necatus,* no. 26781. Left P^2 is present and is a small replica of P^3. The crescents and crests are like those in *M. necatus* and no anterior or posterior intermediate crests are present. M^3 has the well developed posteroexternal style noted in *M. necatus.*

Inferior dentition.—The lower teeth of *M. necatus* and *M.* cf. *furcatus* show a condition of progressive hypsodonty from $P_{\overline{2}}$ and $M_{\overline{3}}$. The deciduous teeth are longer rooted and shorter crowned than the permanent teeth. The premolars are two-rooted but more prismatic than the deciduous teeth.

M. cf. *furcatus,* no. 22450, fragment of jaw from Ricardo with $P_{\overline{4}}$, $M_{\overline{1}}$, and $M_{\overline{2}}$ present, exhibits a very early stage of wear. $P_{\overline{4}}$ would be just erupting from the gum. A like stage of growth is present in the teeth of *O. columbianus,* U. C. M. V. Z., no. 20597.

The primary cusp, no. 22450, lies between an anterior intermediate and posterior crest. The anterior crest is the extreme forward part of the crown. The tooth is not divided into distinct anterior and posterior crests and crescents as in *O. columbianus,* U. C. M. V. Z. no. 20597, but broadens from front to rear. In no. 20597 the anterior crest and crescent are well defined and form two-thirds of the tooth, the posterior third duplicates the anterior part but is much smaller.

$M_{\bar{1}}$ and $M_{\bar{2}}$, no. 22450, are typical straight-sided or prismatic teeth with no cingulum above the alveolar border. The enamel of the tooth crown extends into the dentary to a point midway between the alveolar border and the ventral margin of the bone. The roots are open and relatively broad transversely, and are less than one-quarter of the vertical length of the tooth.

In merycodonts $M_{\bar{1}}$ has two roots, $M_{\bar{2}}$ shows coalescence or atrophy of the roots, and $M_{\bar{3}}$ is a typical hypsodont tooth as in *A. americana.* The roots in the premolar-molar series are not widely separated proximally as in the deer but are parallel with the vertical axis of the tooth. They are indicative of the condition found in the *Capromeryx* dentition where the premolar teeth are mostly single rooted and are grooved medially (Los Angeles Museum no. 988). However, the deciduous teeth of *C. minor,* Los Angeles Museum no. 986, are double-rooted.

We apparently have in *Merycodus* and *Capromeryx* a condition of dental transition in hypsodonty, paralleling in some respects that observed in *Merychippus* of the Perissodactyla.

Schlosser[14] describes and figures cervid and antelopine genera from the Miocene and Pliocene deposits of Asia, among which occur *Protetraceros gaudryi* Schlosser, from the Shansi, Tientsin Pliocene. *P. gaudryi* has dental characters somewhat like those in *Merycodus,* $Dm_{\bar{4}}$ is three-lobed as in other pecora but differs from *Merycodus* in having intercrescentic cusps. The posterior cusp in the worn tooth figured by Schlosser is confluent with the posterior crescent. In $M_{\bar{1}}$ of *Palaeomeryx* sp., Matthew and Cook,[15] there is a condition approximating that in $Dm_{\bar{4}}$ of *P. gaudryi.* $M_{\bar{3}}$ in *P. gaudryi* is hypsodont, $M_{\bar{2}}$ has a small intercrescentic cusp, sometimes present in *Merycodus,* $P_{\bar{2}}$, $P_{\bar{3}}$, and $P_{\bar{4}}$ have an enamel pattern and proportion much like those in *Merycodus* and are more hypsodont than the corresponding teeth in *Palaeomeryx.*

The Asiatic genus makes a close approach to *Merycodus* in character of hypsodonty in certain of its teeth, in which respect it may be regarded as paralleling the development seen in the late Tertiary antilocaprids.

Certain fundamental and primary structures of artiodactyle premolar teeth are apparently quite persistent within the order and

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14 Schlosser, Max von, Die fossilen Saugethiere Chinas. Abhand. Akad. Wissenschaften, Munchen, 1906.

15 Matthew, W. D., and Cook, H. J., Bull. Am. Mus. Nat. Hist., vol. 26, art. 27, 1909.

appear with more or less modification in both the Cervidae and Bovidae. Hence we have a degree of parallel evolution within the pecora. Like conditions of habitat though widely separated geographically may well have a similar effect on members of an order or suborder of mammals, giving rise to parallelism of dental and skeletal structures. Granting this hypothesis, an early antilocaprid genus like *Merycodus* might naturally be expected to exhibit characters closer to a more primitive stock.

In *Merycodus*, the general absence of accessory cusps that are present in the deer, the persistence of the hypsodont character of the dentition and the close resemblance of the teeth to those of *Capromeryx* and *Antilocapra*, indicate or foreshadow the type of teeth we find in the latter genera.

Skeleton

Scapula.—The scapula is represented by the distal third of the bone, the coracoid and acromion processes are not present. The neck, glenoid cavity, and general proportions are apparently similar to those in the genera discussed. However, the anterior, superior, and axillary borders above the neck are indicative of pre- and post-spinous fossae narrower than those in *O. columbianus* and closer in this regard to *A. americana* and *C. mexicana*.

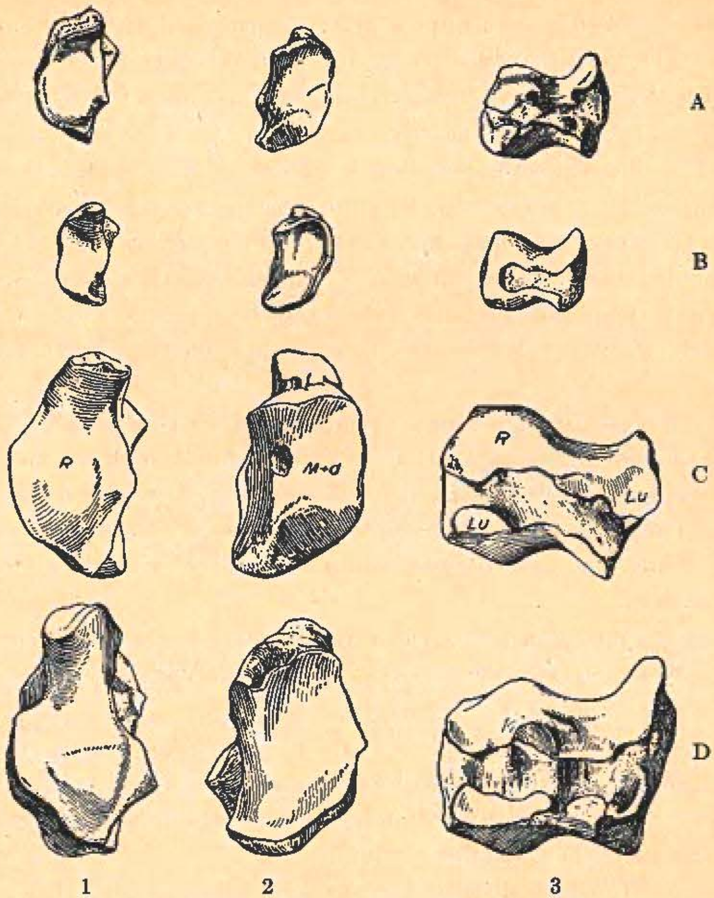
Humerus.—The deltoid ridge is well developed, more so than in *C. mexicana,* while in *A. americana* and *O. columbianus* it is relatively less pronounced. The head is too damaged to permit a comparison.

The olecranon fossa is more open, as in the allied genera; the fossa and trochleae at this point are not overhung by the lateral bounding walls to the extent that they are in *O. columbianus*.

Ulna.—The curvature of the sigmoid notch and the proportions of the olecranon are close to those in the discussed genera. The outer trochlear-condylar facet, as in the antilocaprid forms, has a wider contact with the facet of the radius than in *O. columbianus*. The trochlear facet does not round over its lateral margins in *M. necatus* and allied genera as it does in the deer. Most of the shaft and the distal extremity of the element is missing in *M. necatus*.

Radius.—Proximally the general character of the trochlear facets are similar in all the genera discussed. In *M. necatus* and *C. mexicana* they are more deeply impressed than in *A. americana* or *O. columbianus*, and the outer condylar facet is more sharply emarginated.

In the groove for the trochlear keel the antilocaprid genera do not possess the small deep pit present in *O. columbianus*. Also the small, rugose area is differently disposed than in the deer.



Figs. 1 to 3. Scaphoid. 1, superior view; 2, inferior view; 3, lateral view. Articular facets: *R*, radius; *mtd*, magnum-trapezoid; *lu*, lunar.

A. *Merycodus* cf. *furcatus* Leidy. Spec. No. 26795. × 1.

B. *Capromeryx mexicana* Furlong. Spec. No. 26648. × 1½.

C. *Antilocapra americana* (Ord.). U. C. M. V. Z. No. 8299. × 1.

D. *Odocoileus columbianus*. U. C. M. V. Z. No. 20597. × 1.

The distal face exhibits characters similar to those in the Antilocapridae and Cervidae. As in the deer, the cuneiform facet, posteriorly, is produced with a lateral face, while in *A. americana* it is more anteroposteriorly aligned, and *C. mexicana* in this respect is intermediate between the two forms. The scaphoid facet is vestigial as the scaphoid articulates largely with the ulna facet. *C. mexicana* resembles *M. necatus* most closely in this character. The scaphoid facet in *A. americana* closely approximates that in *O. columbianus* though in the latter the facet has a wider lateral extent.

The discussed genera appear alike in degree of curvature of the shaft. The Antilocapridae possess a relatively more slender shaft than the deer, in this respect *M. necatus* approaches *O. columbianus* more closely than do the others.

Scaphoid.—The proximal face is similar to that in *A. americana* and *C. mexicana;* posteriorly, its transverse diameter is relatively less and not so sharply concavo-convex as in *O. columbianus.*

The distal surface, like that in *A. americana* and *C. mexicana,* is posteriorly more concave, also anteriorly the magnum facet is more distinctly deliminated from its posterior portion than in *O. columbianus.*

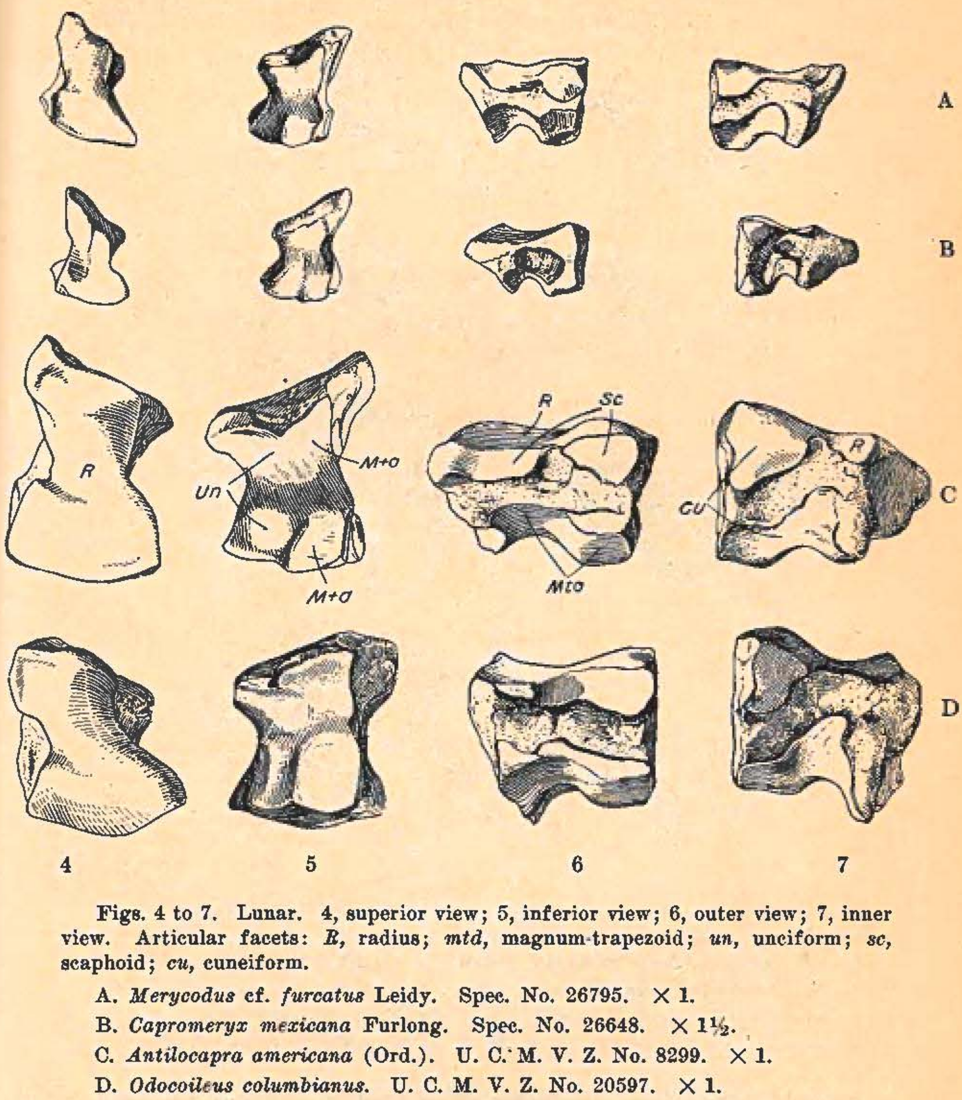
Of the facets for the lunar, the distal one resembles that in *A. americana* and *C. mexicana,* rounded and confluent with the magnum facet, while in *O. columbianus* it forms a right angle with the magnum facet. The proximal facet, as in *A. americana,* has a greater distal extent than in *O. columbianus,* while in *C. mexicana* the two facets are confluent.

Lunar.—The proximal face of the lunar corresponds to that in *A. americana* and *C. mexicana;* its posterior extent is relatively greater than in *O. columbianus.*

The unciform-magnum facets of the distal face are in general contour more like those in *A. americana* and *C. mexicana* than like those in *O. columbianus,* but differ from all these forms in having a greater unciform facet than magnum facet.

The anteroproximal facet for the cuneiform is truncated as in *A. americana* and has a greater distal extent than in *O. columbianus.* This facet in *C. mexicana* is confluent with the distal facet for the cuneiform and is more closely approximated in this respect by *M. necatus* than by *A. americana* or *O. columbianus.* In the antilocaprid forms the mid-proximal cuneiform facet is rounded over and confluent with the facet for the radius. In *O. columbianus* it is delimited with a flat surface.

The anteroproximal facet for the scaphoid is relatively less in distal extent than in *A. americana* or *O. columbianus.* It is more like *C. mexicana* in this respect. The distal facet for the scaphoid



Figs. 4 to 7. Lunar. 4, superior view; 5, inferior view; 6, outer view; 7, inner view. Articular facets: *R*, radius; *mtd*, magnum-trapezoid; *un*, unciform; *sc*, scaphoid; *cu*, cuneiform.

A. *Merycodus* cf. *furcatus* Leidy. Spec. No. 26795. × 1.

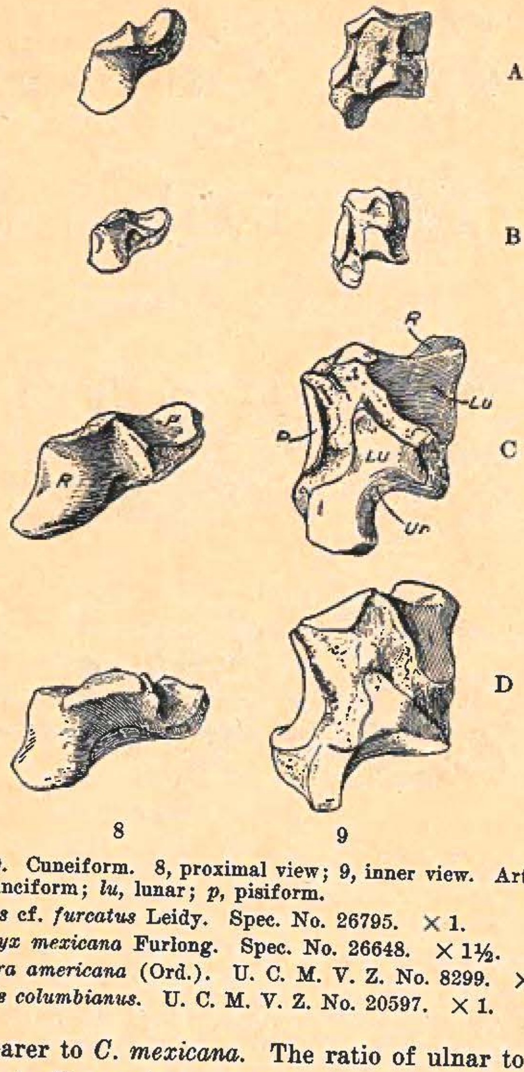
B. *Capromeryx mexicana* Furlong. Spec. No. 26648. × 1½.

C. *Antilocapra americana* (Ord.). U. C. M. V. Z. No. 8299. × 1.

D. *Odocoileus columbianus*. U. C. M. V. Z. No. 20597. × 1.

resembles that in *A. americana.* It is more vertical in position than that of *O. columbianus* and not so vertical as in *C. mexicana.*

Cuneiform.—The proximal surface affords a relatively small facet for the radius, more laterally placed than in *A. americana* or *O. columbianus* and nearer to *C. mexicana.* The ratio of ulnar to radial surface is greater in *M. necatus* and *C. mexicana* than in *A. americana* or *O. columbianus.*



Figs. 8 and 9. Cuneiform. 8, proximal view; 9, inner view. Articular facets: *R*, radius; *un*, unciform; *lu*, lunar; *p*, pisiform.

A. *Merycodus* cf. *furcatus* Leidy. Spec. No. 26795. × 1.

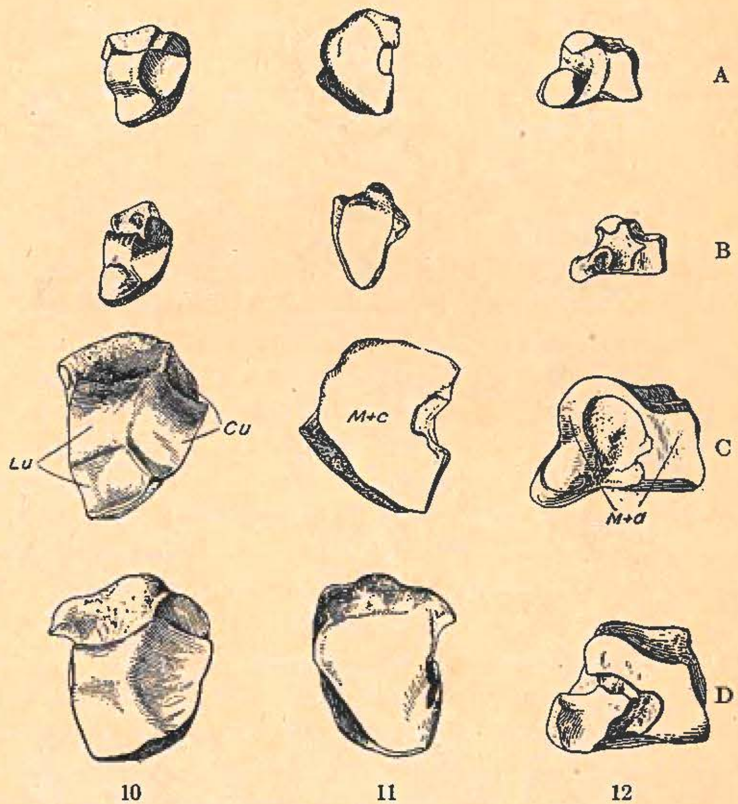
B. *Capromeryx mexicana* Furlong. Spec. No. 26648. × 1½.

C. *Antilocapra americana* (Ord.). U. C. M. V. Z. No. 8299. × 1.

D. *Odocoileus columbianus*. U. C. M. V. Z. No. 20597. × 1.

The distal unciform facet is not so concave as in any of the compared forms and exhibits no other distinctive characters. The lunar facets are close to those in the compared forms.

Unciform.—The proximal faces for the cuneiform and lunar facets in the antilocaprid forms approximate those in *O. columbianus* but the cuneiform facet has a broader transverse area on its posterior face. Also the posterior part of the lunar facet is definitely delimited, whereas in *O. columbianus* it merges into the inner distal lunar facet.



Figs. 10 to 12. Unciform. 10, proximal view; 11, distal view; 12, inner view. Articular facets: *lu*, lunar; *cu*, cuneiform; *mtd.*, magnum-trapezoid.

A. *Merycodus* cf. *furcatus* Leidy. Spec. No. 26795. × 1.

B. *Capromeryx mexicana* Furlong. Spec. No. 26648. × 1½.

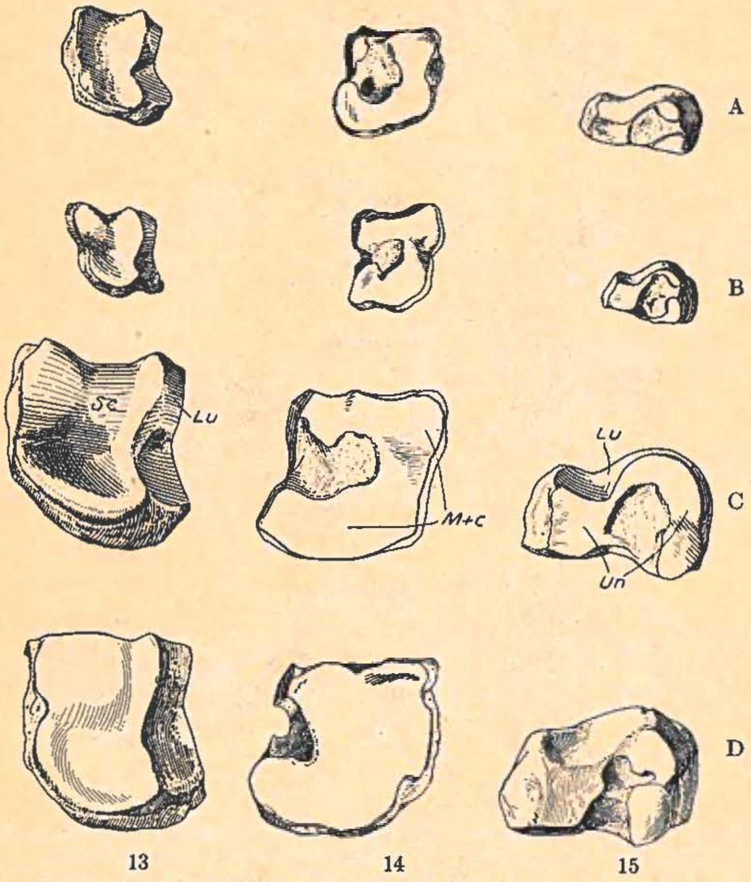
C. *Antilocapra americana* (Ord.). U. C. M. V. Z. No. 8299. × 1.

D. *Odocoileus columbianus*. U. C. M. V. Z. No. 20597. × 1.

The distal surface in the antilocaprid specimens differs from *O. columbianus* in having relatively less area of metacarpal facet.

The facets for the magnum are like those in *C. mexicana* and differ from *A. americana* in being disconnected, and from *O. columbianus* in planation of the posterior facets.

Magnum.—The proximal surface has a broader scaphoid facet as contrasted with the lunar facet and approaches *C. mexicana* in this respect. The scaphoid facet in *A. americana* and in *O. columbianus* is more equal to the lunar facet in breadth, though in *A. americana* the facets more closely approximate those in *C. mexicana* and *O.*



Figs. 13 to 15. Magnum. 13, proximal view; 14, distal view; 15, inner view. Articular facets: *sc*, scaphoid; *lu*, lunar; *mtc.*, metacarpal; *un*, unciform.
A. *Merycodus* cf. *furcatus* Leidy. Spec. No. 26795. × 1.
B. *Capromeryx mexicana* Furlong. Spec. No. 26648. × 1½.
C. *Antilocapra americana* (Ord.). U. C. M. V. Z. No. 8299. × 1.
D. *Odocoileus columbianus.* U. C. M. V. Z. No. 20597. × 1.

columbianus. The anterior part of the lunar facet is not so quadrate in form in the antilocaprid genera as it is in *O. columbianus.*

The distal surface is like that in *A. americana,* the metatarsal facet is more angular than in *C. mexicana* and relatively narrower and more distinctly delimited from the unciform facet than in *O. columbianus.*

The unciform facets are closer to those of *Capromeryx* than to *A. americana* or *O. columbianus.*

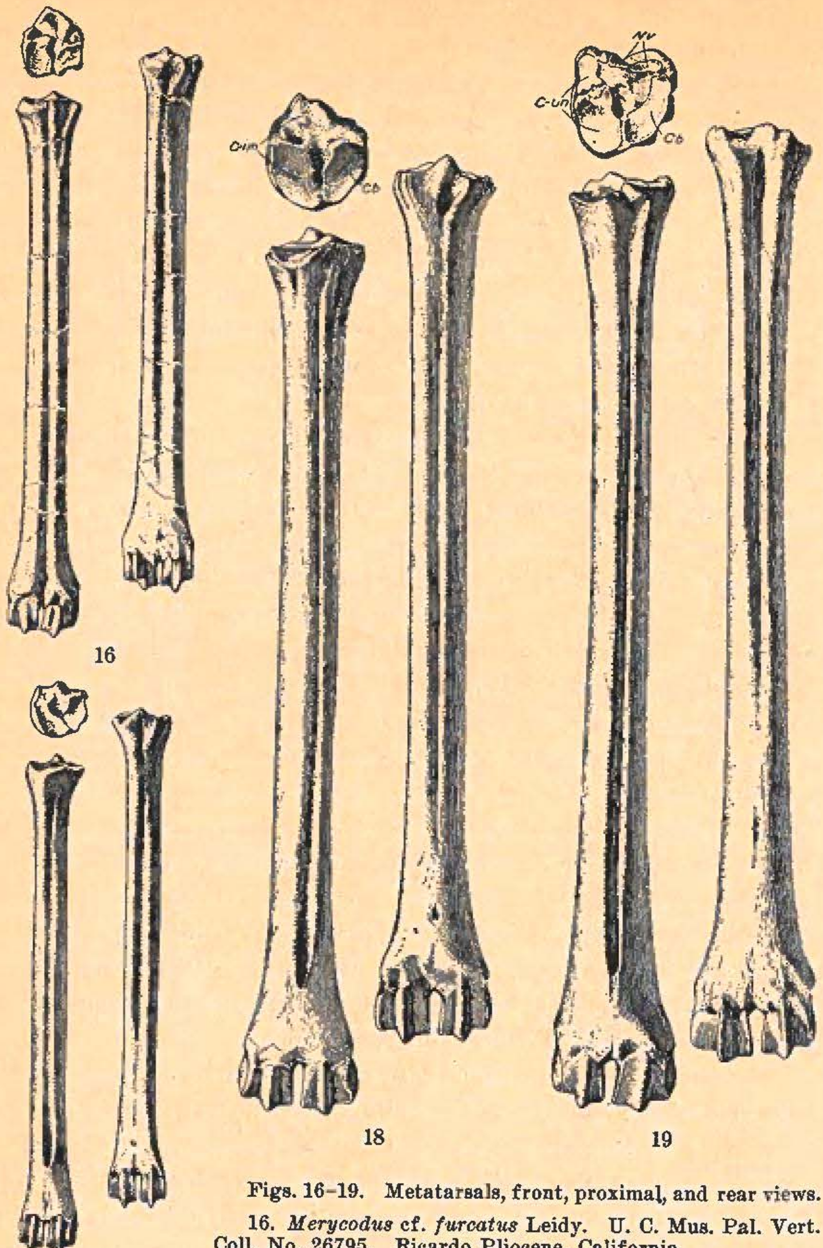
Metatarsals.—The proximal facets for the cuboid and cuneiform are similar to those in *A. americana,* no. 8299 (fig. 19), and *C. mexicana,* no. 26648 (fig. 17). The cuboid facet in anteroposterior diameter is relatively much less than in *O. columbianus,* no. 5866 (fig. 18). The large cuneiform facet (no. 26781, fig. 16) equals or exceeds in length that of the cuboid facet where, as in the deer, it is shorter. The external cuneiform facet is in a plane with its companion facet and not oblique to the internal cuneiform as in *O. columbianus.* There are no small, posterior, transverse facets for the navicular cuboid as in the deer.

The posterior aspect of the shaft is like that in the antilocaprid genera. The groove (figs. 16–19) between the third and fourth metatarsal segments is confined to the central part of the shaft. The raised edges converge proximally, round over to the median line, and give a constricted appearance to this part of the shaft. In *O. columbianus* (fig. 18) the posterior groove, unlike that in the antilocaprid genera, diverges and deepens proximally.

The distal end of the bone shows no characters that are peculiar. The paraxonic character of the limb is like that in all other pecora, but modification has taken place to effect compactness and slenderness of limb structure. The antilocaprid limb structure is in accord with the probable habitat of *Merycodus.* The numerous specimens of *Merycodus* found are corroborative of the assumption that merycodonts were extremely fleet-footed in order to escape the large carnivores with which they were associated. *Antilocapra americana* is considered a fleeter type than the deer, and the Pleistocene *Capromeryx* and probably *Tetrameryx* were similar in this character of speed as is indicated by their limb development.

Metacarpals.—The proximal face shows the unciform facet stepped below but closely opposed to the magnum facet. In *A. americana* and *C. mexicana,* posteriorly, the unciform facet is transversely confluent with the magnum facet; it also lies in the same plane. In *O. columbianus* the facets are separated by a distinct pit that extends to the posterior margin of the bone, the unciform and magnum facets lying in the same plane.

The magnum facet is slightly depressed and rugose ventrally, as in the antilocaprid forms, whereas in the deer it presents a broad, unbroken surface to the margin of the above mentioned pit.



Figs. 16–19. Metatarsals, front, proximal, and rear views.

16. *Merycodus* cf. *furcatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 26795. Ricardo Pliocene, California.

17. *Capromeryx mexicana* Furlong. U. C. Mus. Pal. Vert. Coll. No. 26648. Tequiquiac, Mexico. Pleistocene.

18. *Antilocapra americana*. U. C. M. V. Z. No. 8299.

19. *Odocoileus columbianus*. U. C. M. V. Z. No. 20597. Articular facets: *cu*, cuneiform; *cb*, cuboid area of navicular cuboid; *nv*, navicular-cuboid. × ½.

As in *A. americana* and *C. mexicana* the shaft is relatively more slender than in the deer. The line formed by the fusion of the metapodial elements is not so distinct anteriorly as in *O. columbianus* and is more distinct than in *A. americana* and *C. mexicana.*

The distal face shows characters similar to those possessed by all the compared forms.

Innominate bone.—The acetabulum differs from that in *O. columbianus* and is close to the structure in *A. americana* and *C. mexicana.* The articular surface for the head of the femur practically closes over the top of the cotyloid notch. The cotyloid notch is wide in *O. columbianus* and relatively narrow in *A. americana* and *C. mexicana.*

The crest of the ilium is not present. The great sacrosciatic notch conforms to that in the genera discussed. The anterior border near the acetabular margin has a relatively shallow (rectus femoris muscle) pit as in *A. americana.* This pit is obsolete in *C. mexicana* and large and deep in *O. columbianus.*

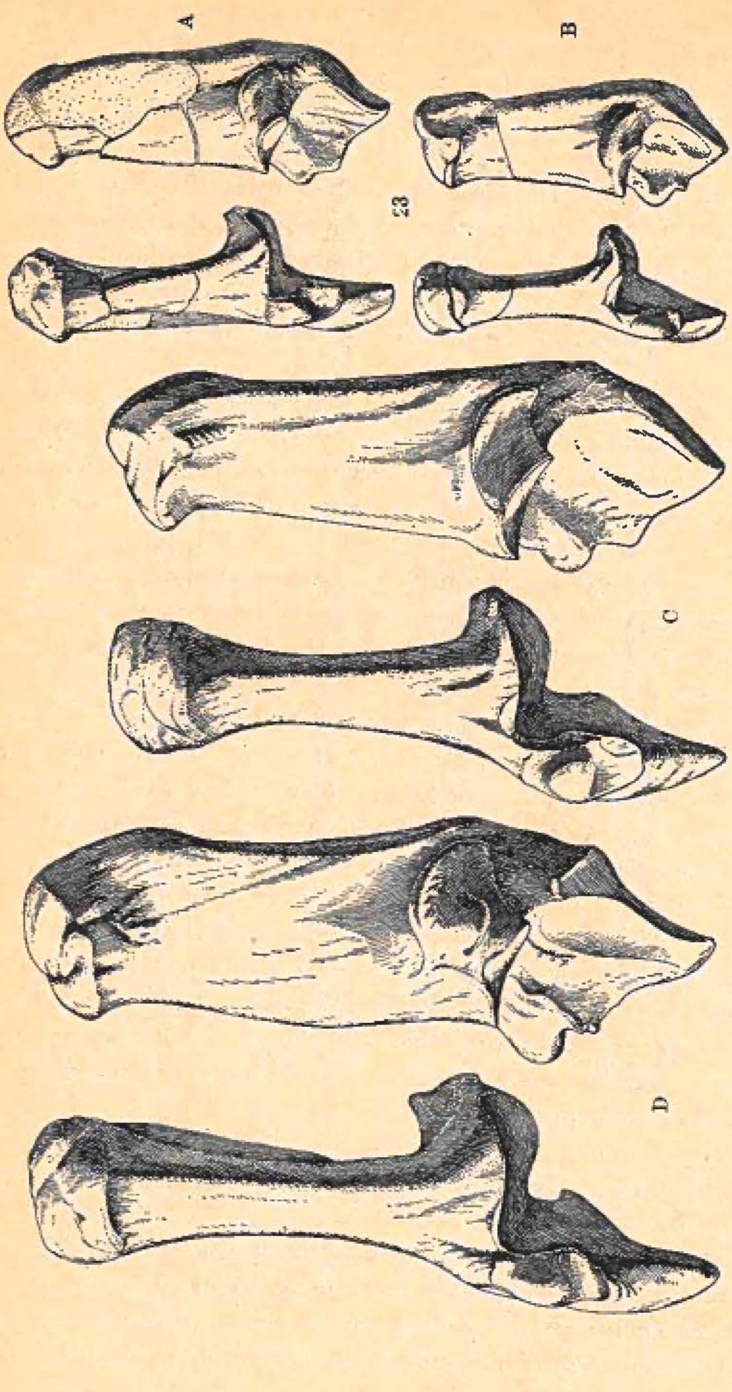
The ascending ramus and tuberosity of the ischium are absent, also the descending ramus of the pubes, but an obturator foramen similar in proportion to that in *A. americana* is indicated by the shape of the inner margin of the cotylid bone.

Sacrum.—Four vertebral segments constitute the sacrum, the same number as in the compared genera, and in general the characters are similar. However, in *M. necatus,* and in the other Antilocapridae, the prezygapophyses have a considerably longer articulating surface for the postzygapophyses of the seventh lumbar vertebra than in *O. columbianus.*

Femur.—The proximal end only is preserved and is very close in character to that of *A. americana.* The digital fossa is deep and underlies the great trochanter to a greater extent than in *O. columbianus.* The intertrochanteric line is closer to the neck and partly closes in the digital fossa, whereas in *O. columbianus* the fossa is more open posteriorly.

Tibia.—The proximal third of the tibia is not present and that part of the cnemial crest remaining would indicate a character similar to that in the compared genera.

The distal face resembles those in *A. americana* and *C. mexicana* and differs from *O. columbianus* in its more deeply impressed facets for the astragalus and in its less pronounced malleolar astragalar facet and tibial facets. The anteroposterior tibial facets in the an-



Figs. 20 to 23. Calcanea. Superior and inner views.
A. *Merycodus* cf. *furcatus* Leidy. Spec. No. 26795. × 1.
B. *Capromeryx mexicana* Furlong. Spec. No. 26648. × 1½.
C. *Antilocapra americana* (Ord.). U. C. M. V. Z. No. 8299. × 1.
D. *Odocoileus columbianus*. U. C. M. V. Z. No. 20597. × 1.

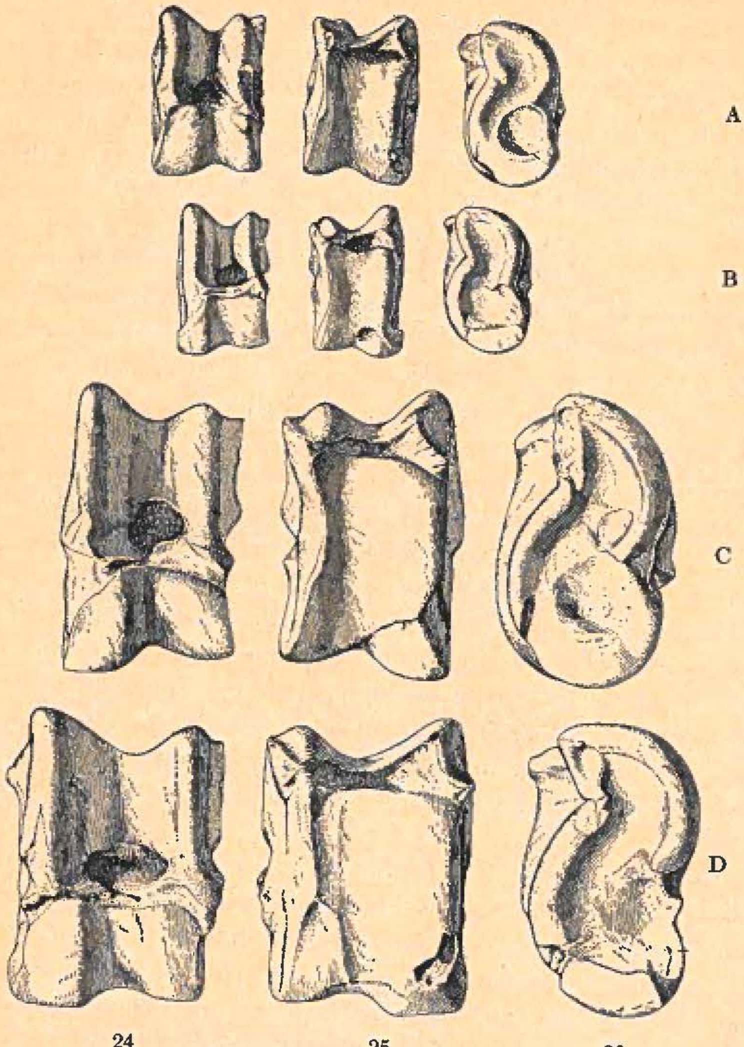
tilocaprid group form a narrow shelf, while in *O. columbianus* the posterior fibula facet is stepped proximally and breaks the uniform plane the facets effect in the other forms.

Calcaneum.—The astragalar facet is, as in *C. mexicana*, more convex transversely than in *O. columbianus*, while in *A. americana* this facet, though not so convex as in *M. necatus* and *C. mexicana*, is more convex than in *O. columbianus*. The cuboid facet in the Antilocapridae is less concave anteroposteriorly and does not extend medially as in *O. columbianus*. The medial extension of this surface in *O. columbianus* gives rise to a distinct astragalar facet not present in the antilocaprid genera.

Astragalus.—The broad calcanear facet is, as in *A. americana* and *C. mexicana*, more deeply grooved than in *O. columbianus* and also shorter in mid-transverse diameter. That part of the navicular facet appearing on the calcanear face is not strongly depressed below the calcanear facet as in *O. columbianus* but is like *A. americana* and *C. mexicana* in being less clearly delimited. The trochlear surface is more oblique in *M. necatus* and the compared genera than in *O. columbianus*. The malleolar facet is not so pronounced and deeply incised in the Antilocapridae as in *O. columbianus*. The cuboid facet in *M. necatus* and its allies is convex anteroposteriorly with a uniform surface, while in *O. columbianus* it is concavo-convex. The navicular-cuboid facet in the antilocaprid group is more deeply grooved than in *O. columbianus*. The navicular facet is on a plane with the cuboid facet; it merges gradually to the median groove and differs in this respect from *O. columbianus* in which the navicular facet is not produced so far distally and converges more abruptly to the median groove. The outer, distal, calcanear facet shows no distinctive characteristics.

Navicular-cuboid.—The proximal face is like that in *C. mexicana* and *O. columbianus*, not so broad relatively, in anteroposterior diameter, as in *A. americana*. The ascending part of the facet of the navicular side is more pronounced than in *A. americana* and in this respect is similar to *C. mexicana* and *O. columbianus*. The calcanear facet is like that in the antilocaprid types and is not produced in a rather sharply ascending surface as in *O. columbianus*, but is more flattened as in *A. americana* and *C. mexicana*.

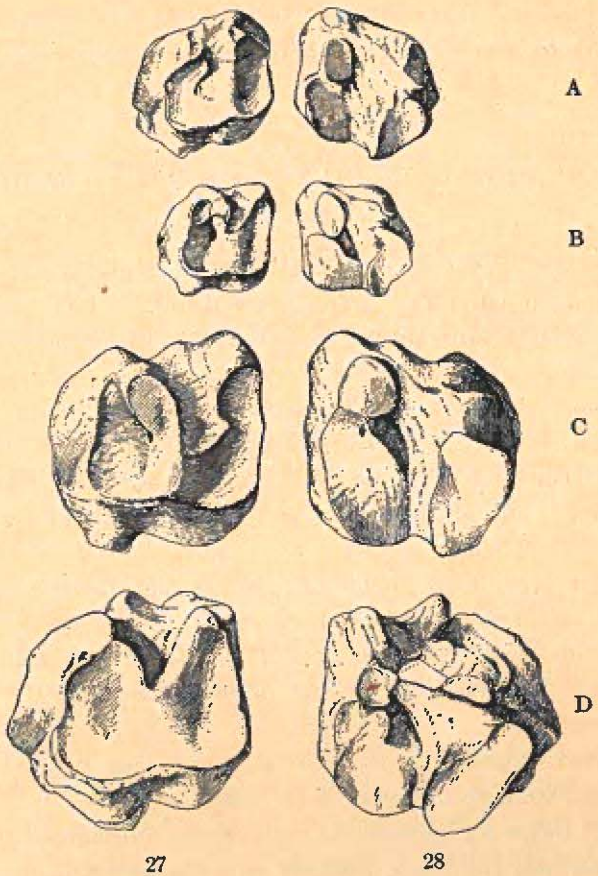
The distal face is much like that in the Antilocapridae. It differs, however, in that the external cuneiform facet is on a lower plane than in any of the compared forms. The internal cuneiform facet is similar to that in the other forms under discussion. The metatarsal facet is like that in *A. americana* and *C. mexicana* and has relatively less area than in *O. columbianus.* As in *A. americana* and *C. mexicana,* it is higher distally above the internal cuneiform than in *O.*



Figs. 24 to 26. Astragali. 24, superior view; 25, inferior view; 26, side view. × ½.

A. *Merycodus* cf. *furcatus* Leidy. Spec. No. 26795. × 1.
B. *Capromeryx mexicana* Furlong. Spec. No. 26648. × 1½.
C. *Antilocapra americana* (Ord.). U. C. M. V. Z. No. 8299. × 1.
D. *Odocoileus columbianus.* U. C. M. V. Z. No. 20597. × 1.

columbianus. As in the other Antilocapridae it lacks the transverse posterior facet, present in the deer for articulation with a corresponding area on the proximal, posterior margin of the metatarsus.



Figs. 27 and 28. Navicular-cuboid. 27, proximal view; 28, distal view.

A. *Merycodus* cf. *furcatus* Leidy. Spec. No. 26795. × 1.
B. *Capromeryx mexicana* Furlong. Spec. No. 26648. × 1½.
C. *Antilocapra americana* (Ord.). U. C. M. V. Z. No. 8299. × 1.
D. *Odocoileus columbianus.* U. C. M. V. Z. No. 20597. × 1.

External cuneiform.—The proximal face is like that in the other antilocaparid types. The navicular facet is less quadrate and relatively smaller than in *O. columbianus.* In this respect *A. americana* resembles the deer more closely.

The distal, metatarsal facet is not rectangular in shape as in *O. columbianus* but is similar to that in *A. americana* and *C. mexicana.*

In the antelope group a small inner facet for the cuboid is present. It is most pronounced in *A. americana* and *C. mexicana,* not so flat in *M. necatus,* and vestigial in the deer.

Internal cuneiform.—The internal cuneiform is like that in *A. americana,* its proximal diameter is relatively greater than in *O. columbianus,* where the element is a simple disc of bone.

STRATIGRAPHIC OCCURRENCE OF BARSTOW-RICARDO MERYCODONTS

The relationships of the Barstow and Ricardo strata, both geologically and faunally, have been discussed by Merriam.[16] Reference to the age relationships of the faunas has also been made by Stock and Furlong.[17]

Merycodus remains occur throughout the fossiliferous horizons in the Barstow syncline. They are present in the Ricardo (in the basal beds below the lava) in Last Chance Cañon, El Paso Range, and they occur also stratigraphically higher in the Red Rock Cañon region.

From our present knowledge of these western Tertiary species no distinctive morphological characters separate those of the Barstow from those of the Ricardo deposits. This also applies to individuals occurring in the lower strata and in beds above the lava in the Ricardo section.

Merycodus apparently enjoyed a fairly long time-range and possessed an extensive distribution in North America. Its occurrence in the Great Basin region suggests a prevalence throughout the Upper Miocene and into the lower Pliocene age, the group being replaced in the later Pliocene by such genera as *Ilingoceros* and *Sphenophalos* from the Thousand Creek deposits of Nevada.

As the Ricardo merycodonts are associated with remains of Amphicyonine dogs (*Hadrocyon*) and typical Miocene rhinoceroses (*Aphelops*) they give support to the view that at least part of the Ricardo deposits are stratigraphically close in age to the Republican River formation, held to be Uppermost Miocene or a transitional stage to the Lower Pliocene.

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[16] *Op. cit.*

[17] Stock, C., and Furlong, E. L., Univ. Calif. Publ. Bull. Dept. Geol. Sci., vol. 16, pp. 43–60, 1926.

SUMMARY

The morphological characters, exhibited in the skull, dentition, and skeletal elements of the specimens used in this report, indicate the presence of at least two species of *Merycodus*, *M. necatus* Leidy and *M.* cf. *furcatus* Leidy. On the basis of the material available it appears possible that the two species occur in the Barstow as well as in the Ricardo deposits.

The most outstanding characters separating the two species are the shape of antlers, the ratio of length of tines to length of beam, and minor characters of size and pattern of teeth. The teeth are so generally uniform in pattern and size, relative to the age of individuals, that a strong specific line of character distinction cannot be drawn.

As compared with the Cervidae, the merycodonts show in their skull structure pronounced differences of facial and cranial proportion. They have a bovid type of orbit and the position and character of their horns are peculiar to the Antilocapridae, aside from the presence of burrs in some individuals.

The teeth of *Merycodus* are progressively hypsodont, although the inferior unworn premolar tooth-pattern resembles that in *Odocoileus columbianus*. The superior teeth closely approximate those in *Tetrameryx schuleri* and *Antilocapra americana*.

The parts present of scapula and os innominatum show a close resemblance to the same elements in the Antilocapridae.

In the detailed discussion of metapodials, carpal and tarsal bones, it has been demonstrated that the elements exhibit characters farthest removed from those of the Cervidae and are closer to those of the Antilocapridae. This is expressed in the position and arrangement of the facets and in the posterior grooving of the posterior cannon bone.

A review of the sum of antilocaprid characters, as shown in the specimens studied, leads inevitably to the conclusion that the major part of the structures reflect the skeletal attributes of the Antilocapridae, as illustrated in *Antilocapra americana* and *Capromeryx mexicana*.

The cervid characters present in the merycodonts are many of them common to all artiodactyls. Their absence in a representative

of a stem group having an ancestral relationship to both Cervidae and Antilocapridae would be most unusual. It would appear quite probable that some of the characters have continued in varying degrees of definiteness through the several American families of even-toed ungulates, becoming, in some groups more than in others, obscured by characters acquired at a later period of time.

Having this concept in mind, the merycodonts may be regarded as a group which has diverged somewhat from the typical Antilocapridae and in this respect the divergence is like that which has taken place in the middle Tertiary *Equidae.*

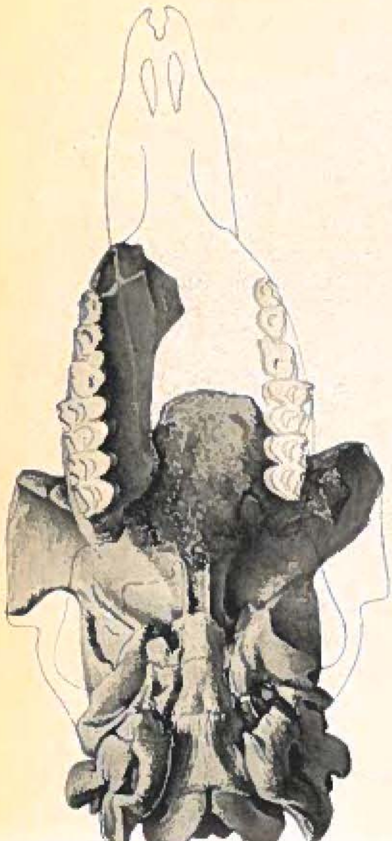
EXPLANATION OF PLATE 24

All figures × ⅔.

Fig. 1. *Merycodus necatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 26781. Barstow Miocene, California. Ventral aspect of cranium and right maxillary.

Fig. 2. *Merycodus necatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 26781. Barstow Miocene, California. Occipital, parietal, and frontal region of skull with antlers as viewed from rear.

Fig. 3. *Merycodus* cf. *furcatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 26795. Ricardo Pliocene, California. Ventral aspect of cranium and maxilli with cheek dentition.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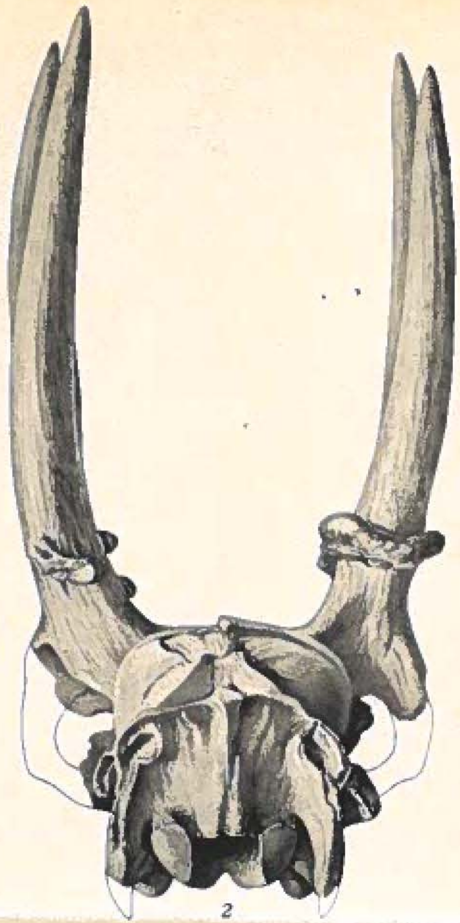
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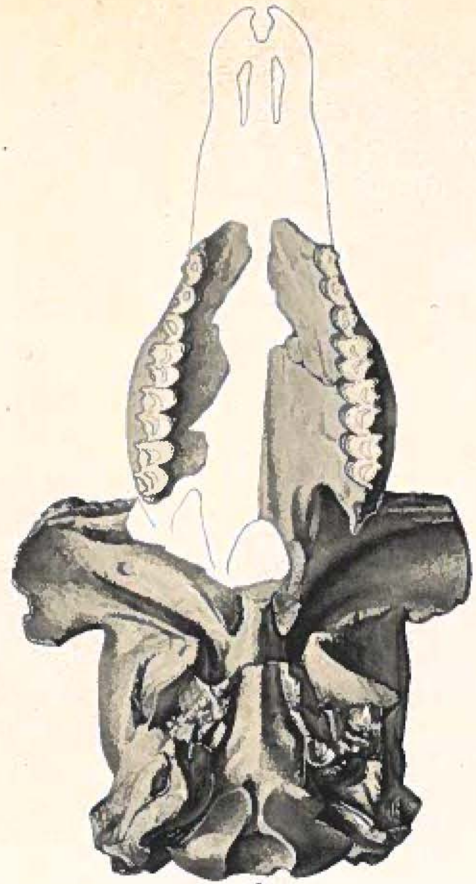
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EXPLANATION OF PLATE 25

All specimens from the Barstow Miocene, California. × ⅔.

Fig. 1. *Merycodus necatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 26781. Side view of skull showing attitude of antler, right ramus, and cheek dentition.

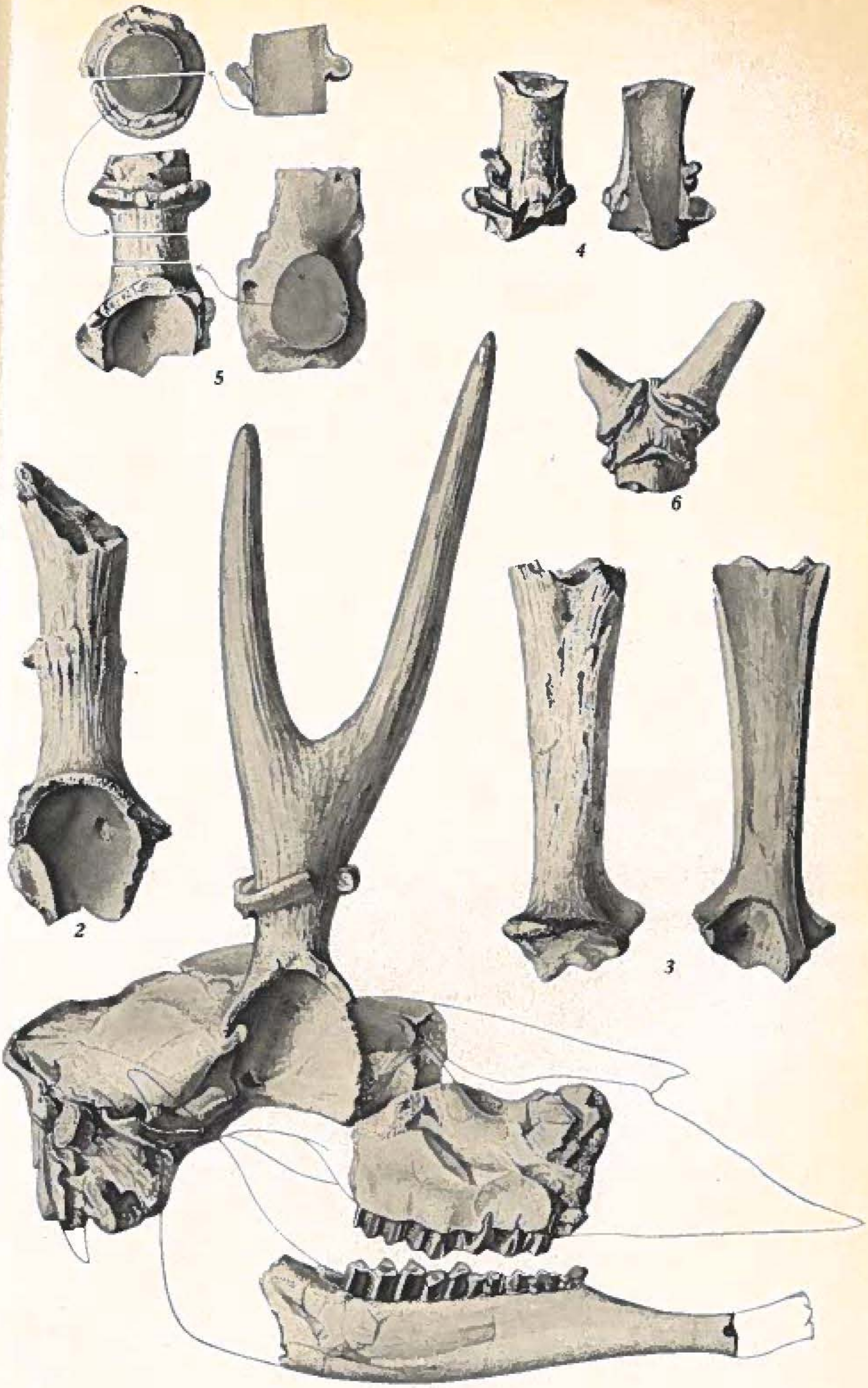
Fig. 2. *Merycodus necatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 27244. Part of antler with burr broken away showing nutrient sinuses passing under burr.

Fig. 3. *Merycodus* sp. U. C. Mus. Pal. Vert. Coll. No. 26801. Illustrates in section the uniform, dense structure of horn.

Fig. 4. *Merycodus necatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 26802. Part of antler showing number of burr growths; section showing dense structure of antler and distinct line of division between beam and burr.

Fig. 5. *Merycodus necatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 26796. Part of antler with cross- and longitudinal sections illustrating nature of burr and inner structure.

Fig. 6. *Merycodus* sp. U. C. Mus. Pal. Vert. Coll. No. 21488. An unusual type of antler that shows the variability in growth of burrs.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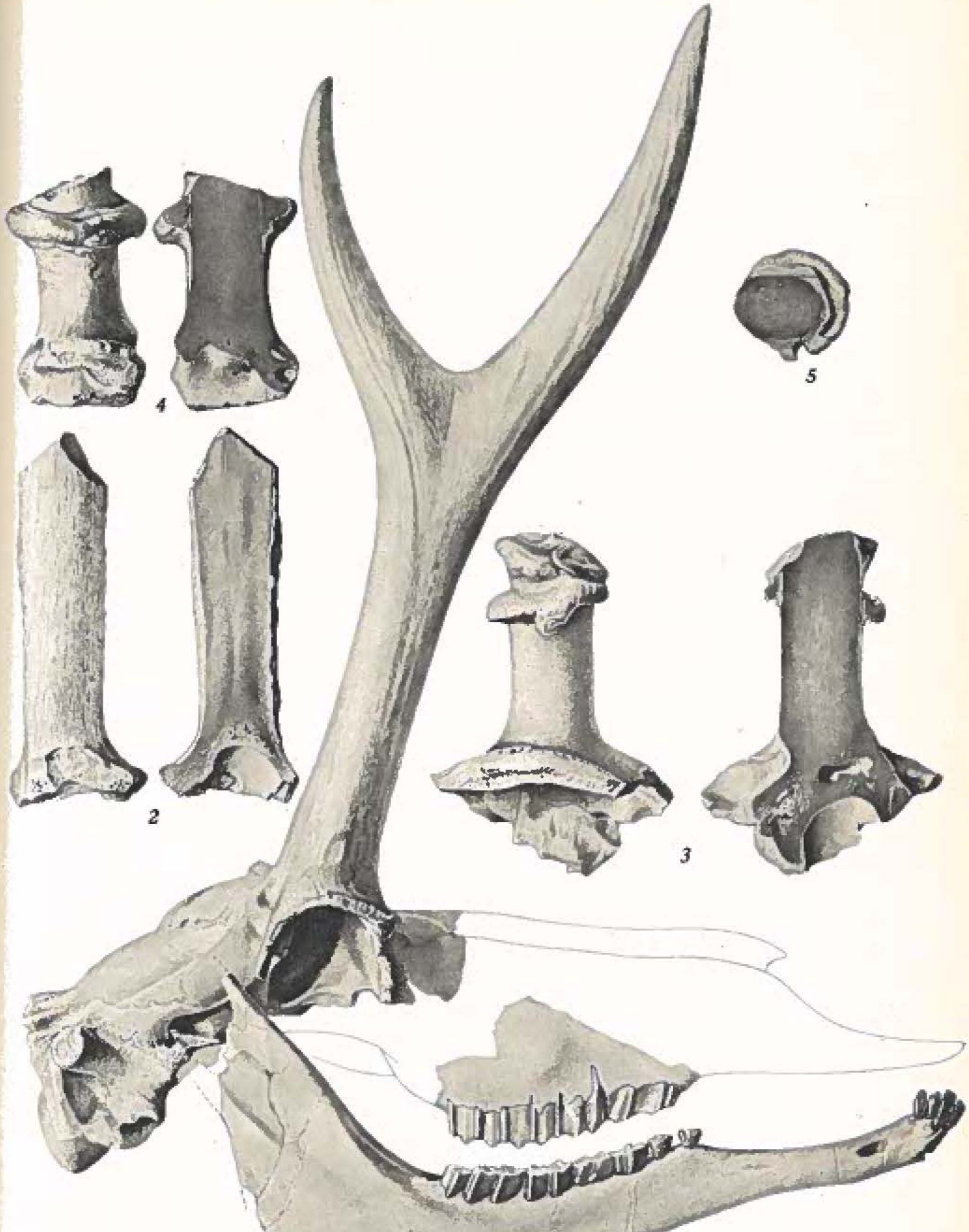
EXPLANATION OF PLATE 26

All specimens from the Ricardo Pliocene, California. × ⅔.

Fig. 1. *Merycodus* cf. *furcatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 26795. Side view of skull showing attitude of antler, also right maxillary and ramus with dentition.

Fig. 2. *Merycodus* sp. U. C. Mus. Pal. Vert. Coll. No. 26798. Part of antler without burr showing dense structure in longitudinal section.

Figs. 3–5. *Merycodus necatus* Leidy. U. C. Mus. Pal. Vert. Coll. Fig. 3, No. 26797; fig. 4, No. 26799; fig. 5, No. 26805. Parts of antler with double and single burrs and structure shown in longitudinal and cross sections.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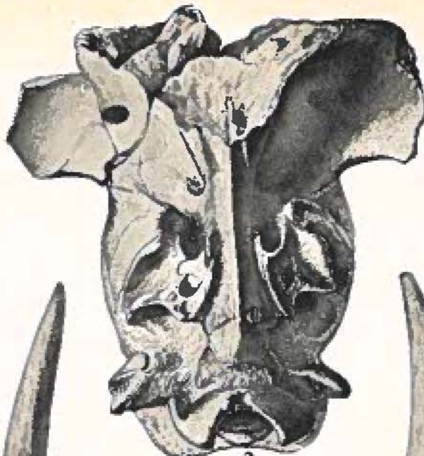
EXPLANATION OF PLATE 27

All figures × ⅔.

Figs. 1–3. *Merycodus necatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 21551. Barstow Miocene, California. Fig. 1, dorsal view; fig. 2, ventral view; fig. 3, posterior view.

Fig. 4. *Merycodus* cf. *furcatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 26795. Ricardo Pliocene, California. Posterior view of cranium showing curvature, backward lateral rotation relative to longitudinal axis of skull and general attitude of antlers.

Figs. 5–6. *Merycodus necatus* Leidy. U. C. Mus. Pal. Vert. Coll. No. 27245. Barstow Miocene, California. Part of antler showing multiplicity of burr growth and position of burrs near point of bifurcation of tines.



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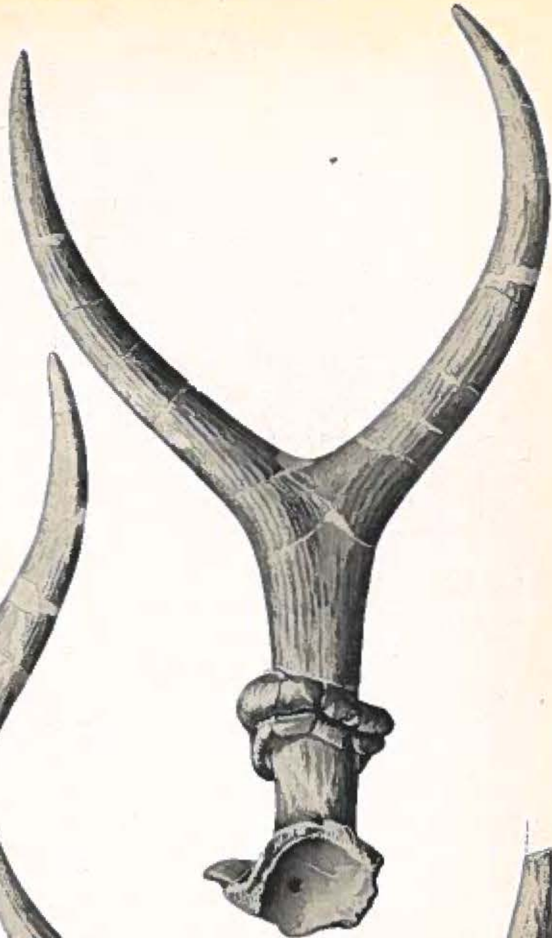
EXPLANATION OF PLATE 28

All figures × ⅔.

Figs. 1–3. *Merycodus* sp. U. C. Mus. Pal. Vert. Coll. Fig. 1, No. 27243, Barstow Miocene, California; fig. 2, No. 27249, Ricardo Pliocene, California; fig. 3, No. 27242. Antlers exhibiting variation in form.



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