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ANTLERS OF *BRETZIA* AND *ODOCOILEUS* (MAMMALIA, CERVIDAE) AND THE EVOLUTION OF NEW WORLD DEER

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Antlers of New World deer (Cervidae), though of considerable taxonomic importance, are rarely found in deposits earlier than Late Pleistocene. The one reasonably well known Blancan deer, *Bretzia pseudalces*, whose antlers are known from deposits in Washington and California, is an odocoileine, closely related to *Odocoileus*. An analysis of antler form and distribution patterns suggests that the immigration and divergence of the New World Odocoileinae (excluding *Alces* and *Rangifer*) occurred in the latest Hemphillian and Early Blancan. Evolution of complexity in antler form in this group begins with a relatively simple pattern which lacks a brow tine immediately adjacent to the burr, possesses a single anteriorly directed tine, and has a larger (sometimes forked) posterior tine. This pattern is seen in *Ozotoceras* and in *Capreolus*. *Bretzia* altered this pattern by spreading the antlers laterally and by developing palmation of the posterior branch. The evolution of antlers of *Odocoileus* seems to begin with development of a helical form incorporating beam and anterior tine. The latter form appeared by the end of the Early Blancan, when *Odocoileus* apparently replaced *Bretzia* in the western parts of North America.

† † †

INTRODUCTION

The most distinctive hard parts of the advanced Cervidae, from the standpoint of classification, are the antlers. Dentitions tend to be conservative, and other features of the skull have not been studied in sufficient detail, even in extant species, to be very useful. It is thus desirable to have a sufficient sample of antlers for study of fossil species. Unfortunately cervid fossils, whether antlers, dentition, or other skeletal elements, are relatively rare.

Antlers are peculiar structures. They can be described as analogous to free-standing bone sculptures. Because they are unconstrained by the anatomical necessities of muscular

attachment or the stresses of bearing the weight of the animal, and because they are shed yearly and regrown at various ages and in varying environmental conditions (such as changing availability of food), they often show extremes of variation. The patterns of variation are, however, under genetic control, and the species from which a complete isolated antler came can generally be recognized by its size and form, if the range of variation in that species is known.

Isolated antlers and skull bones were the primary evidence for recognition of the taxon *Bretzia pseudalces*, an Early Blancan deer from the Ringold Formation in the state of Washington (Fry and Gustafson, 1974). There was considerable doubt initially as to where *Bretzia* fit into the overall pattern of cervid evolution in the New World, despite the relatively good quality and large number of specimens available. Fry and Gustafson (1974) stated that "the unpalmed, multiple-tined antlers of the Recent species of *Odocoileus*, though similar in size to *Bretzia pseudalces*, have few other points of similarity." Evidence that tends to refute the quoted statement and which points toward a close relationship between *Bretzia* and other members of a restricted subfamily Odocoileinae is presented here.

In order to understand the variation in antlers within a genus and species, two related studies were undertaken. Postcranial and dental material associated with *Bretzia* antlers from in and near the type locality were examined closely. The original specimens at the University of Washington (UW) and the Ringold collections at the Los Angeles County Museum of Natural History (LACM), largely obtained by George Beck, Willis Fry, and George Jakway, were studied to make possible a much larger sample of *Bretzia*, particularly of the antlers. A

basic statistical analysis was performed on the available sample of antlers. Additionally, all of the Blancan cervid specimens available from the western United States were examined.

In an attempt to understand the variations in antlers in *Bretzia*, several years have been spent collecting antler measurements and observations on the related genus *Odocoileus* and in analyzing these data. A random statistical sample of antlers from *Odocoileus* is not easy to make; many museum collections have few examples or include mainly large trophy specimens and antlers of unusual morphology. Statistics presented here are based on samples of antlers now in the collections of the Vertebrate Paleontology Laboratory, University of Texas at Austin. The core sample of *O. hemionus*, about 70 antlers, was collected in Brewster County, Texas. It includes shed antlers, many weathered and broken (thus approximating the condition of most fossil specimens), together with a few specimens still attached to skulls. This was supplemented by specimens of *O. hemionus* from Colorado, Nebraska, New Mexico, Oregon, Washington, and Wyoming. The sample of *O. virginianus* was smaller and drawn largely from central Texas, with additional specimens from Iowa and Nebraska. An attempt was made, using a series of 12 measured parameters, to find measurements that consistently differentiate isolated (and occasionally broken) antlers of the two species. A series of consistent differences was then compared to overall morphological patterns to determine what features both species of *Odocoileus* hold in common, so that fossil antlers could be assigned to *Odocoileus* with some degree of objectivity.

RESULTS AND DISCUSSION

Antler Morphology and Variations in *Bretzia*

Knowledge of variation in antlers of *Bretzia* relies on the sample of antlers from the White Bluffs Local Fauna (Fig. 1), which comes from a stratigraphically restricted zone in the upper part of the Ringold Formation. This sample includes 26 antlers in which the position and nature of the first branching point is determinable. Measurements are given in Table I.

The age of this sample is Early Blancan (Pliocene). No radiometric date is available, but age determinations (Gustafson, 1978; Gustafson, 1985; Neville et al., 1985) based on biostratigraphic and paleomagnetic data suggest an age no younger than that of the Hagerman Local Fauna in Idaho and most likely substantially older. Paleomagnetic data are compatible with the Gilbert Reversed Paleomagnetic Epoch, which began about 5.3 m.y.B.P. and ended about 3.4 m.y.B.P. The Blancan land mammal age began after about 4.8 m.y.B.P. Age of the White Bluffs Local Fauna is therefore between 4.8 m.y.B.P. and 3.4 m.y.B.P.

TABLE I. Variation in some characters of *Bretzia* antlers.

Feature	N	\bar{X}	R	s	V
Diameter of beam, antero-posterior, 2 cm above burr	32	30.13	21- 40	4.77	15.83
Anterior tine distance*	26	58.62	18-103	23.26	39.69
Length of anterior tine	4	221.25	135-295	62.79	28.38
Maximum diameter of anterior tine†	22	24.86	8- 35	12.49	50.25
Diameter of posterior branch†	24	36.50	15- 48	8.84	24.22
Angle between basal beam axis and plane of burr	30	77.0°	68- 90°	5.73	7.44

Abbreviations: N = number of specimens measured; \bar{X} = mean of all measurements; R = range (maximum and minimum measurements); s = standard deviation; and V = coefficient of variation. Measurements are in mm, unless otherwise stated.

*Measured on ventral side, from top of burr to a point at intersection of central lines along axes of beam and anterior tine.

†Measured on ventral side 4 cm distad from point at intersection of central lines along axes of beam and anterior tine.

The distinctive characters of the antlers of *Bretzia* are as follows:

1. **Antlers are spread laterally, not held upright above the head.** This attitude of the antlers in adults seems to depend on a substantial bend, concave downward, in the first few inches of beam. In some individuals this proximal portion, or beam, is nearly straight; in others the bend in the beam axis covers an angle of about 30°. The attitude of the antlers also depends on the orientation of the pedicles on the frontal bones of the skull. The pedicles on skulls of *Bretzia* tend to project at a larger angle from the midline of the skull than in *Odocoileus*, though not at the nearly 90° angle seen in *Alces*.
2. **The plane of the burr is at nearly a right angle to the axis of the adjacent beam** (angle measurement in Table I). Statistics for this feature are shown in Table I. Although only an occasional antler approaches the rather acute angle commonly seen in *Odocoileus*, there is some overlap. For comparison, the average angle in *Bretzia* is 77.0° (N = 30) as opposed to 68.7° in *O. hemionus* (N = 56) and 59.3° in *O. virginianus* (N = 18). This feature can allow a preliminary identification of *Bretzia* from a small basal fragment if the burr is preserved.
3. **Distal to the first branching point, the posterior branch is dominant.** This is one of the most consistent features of *Bretzia* antlers. Actually there is one known exception,

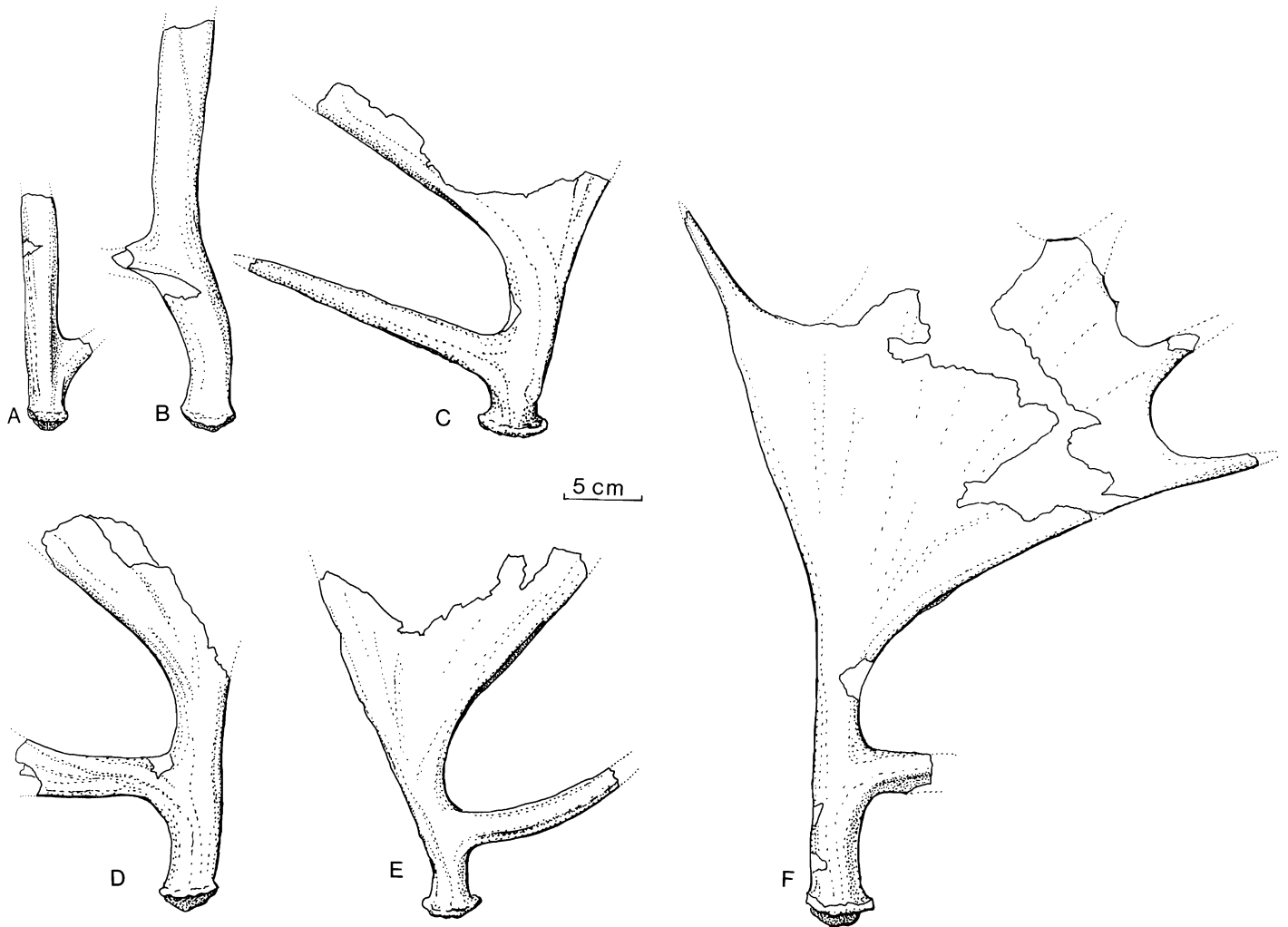


FIGURE 1. Antlers of *Bretzia pseudalces*. A. Juvenile "spike" antler with incipient anterior tine, UW 45,031. B. Second-year antler with base of anterior tine but no palmation (distal end somewhat flattened), UW 41,930. C. Adult antler with complete straight anterior tine and partial palm, UW 42,973. D. Adult antler with anterior tine flattened and probably forked, with relatively narrow palm, UW 42,975. E. Adult antler with curved anterior tine and nearly complete palm, UW 42,974. F. Adult antler, type of *Bretzia pseudalces*, nearly complete palm with multiple tines around margin, UW 42,971.

the type (UW 42,971) in which the anterior tine is almost the same diameter and measures 1 mm larger. The condition in which the posterior branch is larger above the first consistent fork appears to be primitive among the *odocoile* deer.

4. **The first branching point occurs distal to a moderate to long beam or basal section.** This (anterior tine distance of Table I) is the most variable measurement that is available on most antlers of *Bretzia*. The coefficient of variation, 39.7, is high even for features of cervid antlers. When the measurement is small, the tine is nearly adjacent to the burr, though there is always a small gap between the burr and anterior tine. When this measurement is large, the antler assumes a curved shape that nearly approximates the curve of the beam and dominant anterior tine of

Odocoileus. Enough specimens of *Bretzia* are available to show that this variation is continuous and that it is not dependent on the age of the animal. Figure 2 illustrates four examples that show this extreme of variation.

5. **The dominant posterior branch is flattened or spread into a palmate shape.** The shape of the palm ranged from wide, as in the type (Fig. 1), to long and narrow. In most cases the posterior branch begins to show flattening immediately above the first branching point, and in some the flattening begins immediately above the burr. Development of a palmate antler has occurred in a number of cervid phyletic lines (Geist, 1971) but is rarely seen in *Odocoileus*.
6. **There is no basal tine.** *Bretzia* shows little tendency towards the development of rugosity and accessory tines between

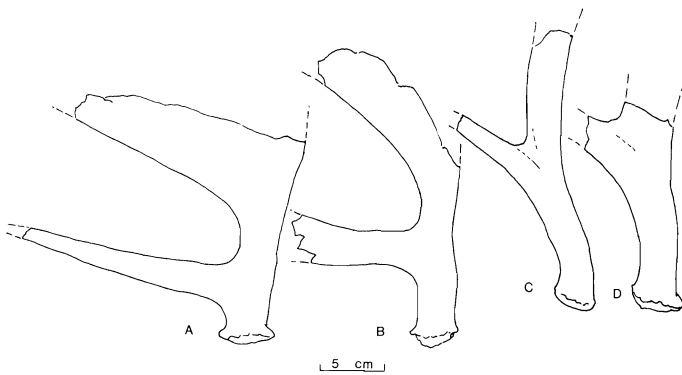


FIGURE 2. Right antlers of *Bretzia pseudalces*, White Bluffs Local Fauna, Ringold Formation, Early Blancan of Washington State, arranged to show range of variation in distance between burr and first major branching point. A. UW 42,973. B. UW 42,975. C. LACM 11,545. D. LACM 11,378.

the burr and first major fork. This is unlike *Odocoileus*, which may have two or more small tines developed on the burr or in the area of high rugosity on the proximal beam (Fig. 3).

Antlers attributable to *Bretzia* on the basis of these characters have been found in Tehama County and Kettleman Hills, California.

Three specimens from Tehama County (UW 22,280, UW 22,281, and LACM 118,597) represent the beams of antlers identical in all respects to specimens of *Bretzia* from the type locality in Washington. In addition, the LACM specimen preserves a fragment of a flattened palm. The specimens are from the Tehama Formation and are Early Blancan in age.

Four fragments of antlers [United States National Museum (USNM) specimens V215,008, V215,004, K60A, and K3,805] are known from Kettleman Hills. Three of these (two of which are shown in Figure 4) closely match *Bretzia* from the type locality. The fourth is a small basal fragment of a juvenile antler in which the angle between the burr and beam is more acute than normal in *Bretzia*. The specimens come from the *Patinopecten* zone of the Etchegoin Formation and are probably also Early Blancan in age.

In both cases the California faunas are poorly known.

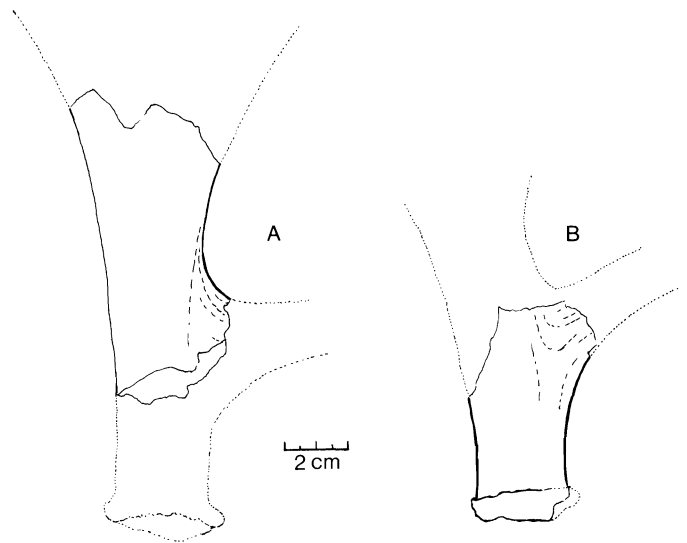


FIGURE 4. Fragments of *Bretzia* antlers, Etchegoin Formation, Kettleman Hills, California, Early Blancan in age. Dotted lines indicate restored outlines. A. USNM K3805. B. USNM 215,004.

Morphology and Variation in *Odocoileus*

Two living species of *Odocoileus* inhabit the Americas. *Odocoileus hemionus* is restricted to regions west of the Mississippi River and ranges from north-central Mexico to the Yukon Territory in Canada. *Odocoileus virginianus* does not range as far north and is absent from most of the Great Basin, but it is the dominant (often the only) deer in the eastern half of North America and Mexico and occurs as far south as northern South America (Hall and Kelson, 1959). The two species are sympatric over much of western North America, although *O. virginianus* prefers brushier habitats at lower elevations, and *O. hemionus* inhabits much of the drier, more open uplands. These species can (but seldom do) interbreed, and both evidently developed from a common ancestry in North America.

There have been several studies (Pocock, 1933; Cowan, 1936; Anderson and Medin, 1969; Roseberry and Klimstra,

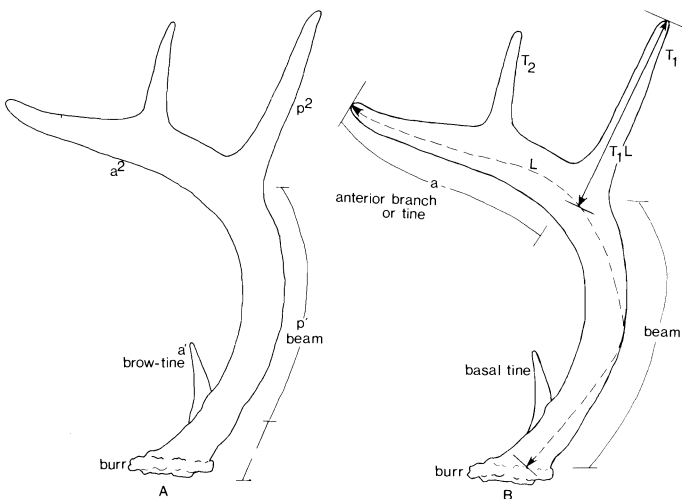


FIGURE 3. Antler terminology for *Odocoileus*. A. Terminology used by Pocock (1933). B. Terminology used here.

1975) of the morphology and variation in the antlers of the two species of *Odocoileus*, but none has emphasized the similarities between the species nor taken a primarily phylogenetic viewpoint.

The first observation that can be made from examination of the antlers is the determination of a pattern that is consistent among antlers of all mature *Odocoileus*. This basic pattern can be considered a generic characteristic of *Odocoileus* and used for comparison of *Odocoileus* antlers to those of other genera (including *Bretzia*). There are two major features of the *Odocoileus* pattern: (1) The beam [the portion of the antler between the burr and the first major branching, branch p^1 of Pocock (1933)] and the anterior branch (from that point forward, Pocock's branch a^2) form a strong, continuous curving structure. The curve approximates a helix (Fig. 5) and can be compared accurately to a section of coil spring. (2) The other common tines can be regarded as rising vertically from the dorsal side of the basic helical structure. There are normally two such tines present in young adult bucks (Fig. 6). A third, the basal tine (Pocock's a^1), is often present (more often in *O. virginianus*), but it is highly variable in size and position.

The two species of *Odocoileus* can usually be distinguished by the ratio of a pair of measurements (Fig. 3), one taken around the outside curve of the helix from the burr to the anterior tip (L) and the second from the base to the tip of the first major vertical tine (T_1L). The first vertical tine is consistently longer on *Odocoileus hemionus* (Fig. 7). No other measurement used in this analysis showed this degree of consistency. The relative length of the anterior branch (a part of the helical structure) and of the vertical tine can be estimated by measuring the greatest diameter of these branches a short distance from the branching point, but a larger degree of overlap is seen in this measurement of the two *Odocoileus* species than in measurements of L and T_1L .

Other characteristics of the antlers that have been suggested for distinguishing *O. hemionus* from *O. virginianus* include: (1) The first major vertical tine (T_1) branches in *O. hemionus*. This is indeed a common characteristic, but only 19 (31.6%) of a sample of 60 antlers in which this character was determinable showed a branching of T_1 . Several others were broken in such a way as to make this indeterminate. The branched T_1 often appeared on only one of a pair of antlers on an individual of *O. hemionus*. In addition, an occasional individual of *O. virginianus* showed a branched tip on T_1 . (2) The number of vertical tines branching from the helical structure was commonly larger in *O. virginianus*. In *O. hemionus* normally only two major vertical tines were present. However, a mule deer may have three or more such tines in a large mature individual, and a whitetail may have only two, especially in young bucks. (3) The basal tine [brow-tine or

a' of Pocock (1933)] was larger and more often present in *O. virginianus*. This was especially true in large mature bucks, but this tine can be quite large in *O. hemionus* and small or absent in *O. virginianus*. The variable presence of this tine is actually

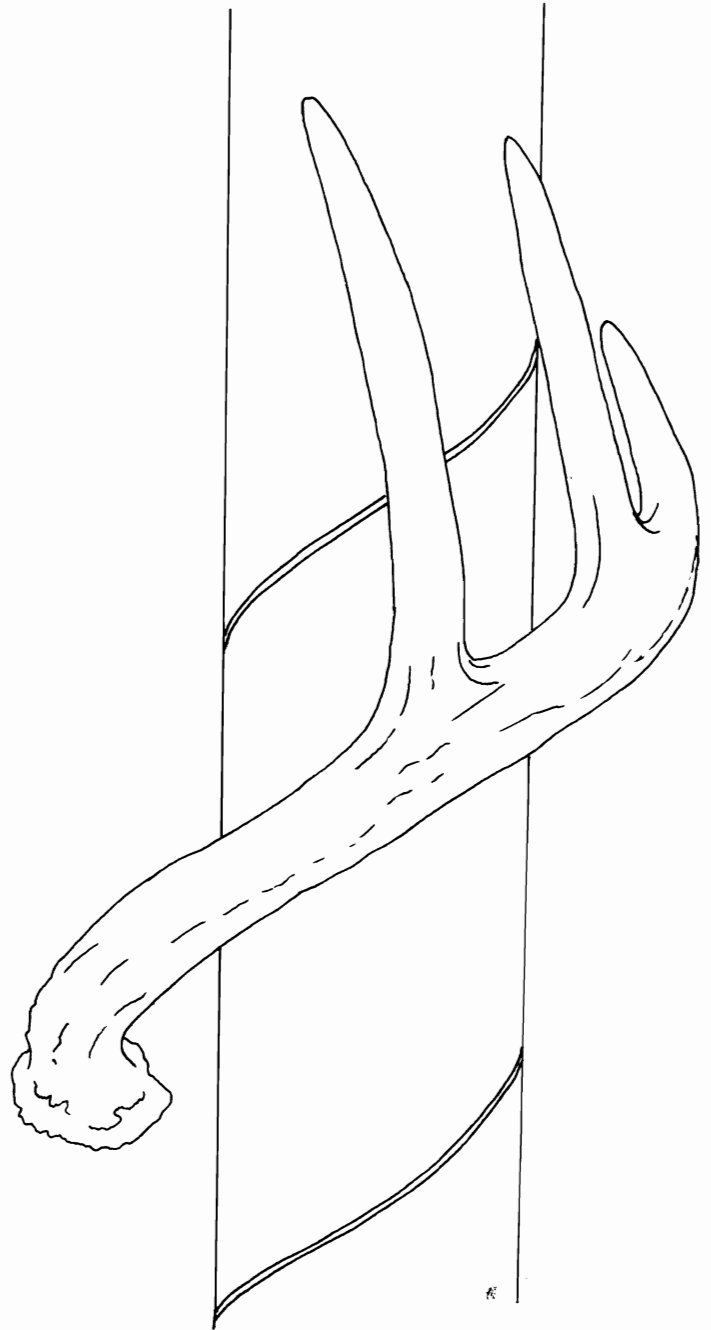


FIGURE 5. Demonstration of helical form of the main structure of the antlers of *Odocoileus*, drawn from a photograph. A right antler of *O. virginianus* has been oriented around a cardboard tube with helical paper wrapping so that the axes of the two helices are coincident and the helical form of the antler parallels the helical markings on the tube.

characteristic of both species and can be considered a generic character. Cowan (1936) noted that the subspecies of *O. hemionus* vary in the frequency of appearance of the structure. Pocock (1933) considered this tine to be a reduced remnant. By comparison with the overall structure of New World deer antlers, I consider it to be a new, or derived, feature in *Odocoileus*.

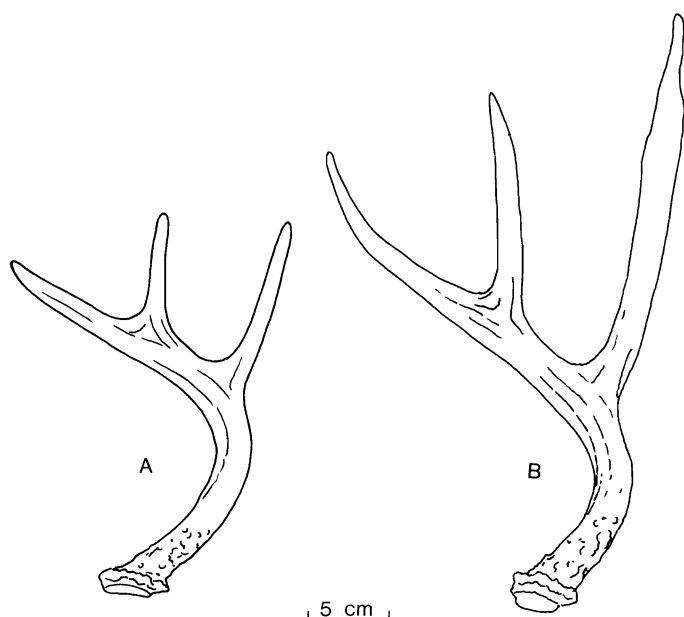


FIGURE 6. "Typical" form of *Odocoileus* antlers, lacking all accessory tines. A. *O. virginianus*. B. *O. hemionus*.

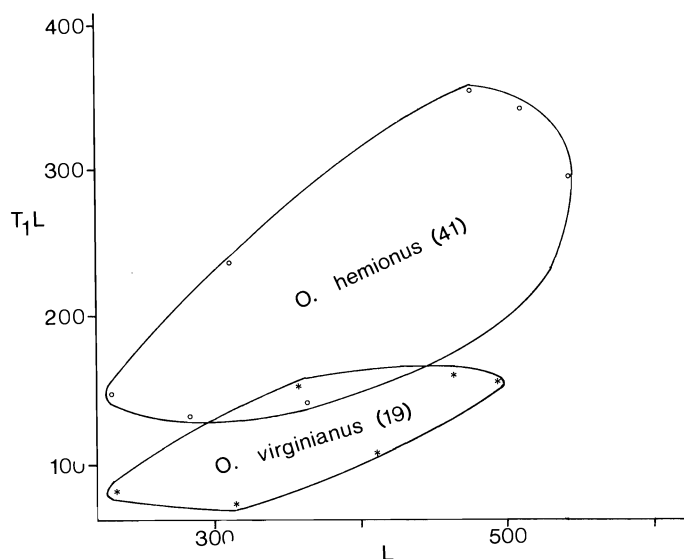


FIGURE 7. Ranges of antler measurements of *Odocoileus hemionus* and *O. virginianus* (see Figure 3 for definition of measurements L and T₁L).

The earliest available example of a mature antler showing the generic characters of *Odocoileus* is a specimen from Hagerman, Idaho (Fig. 8). The antler (USNM 299,483) was collected by George B. Pearce in 1934 from the Glens Ferry Formation. Judging by the measured sections and map published by Bjork (1970), the locality (a small canyon in the northwestern corner of Sec. 4, T. 8 S., R. 13 E.) would be low in the section, certainly lower than the USNM Horse Quarry. Paleomagnetic evidence (Neville et al., 1979) suggests that the antler is from the later part of the Gilbert Paleomagnetic Epoch and is between 3.4 and 3.8 million years old. It shows the usual curvature of the beam, the presence of not one but two basal tines (a feature occasionally seen in modern *Odocoileus*), substantial rugosity near the burr, and, although broken, an apparent branch like that in *Odocoileus*. Although it is not possible to identify features diagnostic of either of the modern species, the rather open curve and relatively small size of the basal tines are suggestive of *O. hemionus*.

Odocoileus brachyodontus from the Rexroad Formation of Kansas may have appeared earlier than the Hagerman deer, but the species has been described only from the dentition, which is very similar in *Odocoileus* and *Bretzia*. Therefore the generic assignment of these specimens cannot be regarded as having been conclusively demonstrated.

Antlers and Phylogeny in New World Deer

In an effort to understand the phylogenetic position of

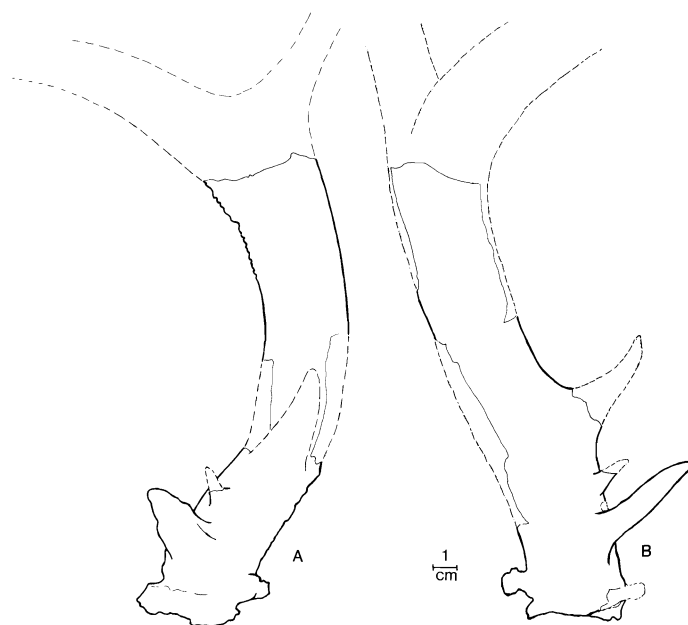


FIGURE 8. *Odocoileus* sp. (USNM 299,483) right antler from the Hagerman Local Fauna, Hagerman, Idaho, Pliocene (3.5-3.8 m.y.B.P.). Dashed lines show reconstructed outlines. A. Medial view. B. Anterior view.

Bretzia in the evolution of the Cervidae, a phylogenetic hypothesis is presented in Figure 9 to account for the observed antler patterns. This is necessarily very preliminary, as it is based on relatively few fossils and only selected anatomical features of the living genera. The branching formation of the phylogenetic hypothesis is based (as in cladistic analysis) on synapomorphies (shared derived characteristics), but the available antler morphology alone does not allow a unique solution to the problem of odocoilene phylogeny.

The numbered branching points of Figure 9 were placed as they are for the following reasons:

1. Most classifications of the advanced Cervidae (i.e., Whitehead, 1972) make a strong distinction between the cervine deer (*Cervus* and its relatives), which are plesiometacarpaline and possess a brow-tine immediately adjacent to the burr, and the odocoilene deer, which are telemetacarpaline (they possess only a reduced distal remnant of the lateral metacarpals) and usually have a variable tineless section to the antlers just above the burr. Those to the right of this point are telemetacarpaline.
2. *Alces* and its close relatives are characterized by gigantism; large palmate antlers; and various skull, dental, and skeletal features. This group is basically Old World in origin and reached North America only in the Late Pleistocene. It could usefully be classified as a separate subfamily, as was done by Frick (1937).
3. *Rangifer* is another specialized cervid that shows considerable divergence from other telemetacarpaline deer, particularly in the antler morphology, and it is unique in the normal presence of antlers in females. Again, as Frick (1937) proposed, *Rangifer* could usefully be placed in its own subfamily. To the right of 3 are all of the small-to-medium sized telemetacarpaline deer, including *Capreolus* and the North and South American genera. These are considered to constitute a restricted subfamily. It is assumed that the antler pattern shown by *Capreolus*, the Old World roe deer (Fig. 10A), is close to the primitive pattern for all of the remaining odocoilenes. This "primitive" pattern includes a relatively long beam; an anterior branch or tine (a); and a longer, forked posterior branch. Since the Pliocene, however, *Capreolus* has evolved independently of other odocoilenes.
4. At some time during the Late Miocene, probably after about 6 m.y.B.P., some ancestral odocoilene deer managed to cross from Siberia into North America, and subsequently spread southward. With suitable unoccupied habitats available nearly to the southern end of South America, the postulated ancestral odocoilene spread rapidly and occupied a diverse series of habitats, diversifying morphologically during the Pliocene and Early Pleistocene. *Capreolus* presumably represents the Old World descendants of the common ancestor of the New World odocoilenes.
5. In tropical areas a niche was available similar to that of the most primitive Old World deer (i.e., *Muntiacus* and *Elaphodus*), which are small forest-dwelling animals. This niche was occupied by *Mazama* and *Pudu*, which are small in size and have simple antlers resembling the first year spike antlers of larger deer of other species (Fig. 10B).
6. The larger odocoilene deer include *Hippocamelus*, the

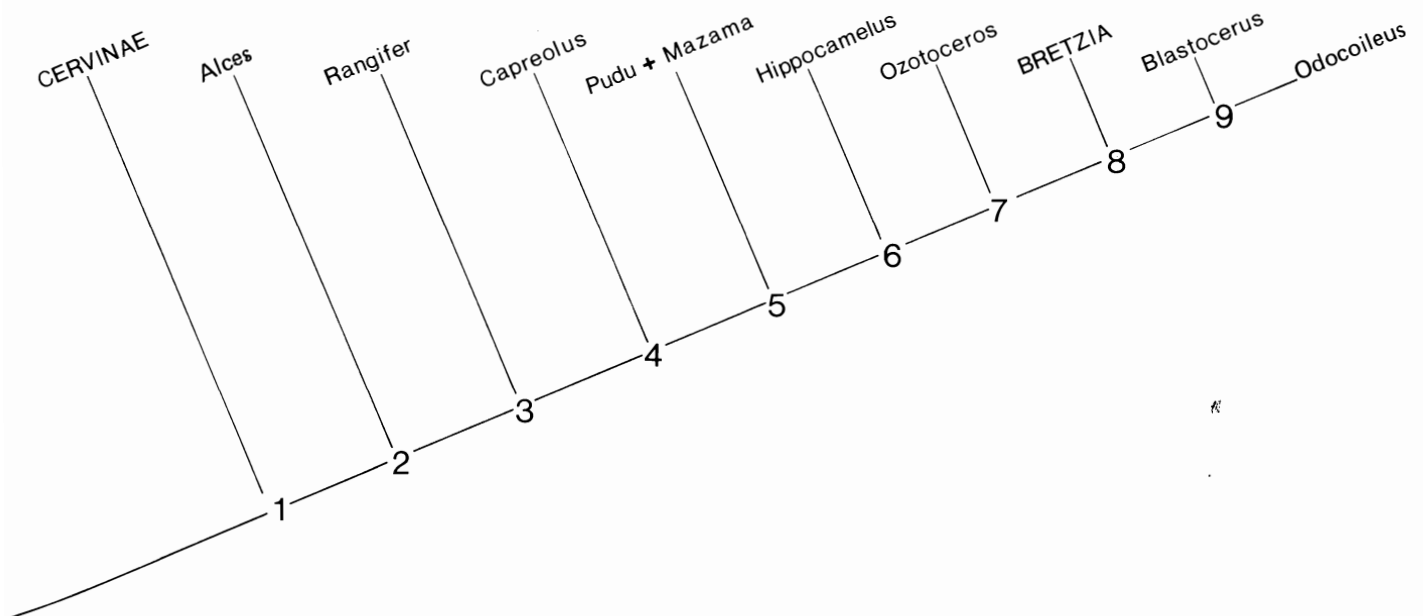


FIGURE 9. Phylogenetic hypothesis to illustrate the position of *Bretzia* among the New World deer.

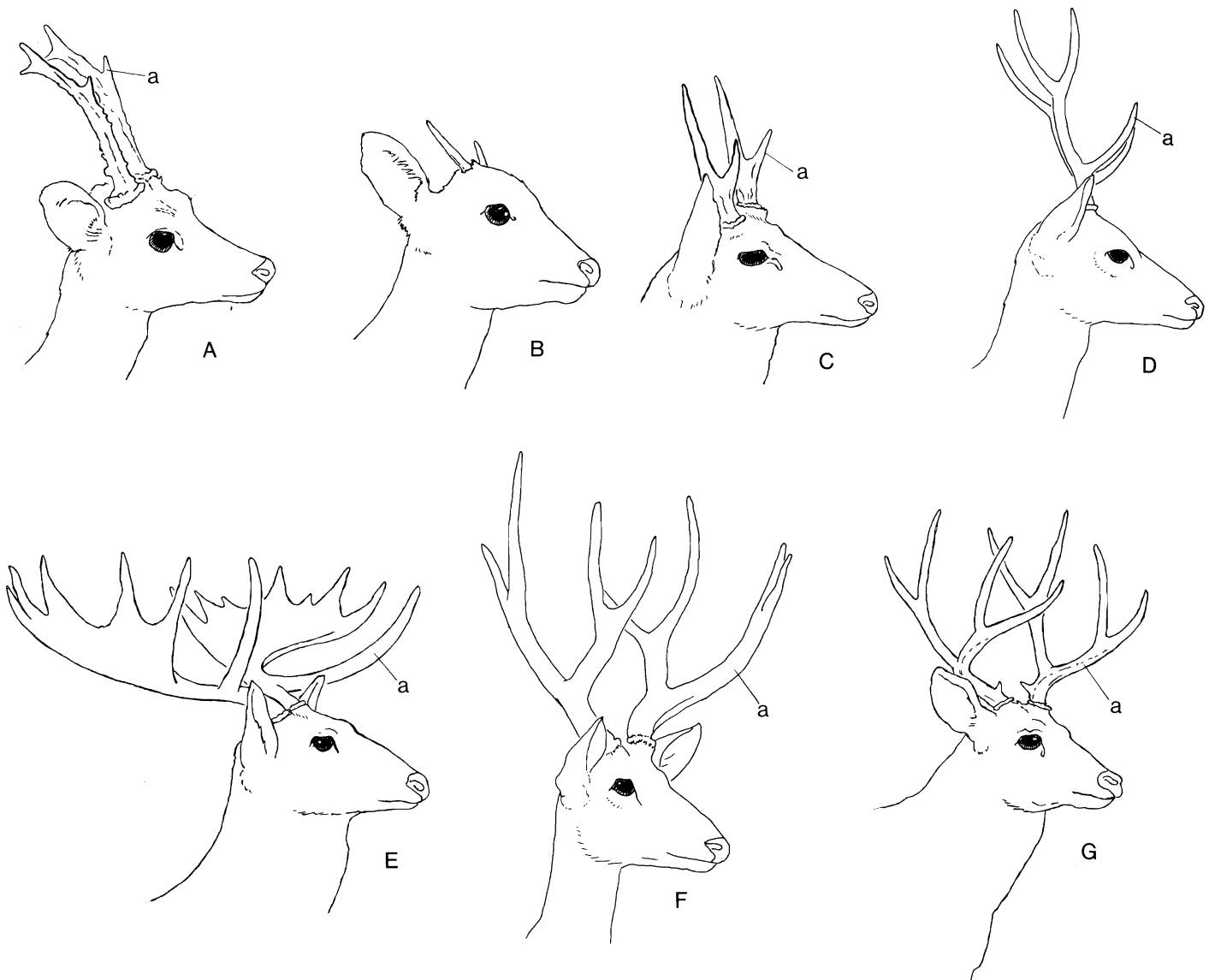


FIGURE 10. Living and fossil odocoilene deer. **A.** *Capreolus*, the Eurasian roe deer. **B.** *Mazama*, the South American brocket. **C.** *Hippocamelus*, the Andean huemul. **D.** *Ozotoceras*, the South American pampas deer. **E.** *Bretzia*, North American, Blancan, Ringold Formation of Washington State. **F.** *Blastocerus*, South American marsh deer. **G.** *Odocoileus hemionus*, North American mule deer. Tines labelled (a) are considered to be homologous (anterior branch or anterior tine).

Andean mountain deer or huemul (Fig. 10C). The antlers are composed of two branches of which the anterior is generally smaller. The posterior branch is occasionally forked. This may be a reduced form of antler.

smaller anterior tine (a) curving upward and inward and a larger, longer, commonly forked posterior branch (equivalent to T₁ of *Odocoileus*). Large specimens of *Capreolus* can have almost identical morphology.

7. The larger-antlered odocoilenes have antler morphologies which can be derived from that of *Ozotoceras* (Fig. 10D). The antlers are held relatively vertically; are branched a short (but variable) distance above the burr; and have a

8. *Bretzia* (Fig. 10E) can be derived from a morphology like that of *Ozotoceras*, though modified so that the antlers are spread laterally and the posterior branch is spread into a palm encompassing the multiple tines of the posterior

branch. The anterior tine (a) is large and may occasionally have been forked, but it was consistently smaller than the posterior branch.

9. *Blastocerus* (Fig. 10F) has enlarged the anterior tine so that it is subequal to the posterior branch, and like the posterior branch, it is forked in many individuals (adding T₂ of Figure 3).

Odocoileus increased the size of the anterior branch (a) and reduced the posterior branch. The combination of beam and anterior branch now forms a strong helical structure. A T₂ tine is routinely added, and new tines (the basal tine or tines) are added to the posterior dorsal side of the beam. Of the two living species, *Odocoileus hemionus* could be said to have the more primitive antler morphology, as the posterior branch (T₁) is large and commonly forked. *Odocoileus virginianus* shows the present extreme in modification, with an enlarged basal tine in most adult males and a greatly reduced (though still occasionally forked) T₁.

CONCLUSIONS

1. *Bretzia* is an odocoilene deer closely related to *Odocoileus*. The cranial, postcranial, and dental remains show definite resemblance to modern *Odocoileus*.

2. The antlers of *Bretzia* fit well into the pattern of evolution of antlers of other odocoilene deer, and certain variations show distinct similarities to a form which could have been the primitive form of the antlers of *Odocoileus*.

3. Finds of specimens of *Bretzia* are restricted so far to the earliest Blancan of the west coast of North America. *Bretzia* seems to have been replaced by *Odocoileus* by the end of the Early Blancan, or by about 3.5 m.y.B.P.

4. *Odocoileus brachyodontus* from the Rexroad Formation of Kansas is probably about the same age as the known specimens referred to *Bretzia*. Lack of specimens of adult antlers makes identification of this species to the genus *Odocoileus* questionable.

5. *Bretzia pseudalces* was preceded in North America by only one known form of deer, represented by undescribed specimens from the Late Hemphillian of Florida. These specimens are being studied at the Florida State Museum.

6. Antlers of *Bretzia* show a series of characteristics that allows tentative identification on the basis of relatively fragmentary antler material. Characters in this series include the orientation of the burr, the form of the proximal beam, the

position and nature of the anterior branch, the small amount of rugosity of the proximal beam, the flattening or palmation of the posterior branch, the lack of a basal tine, and the relative sizes of the anterior and posterior branches (posterior branch equal or larger).

7. The two extant species of *Odocoileus* show a number of common antler characteristics that can be considered generic characters and which allow identification of mature antlers of this genus. These include the helical beam and anterior tine structure, common presence of a basal tine, angle of the burr relative to the beam, tendency towards rugosity of the proximal beam, and the relative sizes of the branches (anterior branch larger in diameter).

8. Antlers of the two extant species of *Odocoileus* can be distinguished more easily by the relative length of the first major vertical tine (T₁) than by other characters.

9. Of the living species of *Odocoileus*, *O. virginianus* appears to have the more derived antler characters and *O. hemionus* the more primitive antler characters, based on comparisons to *Bretzia* and other New World deer.

10. *Capreolus*, *Bretzia*, *Odocoileus*, *Pudu*, *Mazama*, *Hippocamelus*, *Ozotoceros*, and *Blastocerus* appear to be related more closely to each other than to *Rangifer*, *Alces*, or their allies. The subfamily Odocoilinae should include the former series of genera and exclude the latter. This suggestion revives, in part, the classification used by Frick (1937) in which Alcinae and Rangiferinae are independent subfamilies.

11. The antler forms of all New World Odocoilinae are derivable from a single form similar to antlers of *Capreolus* and *Ozotoceros*.

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