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An Early Pliocene North American Deer: *Bretzia pseudalces*, Its Osteology, Biology, and Place in Cervid History

by Eric Paul Gustafson

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Museum of Natural History
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Above*:* *Bretzia pseudalces*, group of males feeding. Adapted from a drawing by J.G. Millais, 1897.

Cover: *Bretzia pseudalces*, reconstruction of skull and antlers.

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ABSTRACT

The cervid genus *Bretzia* was first described in 1974 from antler and skull material found in the White Bluffs local fauna of the Pliocene Ringold Formation in south-central Washington. Cervid specimens from the Ringold deposits had been mentioned in published reports in 1917 and 1953, but not until a series of specimens was collected by Willis E. Fry and donated to the Burke Museum in Seattle, about 1970, was the evidence adequate to provide a preliminary diagnosis of *Bretzia*. The basis of the genus was a series of shed antlers and a portion of the skull of a male individual. Although statements have been made generally characterizing the dentition and postcranial skeleton as similar to *Odocoileus,* the detailed descriptions of these elements have not previously been published.

Bretzia was similar in size to modern *O. hemionus* (mule deer) but differed in antler morphology and details of the skull, teeth, and postcranial skeleton. The antler pedicles are more widely separated than in most Cervidae. The antlers are distinctive, with a single anterior tine and a posterior beam which in adult individuals forms a large palmate structure. Enough antlers are known to present a developmental series including juvenile, adolescent, adult, and senescent forms. Numerous details of the dentition and postcranial skeleton, including the metacarpals show that *Bretzia pseudalces* was a telemetacarpal deer (subfamily Capreolinae). The relationship of *Bretzia* to the living tribes (Alcini, Capreolini, and Rangiferini) is uncertain. *Bretzia* was one of three known genera (*Bretzia, Odocoileus*, and *Eocoileus*) in an early Pliocene (ca. 5 Ma) evolutionary radiation of cervids after the initial immigration from Asia into North America around the time of the Miocene-Pliocene boundary. The Ringold Formation deposits in which the cervid sample was found date to the early Blancan (early Pliocene), probably between 5.0 and 4.8 Ma. The White Bluffs cervid sample largely consists of seasonal (winter and spring) accumulations of bones, antlers, and teeth, which were scattered, weathered, and then buried by spring floods. The proximal environment was a level floodplain with the streams bordered by forest and brush, and surrounded by marsh, small lakes, and grassland. The climate was seasonal but somewhat milder and wetter than at present.

INTRODUCTION

Antlered deer of the family Cervidae are easily the most abundant and familiar large native mammals in North America today. Five genera (*Alces*, *Cervus*, *Mazama*, *Odocoileus*, and *Rangifer*) are present, ranging geographically from the tropics to the Arctic tundra. Of these, only *Odocoileus* has any pre-Pleistocene fossil record in North America. The various cervids include both the trophy animals most desired by hunters and the watchable wildlife easily seen even in areas heavily populated by humans. Antlered cervids appear to have dispersed to North America from Asia about five million years ago and continued on to South America about 1.5 million years later (Webb, 2000). South American faunas include six living genera, of which two are shared with the North (Whitehead, 1972; Groves and Grubb, 2011). To complicate matters, a number of extinct endemic cervid genera appear suddenly in the South American fossil record (Geist, 1998, Webb, 2000). Some studies (e.g., Duarte et al., 2008) suggest that much of this diversification occurred before the ancestral forms left North America. If the latter is the case, then fossils of those ancestral forms should be found in North America.

It is perhaps surprising that the early history of these animals has not been well known. There are two main reasons for what seems to be neglect by paleontologists. First, in most late Neogene deposits, cervids are very rare and, where present, are usually very fragmentary. Second, the group has seemed to be unrewarding for research because of a lack of variety among the known early taxa and because the known specimens, especially dentitions, appear to offer little information about evolution and phylogenetic relationships. Some better specimens exist in various collections but remain unstudied.

An additional problem unique to antlered cervids is the deciduous nature and extreme variation in the forms of the antlers. Antlers are often the most taxonomically distinct fossilized parts and thus are often chosen as the best available type specimens for new genera and species. Being deciduous and only present in the males of most species, antlers present problems in that they are most frequently found detached from the rest of the animal. Identification of a taxon on the basis of dentitions or isolated bones may be impossible if the type specimen is an antler.

There are now two major sources of data on the very early history of North American cervids, both from faunas near the Miocene-Pliocene boundary, not long after the first immigration of cervids. In Florida, the Palmetto fauna, dated at about 5 to 4.7 Ma (Webb et al., 2008), contains two genera, *Eocoileus* Webb, 2000 (an extinct deer with similarities to South American *Ozotoceras*) and *Odocoileus*, the genus which includes modern whitetail and mule deer (see discussion below). The other is the White Bluffs local fauna of Washington State, similar in age (perhaps 4.98-4.89 Ma), which contained the specimens described in this paper of *Bretzia pseudalces* Fry and Gustafson (1974). With new information from these two faunas and from isolated finds elsewhere (i.e., Gustafson, 1985a; Voorhies and Perkins, 1998; Webb, 2000; Morejohn and Dailey, 2004; Morejohn et al., 2005), the history of early North American Cervidae has begun to emerge from obscurity. Assisting the unraveling of New World deer ancestry has been a series of phylogenetic studies of the living deer faunas (i.e., Gilbert et al., 2006, and Duarte et al., 2008). Duarte et al. (2008), in particular, conducted a molecular analysis of cytochrome *b* gene sequences of all the extant New World deer genera and compared their results to cytogenetic data and to external morphology. Their results have provided a phylogenetic hypothesis for the New World deer which can be tested by examination of the fossil record.

The purposes of this study are to describe the osteology of specimens from the White Bluffs local fauna which can be assigned to *Bretzia pseudalces*, to establish the chronological and phylogenetic relationships of *Bretzia* among the Cervidae, to describe the paleoenvironment in which they lived, and to attempt to elucidate some basic factors in the biology of this deer. A substantial number of studies have been done on the geology of the Ringold Formation and various members of the White Bluffs l.f. since the first summary paper (Gustafson, 1978). As a result I have expanded some sections of this paper to accommodate the new information and included an up-to-date faunal list.

MATERIALS AND METHODS

For the purposes of this study, the working hypothesis has been that the vast majority of cervid specimens from a restricted part of the Ringold Formation (the White Bluffs cervid sample) can be assigned to the single species *Bretzia pseudalces*. The limited range of variation in size and characteristics for most (non-antler) specimens supports this view, and the much-more-variable antler material can generally be assigned to a reasonable set of developmental stages in one taxon. There are other possible taxonomic scenarios; for example, it is not unknown for two distinct but similar species of cervid to occupy the same geographic area. This happens with *Odocoileus hemionus* and *O. virginianus* in several areas in North America today. In the latter case, with a sample of the size and quality of the White Bluffs cervid sample, it might not be possible to separate the two species, and certainly most of the bones would be impossible to identify to the species level. Sexual dimorphism was certainly present in *Bretzia* in the presence or absence of antlers, and by analogy with modern cervids probably in body size, providing an immediate justification for bimodal statistical distributions should such be found. In addition, when making size comparisons it is significant that both modern *Odocoileus* species exhibit considerable size variation between geographically separated populations, in each case providing more variation in size (i.e., between populations of *O. virginianus* between Minnesota and Florida, or between populations of *O. hemionus* between Colorado and coastal Oregon) than is seen in the White Bluffs cervid sample (Rue, 1997; Wallmo, 1987). Cervids with substantially different size and morphology representing multiple genera often occur sympatrically in modern faunas, but there is no evidence of such diversity in this sample.

Fossil specimens from the Ringold deposits included here are from the collections of the Burke Museum of Natural History and Culture in Seattle, Natural History Museum of Los Angeles County, University of California Museum of Paleontology, Charles R. Conner Museum at Washington State University, University of Oregon Museum of Natural and Cultural History, Geology Museum of Whitman College, Walla Walla, Washington, and Museum of Geology at the South Dakota School of Mines and Technology in Rapid City. Fossils of other cervid taxa were examined at the American Museum of Natural History, Natural History Museum of Los Angeles County, Florida Museum of Natural History, Natural History Museum (London), Berlin Museum of Natural History (Museum für Naturkunde, Berlin), and Museum of Evolution in Uppsala, Sweden. Some of the modern comparative material is from the author's collections. Other modern deer specimens were provided by the University of Oregon Museum of Natural and Cultural History, C. Dailey of Sierra College, California, Natural History Museum of Los Angeles County, Florida Museum of Natural History, American Museum of Natural History, Natural History Museum (London), Vienna Museum of Natural History, Philadelphia Academy of Sciences, and Burke Museum of Natural History and Culture, Seattle. The author's collection of *Odocoileus hemionus hemionus* from eastern Oregon provided a statistical sample, allowing for comparisons of the sample of *Bretzia pseudalces* with a modern localized population of a single species. Comparisons to *Odocoileus* are to this population.

Specimens of Recent species used for anatomical comparison were chosen partly on a practical basis, using easily-available species, and partly to represent the several surviving cervid clades. Among the Cervinae (plesiometacarpal deer, Fig. 2), comparisons were made with *Muntiacus* (naturalized, non-native specimens from Britain), *Dama dama* (captive specimens from deer farms), and *Cervus canadensis* (wild specimens from eastern Oregon). Capreolini examined (telemetacarpal deer, those with reduced proximal lateral metacarpals and undivided posterior choanae) include *Capreolus capreolus* (British specimens) and *Alces americana*. Among the telemetacarpal Rangiferini (deer with the posterior choanae divided by a vomerine septum) comparisons have been with *Odocoileus hemionus* and *O. virginianus* (wild specimens), as well as *Mazama americana* (wild specimens; captive specimen from the San Diego Zoo), *Pudu puda* (wild and captive specimens), *Ozotoceros bezoarcticus* (wild and captive specimens), *Blastocerus dichotomus* (wild specimens), and *Hippocamelus antisensis* (wild specimens). For most of the larger South American forms, only cranial specimens were examined. The vast majority of comparisons have been made using *Odocoileus*. This is partly because of the availability of a large suite of modern specimens of mule deer, and partly because this is the genus with which specimens of *Bretzia* are most likely to be confused.

Taxonomy of the Cervidae used herein follows Groves and Grubb (2011), both in the higher ranks (Artiodactyla, not Cetartiodactyla; using Capreolinae and Rangiferini instead of Odocoileinae and Odocoilini respectively, for example) and at the genus and species level (i.e., using *Cervus canadensis* instead of *Cervus elaphus* for wapiti and *Alces americana* instead of *A. alces* for North American moose). The latter work, unlike earlier taxonomies, was able to take into account recent phylogenetic studies based on DNA analysis, mostly of living species. The conclusions of such studies (i.e., Gilbert et al., 2006, Duarte et al., 2008, and Hassanin et al., 2012) has simultaneously clarified and confused our knowledge of cervid clades, and the extensive new data has not yet been fully absorbed nor tested against the fossil record.

ABBREVIATIONS

AMNH = American Museum of Natural History, New York City, New York

AMNH F:AM = Frick Collection, AMNH, New York City, New York

LACM = Natural History Museum of Los Angeles County, Los Angeles, California

SDSM = South Dakota School of Mines and Technology, Rapid City, South Dakota

UCMP = University of California Museum of Paleontology, Berkeley, California

UF = Florida Museum of Natural History, University of Florida, Gainesville, Florida

UMMP = University of Michigan Museum of Paleontology, Ann Arbor, Michigan

UOMNH = University of Oregon Museum of Natural and Cultural History, Eugene, Oregon

UWBM = Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington

WHC = Whitman College, Walla Walla, Washington

CRCM = Charles R. Conner Museum, Washington State University, Pullman, Washington

Ma = millions of years before the present

N = number of specimens in sample

L = left

R = right

AP = anteroposterior

T = transverse

l.f. = local fauna

DENTAL TERMINOLOGY

Origins—Dental terminology in ruminant artiodactyls, including cervids, has varied considerably among authors. Modern researchers accept the general tritubercular pattern of cusps as primitive, as established by Cope (1874; 1883) and Osborn (1888; 1907). This tritubercular theory forms the basis for almost all studies of mammalian dental evolution. An examination of the wide variety of early (Eocene) artiodactyls (i.e., in Prothro and Foss, 2007), shows that these dentitions had origins in animals with tritubercular dentitions similar to those of other placental mammals.

Available terminology—Among relatively recent works, the terminologies used by Heintz (1970, largely in French), Hershkowitz (1982), Hamilton (1973), Janis (1987), Gentry and Hooker (1988), Dong (1993) and Gentry et al. (1999) have been influential. The most significant differences have been in the name of the main posterolingual cusp on the upper molars. For most mammals, and until recently for cervids, this cusp has been called the hypocone. Wortman (1898) proposed that this cusp, in some selenodont artiodactyls, is actually homologous to the metaconule of other mammals. The latter term has been adopted here and by many modern workers, though sometimes inconsistently. For example, Gentry and Hooker (1988) use metaconule, but Gentry et al. (1999) use hypocone for the same cusp.

Cervid tooth cusps, particularly those with selenodont or crescentic form, have attached crests which add to the chewing efficiency but which obscure the primitively conical cusps. Some authors use the term “wings” (as in anterior or poster wings of the protocone). This term has more often been supplanted by the term “crista” (cristids for the lower teeth) in recent publications. Adding prefixes gives direction and cusp to which the crista is attached, as in “preprotocrista” for a crest projecting from the anterior side of the protocone.

More recently, Burmann and Rossner (2011) have reviewed the dental terminology of the Ruminantia, comparing the terms used by several influential authors and proposing some standardization. They state that their compilation “does not pay attention to the deeper issues of cusp and cuspid homologies…” and suggest terms “referring to the spatial position on the tooth with respect to the basic cusps and cuspids” (p. 762). In addition, Burmann and Rossner (2011) propose an entirely new set of terms for the premolars, based on the geographic positions of structures on the teeth. I am reluctant to use

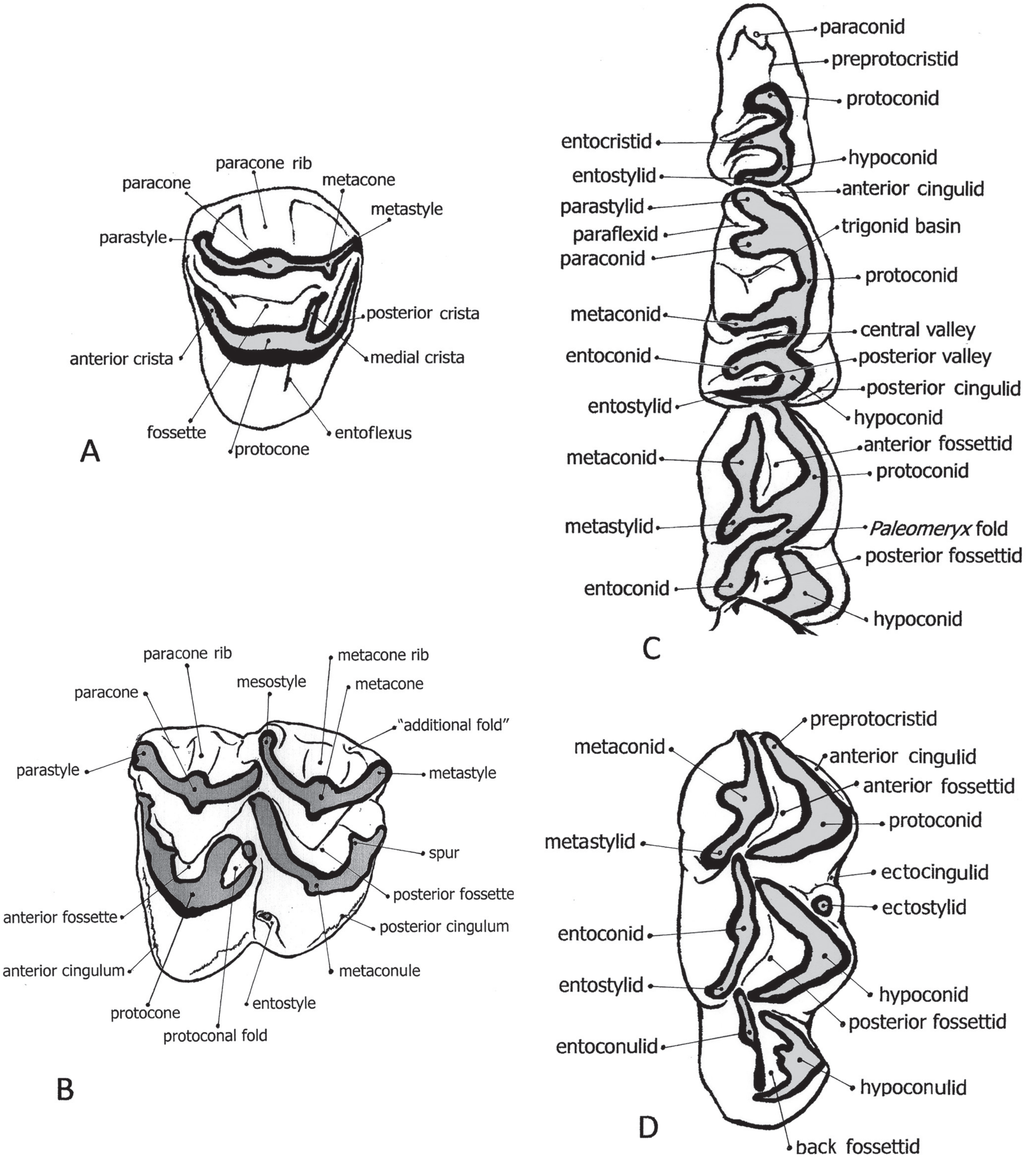

FIGURE 1. Dental terminology: A) L upper premolar (anterior to left; labial at top); B) L upper molar (anterior to left, labial at top); C) R lower premolars (anterior at top; labial at right); D) R lower 3rd molar (anterior at top, labial at right). The teeth are abbreviated in text and figures with capital letters (I for incisor, C for canine, P for premolar, M for molar); tooth number in superscript for uppers, subscript for lowers; deciduous teeth are indicated by a prefix lower case d (i.e. dP^3 for third upper deciduous premolar).

this new set of terms, for two reasons. First, the older terms are well-entrenched in the literature and the new terms would make comparisons between this and previous research difficult. Second, the premolars in cervids have evolved in parallel with molars, first in adopting a trigonid-talonid (tritubercular) pattern (especially on P_2 and P_3) and then evolving a selenodont pattern which overlies the tritubercular pattern. This means that possibly homologous structures of similar shape and position in the premolars and molars would be given different names.

Cusp homology and patterns specific to cervids—The evolutionary tendency among the cervids has been for an increase in the chewing battery by modifying the posterior premolars (especially P_3-P_4 and P^3-P^4) to be included in the selenodont molar row. In the lowers this situation is produced by molarization (here meaning "acquiring selenodonty") of P_4 to resemble the molars. In the uppers the deciduous third premolar is partly selenodont and the deciduous fourth premolar (dP^4) is already completely molariform, and at one point before the dP^3 and dP^4 are lost and while the M^3 is erupting, the animals have the appearance of having four or five upper molars. After the deciduous premolars are lost and the posterior premolars erupt, the functional effect is to continue the presence of an additional anterior molar, with each of the two posterior premolars forming half of a functionally four-cusped chewing structure.

Use of the term *homology* in the cusp patterns of mammalian dentitions suggests an identity in the origin or process of formation of these structures on a genetic basis. The distinctive characters of each tooth are not determined by any one specific gene but by the overlapping or combinational activities of numerous genes (presence and also absence) which determine the tooth shape (Coburne and Sharpe, 2003). Mammalian teeth develop along restricted linear zones in the jaw margins, and, early in embryonic development, begin to differentiate into zones which typically separate teeth into incisors, canines, premolars, and molars. Each tooth passes through several stages beginning from a tooth bud, and later developing structures called enamel knots (in two stages) which determine where formation of the enamel occurs. The positions of secondary enamel knots determine the species-specific pattern of cusps, which generally differ between teeth. Regulatory genes determine the sequence with which the specific structures form (Jernvall and Thesleff, 2000).

Molarization (the acquisition of molar-like cusp patterns and tooth shape) appears in the premolars of many mammalian taxa. It often affects the premolars in a predictable sequence. Generally the posterior premolars begin to take on the cusp pattern of the molars, probably by appearance during early development of secondary enamel knots in positions typical of the molar teeth. The process appears to move sequentially forward. In some lineages (e.g., horses and rabbits) the resemblance of premolars to molars is extreme, though usually the anterior-most premolar remains distinctive. The process is reasonably interpreted as depending on the activation of genes in the developing premolars which are normally only expressed in the molar series. This process moves forward from the area of the anterior molar. In other words, the molarized cusps of the premolars are likely genetically homologous to the equivalently shaped and positioned cusps of molars.

The pattern of molarization in the premolars of cervids is strongly suggestive of the gradual addition of molar characteristics in their genetic development; first, by adding a generalized tritubercular form (very ancient for molars), then superimposing features which lead to selenodonty. As a result, I consider the use of the more traditional names for the premolar cusps, which suggest homology, to be justified on a genetic basis.

Terminology used in this paper—Terminology of the major tooth structures used in this paper (Fig. 1) is compatible with those of Janis (1987), Gentry and Hooker (1988), Dong (1993) and (for major molar structures) Burmann and Rossner (2011).

METACARPAL TERMINOLOGY

Extant deer are divided into two major groups at the subfamily level, the Capreolinae and Cervinae. The distinctive anatomical difference between these subfamilies is in the nature of the reduction of the lateral metacarpals (Brooke, 1878), i.e., metacarpals II and V (Fig. 2; see also Fig. 48). All cervids have completely lost metacarpal I and its digits, the equivalent of our thumb, and have the medial metacarpals (III and IV) fused into the cannon bone. In the Miocene deer (which are *holometacarpal*) the lateral metacarpals are almost as long as the medial metacarpals and have a central shaft. All modern deer have lost the central shaft of the lateral metacarpals. The Old World deer (the Cervinae) also lose the distal end of the lateral metacarpals but retain parts of the proximal ends, a condition called *plesiometacarpal*. The New World deer (Capreolinae), which also includes roe deer (*Capreolus*), plus moose (*Alces*) and reindeer (*Rangifer*), have lost the proximal ends of the lateral metacarpals, but retain the distal end. This condition is termed *telemetacarpal*. There actually is some variation in the degree of reduction among various taxa; for instance Morejohn and Dailey (2004) describe the presence of a tiny remnant of proximal metacarpal II in *Odocoileus* which had been previously overlooked. In general, however, this anatomical distinction seems to agree with taxonomy based on recent phylogenetic studies.

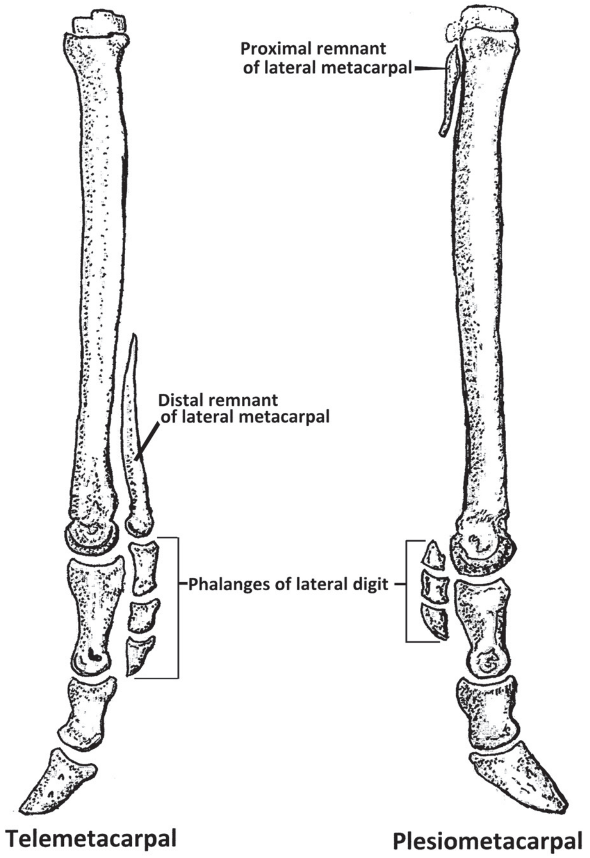

FIGURE 2. Cervid front foot (metacarpal) terminology. Foot bones as seen from the side. All modern deer have lost portions of the lateral metacarpal bones. The New World deer (Capreolinae, including also roe, caribou and moose) retain the distal (lower) part of the lateral metacarpals (telemetacarpal, on left). The Old World deer (Cervinae) retain only the upper (proximal) remnant of the lateral metacarpals (plesiometacarpal, on right).

GEOLOGY AND AGE OF TYPE LOCALITY

The type locality, or the location from which the type specimen for the genus and species *Bretzia pseudalces* was excavated, is UWA9577, a small hand-dug quarry in a thin gravel layer in the Ringold Formation about 15 meters below the White Bluffs tuff (Fry and Gustafson, 1974; Gustafson, 1978; Fig. 3). The spot is in the bluffs just south of the mouth of Ringold Coulee, in Sec. 25, T12N, R28E, Eltopia Quadrangle, Franklin County, Washington.

The Ringold Formation is a continental basin-filling sedimentary deposit in south-central Washington (Map, Fig. 3). The majority of deposits mapped as Ringold Formation are in the Pasco Basin, surrounded by the Horse Heaven Hills to the south, Rattlesnake Hills and other highlands to the west, the Saddle Mountains to the north, and the gently-sloping Palouse Slope of the Columbia Plateau to the east. Underlying the sediments are the late flood basalt flows of the Columbia River Group, particularly the Elephant Mountain flow, which had formed a broad flat plain in central Washington and northern Oregon about 10 Ma. Deposition of Ringold sediments began in the late Miocene, by about 8 Ma (Lindsey, 1996) with the onset of basin formation and other deformation of the basalts. The ancestral Columbia River, which originally flowed from the present position of Sentinel Gap in the Saddle Mountains in a southwestward direction, was diverted during Ringold deposition to flow southeast through the Pasco Basin to Wallula Gap (Lindsey, 1996; compare maps, Fig. 3 to Fig. 47)

The main exposures of the Ringold Formation are in a series of steep exposures called the White Bluffs. These bluffs follow the east bank of the Columbia River from a point just north of Richland, northward for a distance of about 42 km (25 miles). The bluffs average about 130 m high and occur from about river level at about 150 m to 295 m above sea level. Additional sediments extend downward to the underlying basalt flows (Brown and McConiga, 1960).

Gustafson (1978, 1985b, 2012) divided the section into three informal members, largely following Newcomb (1958), Newcomb et al. (1972), and Brown and McConiga (1960). The divisions (Figs. 3 and 4) were the lower Ringold, a middle series of conglomerate and sand called the Taylor Flat conglomerate, and the upper Ringold.

Lindsey's members of the Ringold Formation—Lindsey (1996) examined the Ringold Formation in both exposures and well records and described the section in much more detail than had previously been done (Fig. 4). Lindsey proposed a fourfold division of the post-basalt sediments in the Pasco Basin;

The oldest sediment (not exposed at the surface in the Pasco Basin) is a basal conglomerate which Lindsey identifies with the Snipes Mountain conglomerate, best known from exposures in the Yakima Valley farther west. It seems to record a stage at which the ancestral Columbia flowed to the southwest, partly bypassing the Pasco Basin.

Above that is a thick sequence of varied clay, silt, sand, and conglomerate, the "member of Wooded Island," subdivided into lettered units. The uppermost of these, his unit E, includes the deposits I termed the Taylor Flat conglomerate (Gustafson, 1977; 1978). Some of the lower sediments of this member are exposed near the southern margins of the basin (Gustafson, 2012), but only the uppermost parts of unit E are exposed in the White Bluffs.

Third stratigraphically is his "member of Taylor Flat." His name is unfortunately similar to my name (Gustafson, 1978) for the underlying conglomerate, and care should be used in referring to each. This "member of Taylor Flat" includes the primarily fluviatile sediments between the conglomerate and the first lake sediments,

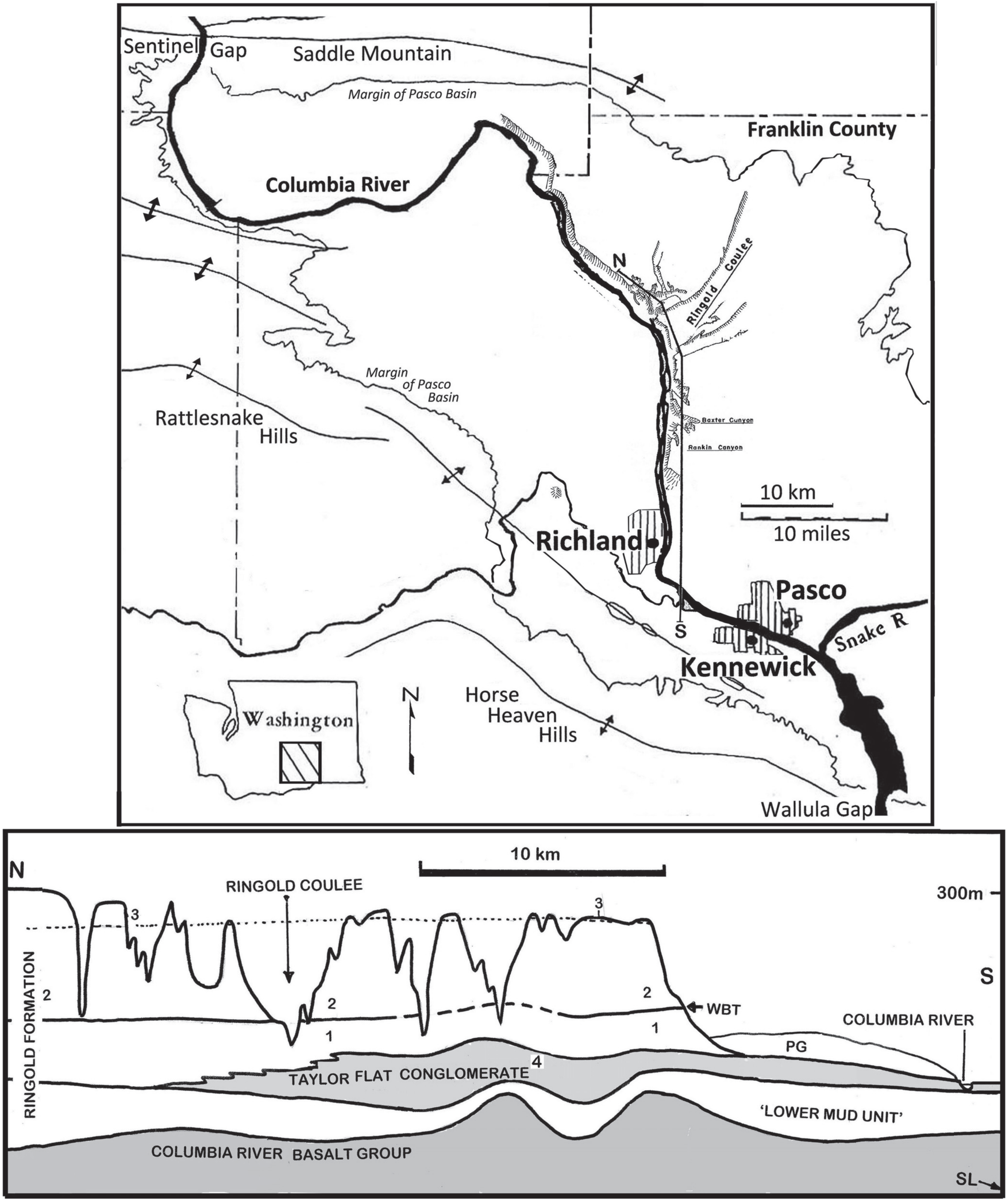

FIGURE 3. Top; map of the Pasco Basin area of central Washington, showing location of cross-section (N-S). Margin of Pasco Basin drawn at about 330 meters (1000 feet) elevation. Bottom; Cross section of the Ringold Formation from the north end of Savage Island, south to the Columbia River. 1) Level of the lower White Bluffs local fauna; 2) level of the upper White Bluffs l.f.; 3) level of the Blufftop l.f.; 4) level of the River Road l.f. SL=sea level, PG=Pleistocene gravel. WBT=White Bluffs tuff. Modified from Brown and McConiga, 1960 and Gustafson, 2012.

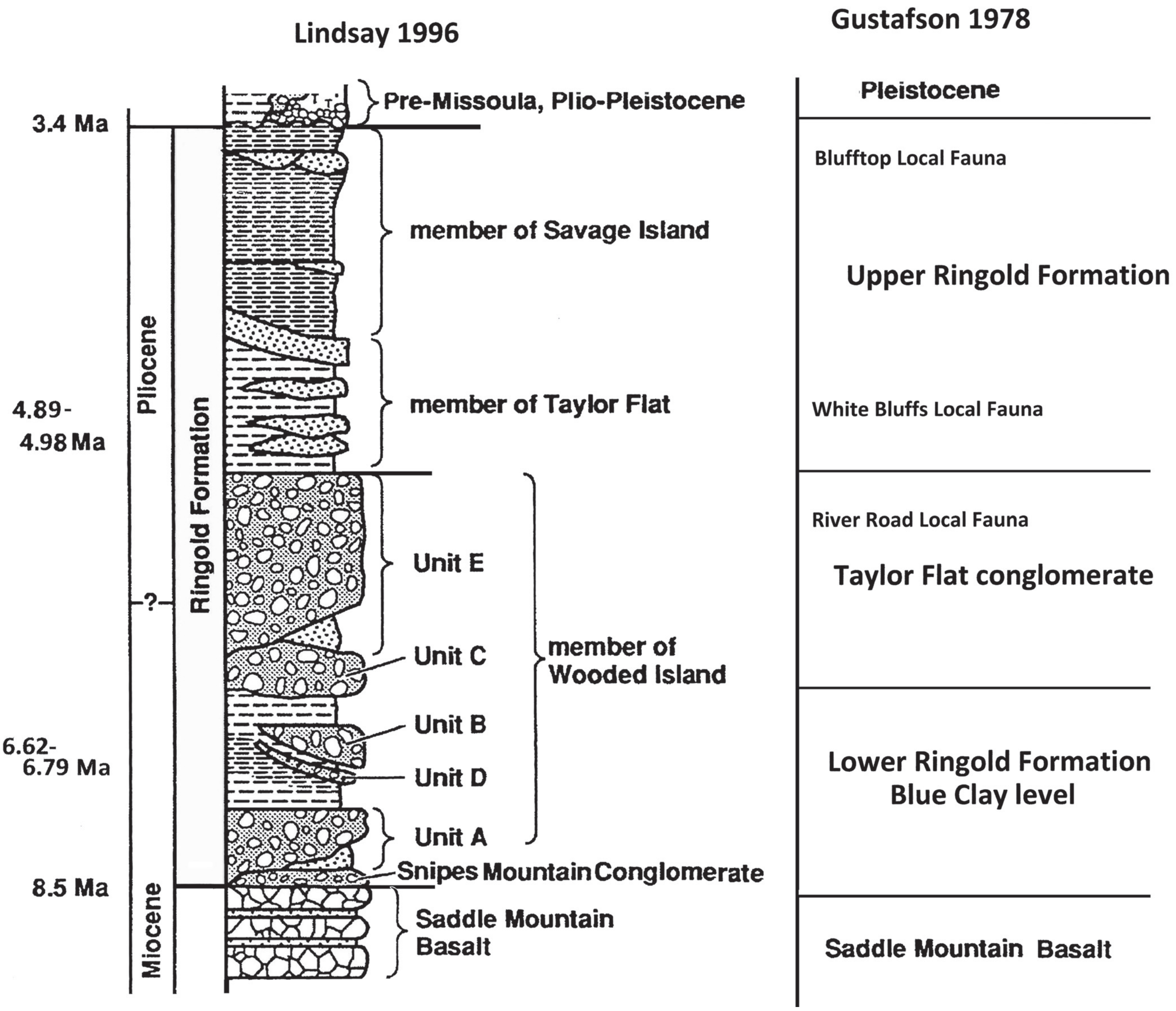

FIGURE 4. Left: Stratigraphic section, modified from Lindsay, 1996, showing superpositional relationships of his members of the Ringold Formation and dated levels. All *Bretzia* specimens described here are from the member of Taylor Flat. Right: Stratigraphic terminology as used by Gustafson, 1978, with levels of Ringold local faunas indicated.

and is the part of the section from which the White Bluffs local fauna is derived. Lindsey (1996, p. 34) describes this member thus; "the member of Taylor Flat records deposition in sandy fluvial channels and on adjacent floodplains and overbank deposits. The change from the underlying gravels of the member of Wooded Island to this member indicates a change from fluvial gravel depositional systems to fluvial systems characterized almost exclusively by sand deposition." Interspersed with the sand are finer overbank and pond sediments and occasional thin gravel deposits. A single notable volcanic ash layer (the White Bluffs tuff) is useful as a stratigraphic marker (Fig. 3). Fossil localities in the member of Taylor Flat are commonly of two types. The most obvious to collectors are thin gravel layers, most of which (but not all) are stratigraphically above the White Bluffs tuff. Such gravels are streambed and point-bar deposits. Streams concentrated bones along with other larger objects, such as wood, clay clasts, and stones as bed load. The cobbles and gravel presumably were carried out of a main river channel during major floods. Bones and teeth in these beds comprise most of the megafaunal remains of the White Bluffs local fauna. Skeletons were usually entirely disarticulated and eroded to varying degrees. The second group of localities comprises silty beds which most commonly preserve fish and small mammals, of which microtine rodents are the most abundant. These probably record marshy areas and oxbow lakes.

The fourth, stratigraphically highest member, is Lindsey's (1996) "member of Savage Island," composed of three consecutive lake sequences, each starting with a diatomite and recording the filling of each lake with mostly silt and sand. The Blufftop local fauna (Gustafson, 1985b) comes from the upper part of the second lake sequence in this series.

Age of the deposits—The age of the "member of Taylor Flat" and thus the White Bluffs local fauna has been estimated using radiometric dates, biostratigraphy, and paleomagnetic dating.

Radiometric dates—There are no radiometric dates from the upper Ringold Formation. Lindsey (1996) reports three radiometric dates (^{40}Ar/^{39}Ar) derived from volcanic ash in well cores in the "lower mud unit" of the Ringold Formation (part of his "member of Wooded Island" between unit A and unit C) elsewhere in the Pasco Basin. The dates are 6.79 +0.13 Ma, 6.67 +0.18 Ma, and 6.62 +0.09 Ma. These dates set a maximum age of less than about 6.6 Ma for both the River Road and White Bluffs local faunas.

Biostratigraphic correlations—A revised list of the White Bluffs local fauna is given here. The most significant previous works describe the overall fauna (Gustafson, 1978), and more recently the fishes (Smith, Morgan, and Gustafson, 2000), the bear (Tedford and Martin, 2001), the horse (Albright, 1999), rhinos (Gustafson, 2012), microtine rodents (Repenning, 1987; 2003), and an unpublished review of the SDSM collections (Ciccimurri, 1999). Each study has noted the fauna's Blancan age and most have noted characteristics which place it early in the Blancan North American Land Mammal Age.

The White Bluffs microtine (*Mimomys sawrockensis*) is known from the upper Alturas Formation in California, where it occurs below a basalt dated at 4.7 + 0.5 Ma and just below a tephra deposit dated by chemical fingerprinting techniques at 4.8 Ma (Repenning, 2003). By Repenning's correlations, the presence of this microtine clearly establishes the White Bluffs l.f. as early Blancan (Blancan I of Repenning, 1987; Bell et al., 2004). Other taxa suggest a Hemphillian influence on the White Bluffs local fauna. Those taxa, found elsewhere in Hemphillian faunas (and sometimes also in early Blancan faunas), include the rabbits *Nekrolagus progressus* and *Hypolagus ringoldensis*, the rhino *Teleoceras hicksi*, the bear *Plionarctos harroldorum*, the canids *Eucyon davisi* and *Borophagus hilli*, the marmot *Paenemarmota sawrockensis*, the camel *Megatylopus* aff. *gigas*, and possibly ?*Pliotaxidea*, a badger. Gustafson (2012) established a stratigraphic overlap (within the member of Taylor Flat) between *Teleoceras hicksi* and *Mimomys sawrockensis.* This overlap suggests a date just after the microtine dispersal event which is used by Bell et al. (2004) to define the beginning of the Blancan North American Land Mammal Age at around 4.9 Ma.

Paleomagnetic dating—The White Bluffs l.f. occurs in mostly magnetically-reversed section, just above a transition from normal to reversed (Packer, 1979; Packer and Johnston, 1979; Gustafson, 1985b). Two such transitions are known in the magnetic time scale in the time period near (and younger than) the Hemphillian-Blancan boundary; one at 4.98 Ma and one at 4.80 Ma. The White Bluffs local fauna is not likely to be younger than the end of Gilbert 3n2r, at 4.62 Ma. This interpretation places the White Bluffs l.f. between 4.62 and 4.98 Ma. Because of the Hemphillian aspects of the fauna the lower reversed zone appears to be the better correlation. If this is correct, this correlation (to Chron C3n.3r) constrains the White Bluffs l.f. to between 4.98 and 4.89 Ma. Tedford et al. (2004), place the time of the latest Hemphillian (Hh4)-Blancan transition in the same approximate time zone (4.6-4.9 Ma). This is also a close match to the current estimate for the latest-Hemphillian Palmetto fauna of Florida, at 5.0 to 4.7 Ma (Webb et al., 2008), and is consistent with the Hemphillian-Blancan boundary date at the Yepomera fauna in Mexico at about 4.8 Ma.

These several lines of evidence are consistent with an age for the White Bluffs local fauna (and therefore the type series of *Bretzia pseudalces* specimens) of very early Blancan, at about 4.98-4.89 Ma, and very close to the Hemphillian-Blancan boundary.

White Bluffs local fauna and associated flora of the Ringold Formation

Flora

Diatoms (not identified) Lindsay, 1996.
Pollen (Leopold and Nickmann, 1981)
Wood (oak, alder) George Beck (1937d, 1938a); unidentified, Gustafson 1978 (A6503).
Leaves (not identified) , 3 localities.

Invertebrates

Fresh-water snails (several species) McKnight, 1923; Taylor, 1966.

Vertebrates

Fishes

Acipenseridae
Acipenser transmontanus (white sturgeon)

Cyprinae
Mylocheilus heterodon (peamouth chub)

Catostomidae
Chasmistes sp. cf. *batrachops* (sucker)

Ictaluridae
Ameiurus reticulatus (bullhead catfish)

Esocidae
Esox columbianus (muskellunge or muskie)

Centrarchidae
Archoplites molarus (sunfish)

Amphibians

Unidentified amphibians

Reptiles

Chelonia
Clemmys marmorata (pond turtle)
Chrysemys? sp. (pond turtle)
Testudo or *Geochelone* sp. (large tortoise)
Unidentified snake and/or lizard

Mammals

Insectivora

Scapanus sp. (mole)

Lagomorpha

Hypolagus ringoldensis (rabbit)
Nekrolagus progressus (rabbit)

Pilosa

Megalonyx leptostomus (ground sloth)

Rodentia

Paenemarmota sawrockensis (marmot)
Spermophilus sp. cf. *S. johnsoni* (ground squirrel)
Spermophilus? *russelli* (large ground squirrel)
Ammospermophilus hanfordi (antelope ground squirrel)
Thomomys sp. cf. *T. gidleyi* (pocket gopher)
Castor californicus (beaver)
Dipoides rexroadensis (extinct beaver)
Peromyscus nosher (deer mouse)
Neotoma sp. cf. *N. quadriplicatus* (wood rat)
Mimomys sawrockensis (vole)

Carnivora

Eucyon davisi (dog or coyote)
Borophagus hilli (hyaena-like dog)
Chasmaporthetes ossifragus (hyaena)
Pliotaxidea sp. (badger)
Trigonictis macrodon (extinct mustelid)
Bassariscus sp. cf. *B. astutus* (ringtail)
Felis sp. (large cat)
cf. *Homotherium* (saber-tooth cat)
Plionarctos harroldorum (bear)

Proboscidea

Mastodon americanum (mastodon)

Perrisodactyla

Tapirus sp.
Teleoceras hicksi (short-legged rhino)
"Plesippus" francescana (zebra-like horse)

Artiodactyla

Platygonus pearcei (peccary)
Megatylopus sp. aff. *M. gigas* (large camel)
Hemiauchenia blancoensis (llama-like camel)
Bretzia pseudalces (extinct deer)
Antilocaprid (pronghorn-like antelope)

HISTORY OF INVESTIGATIONS

BRETZIA FROM THE RINGOLD FORMATION

Although *Bretzia* was not described until 1974, the first listing of the White Bluffs local fauna, by Merriam and Buwalda (1917), reported cervid partial antlers, from locality 3031, three to four miles below Hanford near Savage Island. They identified the specimens only as "Cervid" and stated: "Deer are represented by fragments of antlers, some of which show the burr well-preserved. The deer of the Pleistocene and later Tertiary are not as yet well enough known to furnish a good basis for comparison of the fragments represented in the White Bluffs collection" (Merriam and Buwalda 1917, p. 258).

Strand and Hough (1952) reported a cervid metapodial from the far south end of the White Bluffs, at the top of the Taylor Flat conglomerate. Although identified as *Rangifer* (caribou) in their paper, it is probably *Bretzia*.

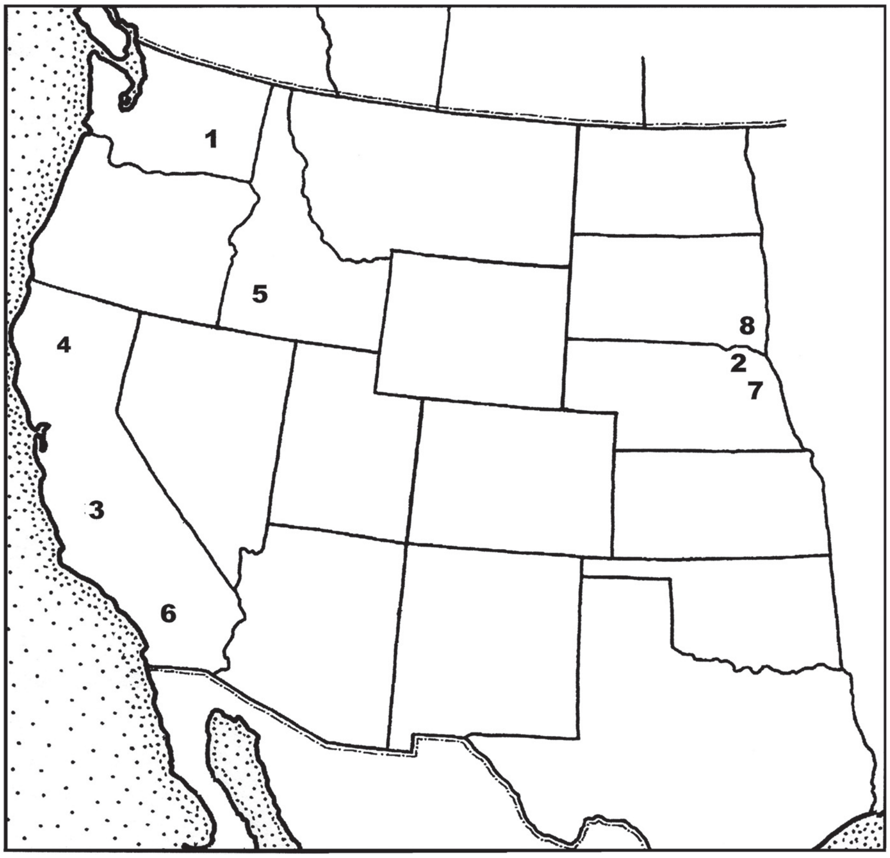

FIGURE 5. Map of western United States showing reported occurrences of *Bretzia*;
1. Ringold Formation, Washington
2. Santee fauna, Nebraska
3. Upper Etchegoin Fm., California
4. Tehama Fm., California
5. Birch Creek, Idaho
6. Aguanga, California
7. Stanton County, Nebraska
8. Lincoln County, South Dakota

From about 1955 through the early 1970s, collectors intensively worked the Ringold localities. These included institutional collectors (i.e., V.S. Mallory from the Burke Museum and G. Jakway from LACM) and many amateurs, most prominently Willis Fry, Wayne Harrold, and William Shawver. During this period, most of the specimens used here were found. An article published in Gems and Minerals magazine in 1967 described and illustrated one of Shawver's antler specimens, noting a resemblance to fallow deer because of the palmation. Fry subsequently donated a series of antlers to the Burke Museum which formed most of the basis for the taxonomic description of *Bretzia*. The other amateur collections have now been deposited into institutional collections.

Fry and Gustafson (1974) named *Bretzia pseudalces* from antlers and a male skull fragment with pedicles. The available specimens were sufficient to establish the basic characters and age-variation of antlers within the species. Although the closest relatives were in doubt, some relationship to Eurasian *Cervavitus* was postulated.

Gustafson (1978), in a description of the White Bluffs local fauna, published the first reconstruction of the head of *Bretzi*a, placed it in faunal and geological context, noted that it seemed to be among the most abundant of the large mammals in the fauna (rivaled only by the peccary *Platygonus* and two types of camels), and established an early Blancan date for the fauna.

Comparing antlers of *Bretzia* and *Odocoileus*, Gustafson (1985a) listed the distinctive antler characters of *Bretzia*, described variation in these antlers, and proposed a phylogenetic hypothesis to account for the evolution of the forms of the antlers of the New World deer. The study particularly suggested that the primitive antler form was a three-tined antler similar to *Ozotoceros*. Characters were noted which are distinctive for *Odocoileus* and allow generic identification from fragments of antlers. *Bretzia* was recognized from Blancan faunas in California (Etchegoin and Tehama Formations) and *Odocoileus* was recognized from the Blancan of Idaho, all from antler fragments. A general similarity between the dental and postcranial anatomy of *Bretzia* and *Odocoileus* was asserted, without further description.

Ciccimurri (1999), in an unpublished thesis, cataloged and described the Wayne Harrold collection from the White Bluffs, which is now at SDSM. This was the first description of teeth and postcranial elements assigned to *Bretzia pseudalces*. Notably, she described characters of the M^3 and tarsal bones which suggested some relationship to the Alcini. These will be discussed below.

BRETZIA FROM OTHER LOCALITIES

Fossils referable to the genus *Bretzia* are now reported from across the western United States and from deposits ranging in age from 5 Ma (near the Hemphillian-Blancan boundary) to late Rancholabrean or late Pleistocene, perhaps less than a few tens of thousands of years old (Fig. 5). The list includes the following;

Santee Ash, NE Nebraska, Late Hemphillian—Voorhies and Perkins (1998) report a partial mature antler fragment probably referable to *Bretzia in situ* 2 meters below the Santee Ash (dated at 5.0±0.2 Ma). The antler fragment was found in association with a diverse late Hemphillian mammalian fauna and is the oldest radiometrically dated North American cervid.

Upper Etchegoin fauna, California, Early Blancan—Merriam (1915, Figs. 46-48b) described and illustrated fragments of antlers from four localities in the "upper Etchegoin area," near Coalinga, California. Gustafson (1985a, Fig. 4) reported four more specimens, assigning these to *Bretzia* without a specific designation. In a report on the paleomagnetic stratigraphy of these deposits, Prothero (2010) states: "the upper Etchegoin Formation is reversed in polarity and appears to correlate with Chron C2Ar (3.6-4.2 Ma)."

Tehama Formation, Tehama County, California, Early Blancan—Gustafson (1985a) identified three antler specimens from Tehama County, California as *Bretzia.* The specimens are from the Tehama Formation and are early Blancan in age.

Birch Creek, Glenns Ferry Formation, Idaho, Late Blancan—Morejohn, Hearst and Dailey (2005), describe specimens including an antler and carpals from the late Blancan (Blancan V) Glenns Ferry Formation, Birch Creek locality, Idaho, as *Bretzia*. This is the only published previous report which describes postcranial elements of the *Bretzia* skeleton. The locality is believed to date to 2.4 Ma.

Riverside County, California, early Irvingtonian?—Frick (1937, p. 200, Fig. 20B) recorded a partial antler (AMNH F:AM 31776) "from the vicinity of Aguanga," Riverside County, California as *Cervus aguangae.*" The antler has several characters which resemble *Bretzia* specimens from the White Bluffs l.f., particularly a juvenile antler (UWBM 41930). It does not show the characteristic palmation of the adult specimens of *Bretzia.* It also resembles some specimens of *Eocoileus* and the South American genera *Morenoelaphus* and *Paraceros.* Without a series of examples, this specimen cannot be interpreted as being a juvenile antler or an adult form. The species should be considered a *nomen dubium*. The fauna from this locality appears to be early Irvingtonian.

Stanton County, Nebraska, and Lincoln County, South Dakota, Late Pleistocene-Holocene—Gunnell and Foral (1994) described a new species*, Bretzia nebrascensis* from two complete antlers (UMMP 42220, the holotype, and UMMP 42221 from Stanton County, Nebraska and Lincoln County, South Dakota). This latest Pleistocene or early Holocene species shows consistent differences from *B. pseudalces*, particularly in that the anterior tine branches off at the burr instead of some distance above it. These specimens expand the range for *Bretzia* both temporally and geographically.

RECENT WORK ON OTHER LATE CENOZOIC NORTH AMERICAN CERVIDS

Webb (2000) described *Eocoileus gentryorum* from the latest Hemphillian Palmetto Fauna of Florida, from antlers, cranium, and dentition. In size and form of antlers this deer resembles the pampas deer of South America, *Ozotoceros bezoarticus.* The Palmetto Fauna comes from mines in the upper Bone Valley Formation, and most specimens are found in mine tailings or on working faces (Webb et al., 2008). The fauna is considered latest Hemphillian (Hh4), about 5.0 to 4.7 Ma, largely on the basis of the occurrence of several Blancan taxa in an otherwise Hemphillian assemblage and on data on sea level changes in the latest Miocene.

Antler fragments of a deer with characteristics of *Odocoileus* have been found in the same mines as the Palmetto fauna. *Odocoileus* was not included in the most recent list of Palmetto Fauna taxa (Webb et al, 2008) because of the suspicion of contamination from later deposits. I examined a group of specimens quarried from the upper Bone Valley sediments *in situ*, now in the Florida Museum of Natural History. This collection includes several partial antlers with the diagnostic characteristics of *Odocoileus*. These are now the earliest known specimens of the genus.

Fragmentary unidentified deer occur in other faunas, for example the late Hemphillian Walnut Canyon local fauna of New Mexico (Morgan et al., 1997), suggesting that, while rare as fossils, cervids were widespread in the late Hemphillian.

Wheatley and Ruez (2006) added a cervid tooth to the previously known antler of *Odocoileus* from Pliocene deposits at Hagerman, Idaho (Gustafson, 1985a). The Glenns Ferry Formation deposits are dated to between 4.0 and 3.5 Ma. This study also discussed *O. brachyodontus* Hibbard (1941), from the early Blancan of Kansas. The latter remains the only described species of *Odocoileus* currently recognized from the early Pliocene of North America (Webb, 1998), although still from very fragmentary material.

Morejohn and Dailey (2004) described a skeleton (lacking most of the skull) of the Irvingtonian deer *Odocoileus lucasi* from California. Their study is significant partly for a clarification of the status of this species, but also because of the extensive examination of the postcranial osteology of cervids included in this study.

The record may be summarized thus; modern cervids seem to appear in North America just before the Hemphillian-Blancan boundary, near the end of the Miocene. They differentiated rapidly, so that the first fossil forms to appear, all at about the same time, are of three distinct genera, none of which is known from Asia. The morphology of *Eocoileus,* close to *Ozotoceros*, suggests that it may be near the ancestry of the "Gray clade" (including *Ozotoceros, Blastocerus, Hippocamelus*, and some species of *Mazama*) of Duarte et al. (2008) which formed the source for subsequent differentiation in South America. The as-yet-unstudied early *Odocoileus* specimens would apparently be part of that study's "Red clade" and represent the ancestry of both *Odocoileus* and some species of *Mazama*. Together they represent the potential ancestry of the living New World capreoline deer. The third genus, *Bretzia*, also a capreoline, has yet to be placed with its closest relatives.

The other living deer in North America, the elk or wapiti (*Cervus canadensis*), the caribou (*Rangifer tarandus*), and the moose (*Alces americana*, and its Pleistocene relative *Cervalces*) dispersed into North America during the Pleistocene, apparently less than 1.8 Ma (Kurten and Anderson, 1980; Tedford et al., 2004).

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Family Cervidae Goldfuss, 1820
Subfamily Capreolinae Brookes, 1828
Tribe incertae sedis
Genus Bretzia Fry and Gustafson 1974

Type species—Bretzia pseudalces Fry and Gustafson, 1974

Included species—Type species and *Bretzia nebrascensis* Gunnell and Foral, 1994

Distribution—Early Pliocene (ca 5 Ma) to late Pleistocene (Rancholabrean); western North America (Washington, Idaho, California, South Dakota and Nebraska).

Diagnosis—Medium-sized cervid, antlers with long anterior tine held in mostly vertical position, beam long, and cervicorn in adolescent stage, short in adults, spreading into a vertical palm with multiple tines on distal edge, skull with large pedicles at 90-degree angle or more to each other, pedicles extend laterally to or beyond orbits, P^3-P^4 with lingual cingulum, M^3 with enlarged basal metastyle, metacarpals without facets for articulation of lateral proximal metacarpals.

Bretzia pseudalces Fry and Gustafson 1974

Holotype—UWBM 42971, nearly complete left antler from locality UW A9577, Ringold Formation, White Bluffs local fauna.

Paratypes—UWBM numbers 41930, 42972-42975, 45016, 45031, 45032, all partial antlers, and UWBM 37733, skull fragment.

Referred specimens: *Dentary/lower dentition:* LACM 10958, LACM 11816, LACM 118599, LACM 118600, LACM 120093, LACM 120094 , LACM 120096, LACM 120155, LACM 120159, LACM 154776-154779, LACM 154781. SDSM 22214-22230. UWBM 41520, UWBM 42986, UWBM 46200, UWBM 46211, UWBM 47418, UWBM 49483, UWBM 50398, UWBM 50402, UWBM 51617, UWBM 53062, UWBM 92880-92892, UWBM 95525, UWBM 95596, UWBM 95597, UWBM 95599, UWBM 95603, UWBM 95604. WHC-0005. CRCM 58-132, CRCM 58-149, CRCM 58-151.

Upper dentition: LACM 118598, LACM 120169, LACM 154775, LACM 154780. SDSM 22194, SDSM 22196-22201. UWBM 41938, UWBM 42222, UWBM 42987, UWBM 46832, UWBM 47397, UWBM 51475, UWBM 52677, UWBM 92883, UWBM 92892A, UWBM 92894, UWBM 95598, UWBM 95600-95603.

Skull: LACM 10921-10923, LACM 120099, LACM 120161. SDSM 22203, SDSM 22204. UOMNH F-32203. UWBM 37733, UWBM 41478, UWBM 45016, UWBM 53074, UWBM 95606. WHC-0001.

Antlers: LACM 10910, LACM 10933, LACM 10934, LACM 10945, LACM 10947, LACM 10968, LACM 11369, LACM 11375, LACM 11377, LACM 11378, LACM 11379, LACM 11380, LACM 11381, LACM 11392, LACM 11545, LACM 11548, LACM 11549, LACM 120098, LACM 120100, LACM 120154, LACM 120157, LACM 120161, LACM 120163, LACM 120165-120168, LACM 154791-154803. SDSM 22205, SDSM 22207, SDSM 22208, SDSM 22210-SDSM 22213, SDSM 22420, SDSM 42894. UWBM 35245, UWBM 41930, UWBM 42009, UWBM 42555, UWBM 42971-42975, UWBM 45031, UWBM 45032, UWBM 49478, UWBM 51755, UWBM C0076, UWBM 92877, UWBM 95605, UWBM 95606-95611, UWBM 95616, UWBM 95617. WHC-0009—0015.

Vertebrae: LACM 154783, SDSM 22231, UWBM 95614.

Scapula: UWBM 51761.

Humerus: UWBM 95620.

Ulna: UWBM 42143.

Radius: LACM 154784, SDSM 22237, UWBM 95613.

Metacarpals: LACM 154790, UWBM 46204, UWBM 95623.

Pelvis: UWBM 49519.

Femur: LACM 154785, LACM 154786, SDSM 22239.

Tibia: LACM 10928, LACM 154787-154789. SDSM 22240, SDSM 22309. UWBM 35226, UWBM 92878, UWBM 95621, UWBM 95622. WHC-0003.

Astragalus: SDSM 22241-22243. UWBM 41998, UWBM 53066.

Calcaneum: SDSM 22244, UWBM 49480, UWBM 95612, WHC-0002.

Cubonavicular: SDSM 22245.

Metatarsals: LACM 10959, LACM 120151, LACM 143477. SDSM 22246, SDSM 22250. UWBM 40463, UWBM 95615, UWBM 95618, UWBM 95619, UWBM 95623. WHC-0004.

Age and distribution—Early Blancan (ca. 5.0-4.8 Ma), Washington State.

Emended diagnosis—Distinguished from *B. nebrascensis* by consistent and frequently large gap between burr and anterior tine.

DESCRIPTION

Dentary—The dentary is generally typical of advanced cervids of medium size (Fig. 6, 7, 8). The coronoid process is tall and posteriorly recurved, but none of the fossils preserve this process complete. In smaller cervids (*Pudu, Mazama, Capreolus*) the ascending ramus tends to be more vertical; in larger cervids (*Alces, Cervus*, and especially *Rangifer*), it tends to lean backwards at a considerable angle; in *Bretzia* it is intermediate, though a few degrees further off vertical than in *Odocoileus.* The articular process is small, placed well above the tooth row, with the articular surface slightly convex. The angular process is large, moderately concave, and has a rounded border. The posterior margin of the dentary is less indented (that is, straighter and more vertical) between the articular process and the angular process than is usually the case in *Odocoileus*. In the latter the angular process often projects much further to the rear. This posterior margin in *Bretzia* resembles *Cervus canadensis*, *Dama* or *Alces* more than *Odocoileus*. The depressed area for attachment of the masseter muscle is larger than in *O. hemionus*.

The horizontal ramus is curved, with a convex ventral border. The cheek tooth row is also slightly curved, concave dorsally. There is a long diastema between the incisiform canine and the P_2; P_1 is absent. The length of the diastema can be estimated in three specimens, though not accurately measured. In the best-preserved specimen (UWBM 46211) the diastema is about 60 mm, whereas in the sample of *O. hemionus* it ranges from 62 to 70 mm. Although the distance from the anterior premolar to the large mental foramen is about the same in the three *Bretzia* specimens as in my sample of *O. hemionus*, the portion of the diastema anterior to that foramen appears to be relatively shorter in *Bretzia*, and the dentary at the diastema in *Bretzia* is somewhat thicker and deeper. Compared to *Dama*, the diastema in *Bretzia* is considerably longer, both relatively and absolutely.

One nearly complete dentary (WHC-0005, Fig. 7) is known. A second (Fig. 6) has been reconstructed using three other specimens (UWBM 41520, UWBM 46211, LACM 120095).

Lower Dentition, general—As with cervids in general the adult lower dentition of *Bretzia* is composed of three

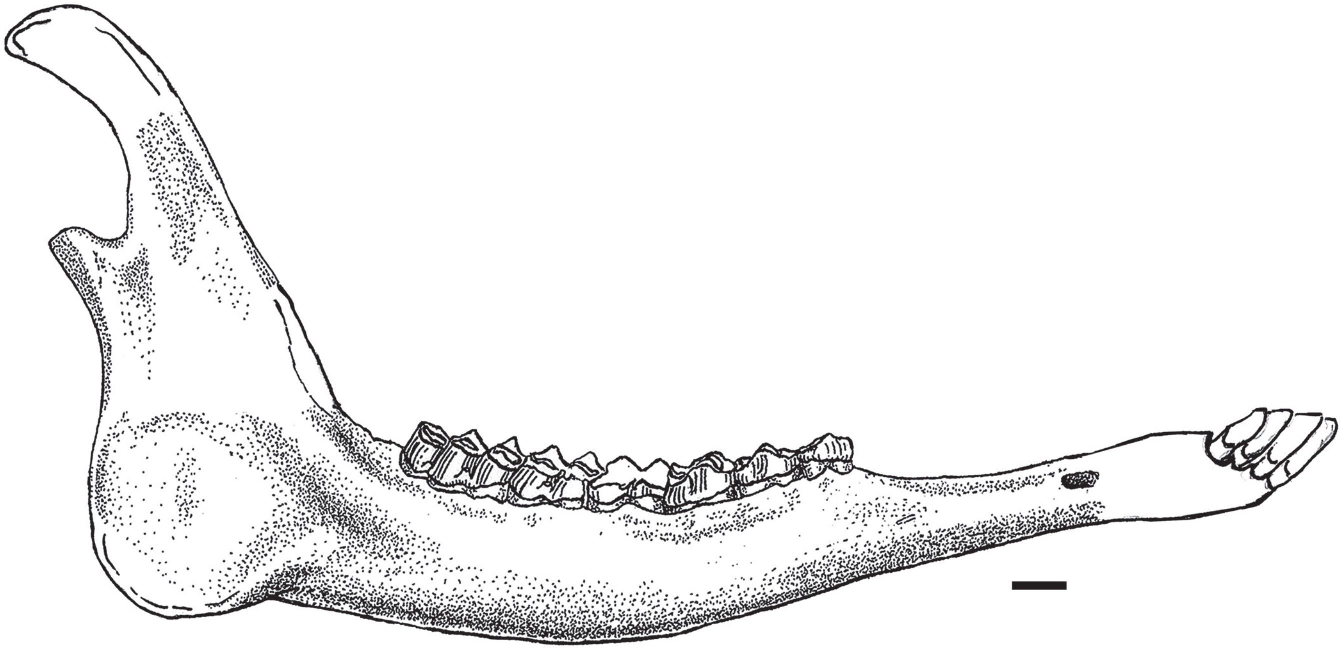

FIGURE 6. *Bretzia pseudalces*, lower jaw reconstruction from UWBM 41520, UWBM 46211, and LACM 120095. Top of coronoid process and anterior dentition reconstructed. Scale bar equals 1 cm.

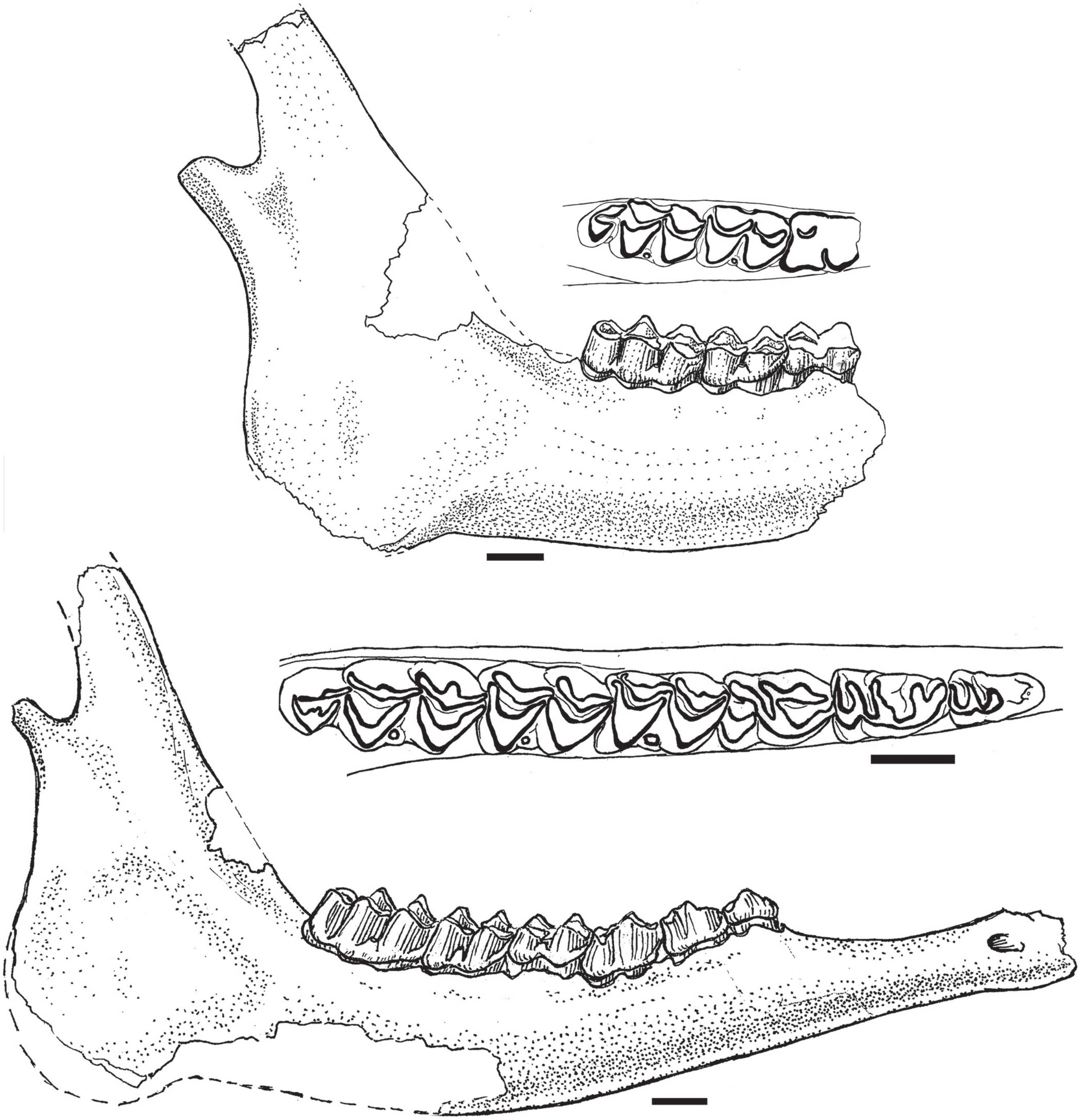

FIGURE 7. *Bretzia pseudalces*, dentary with occlusal views of dentition. Top, LACM 120095, partial R dentary with M_1-M , lateral view of dentary and occlusal view of teeth. Bottom, WHC 0005 (UWBM 92895), R dentary with P_2-M_3, lateral view of dentary with (enlarged) occlusal view of teeth. Scale bars equal 1 cm.

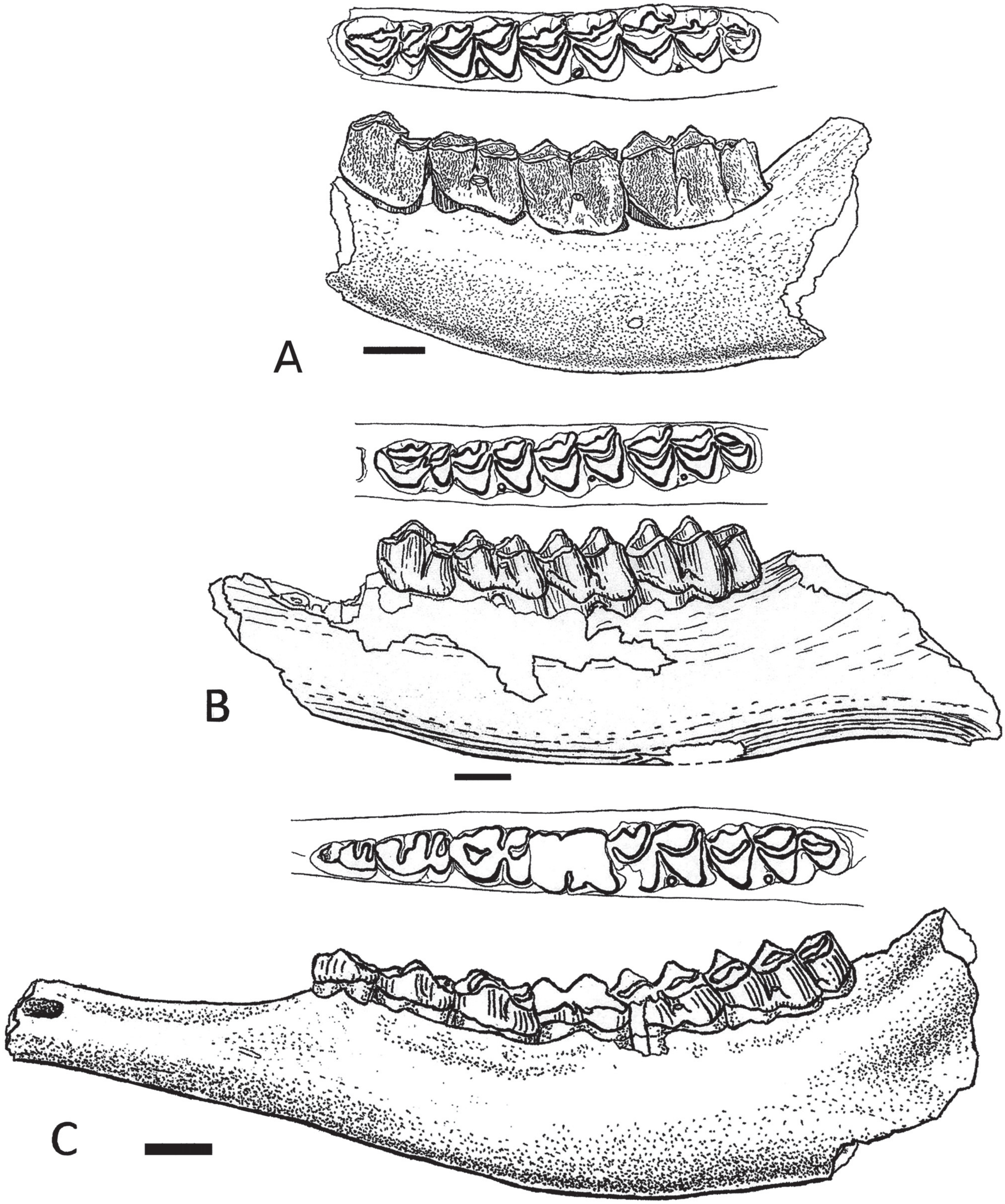

FIGURE 8. *Bretzia pseudalces*, A, UWBM 92882, partial L dentary with P_4-M_3, teeth only slightly worn; B, UWBM 95604, partial L dentary with P_4-M_3, teeth at young-adult wear stage; C. UWBM 41520, partial L dentary with P_2-M_3, teeth at mature adult wear stage. Scale bars equal 1 cm.

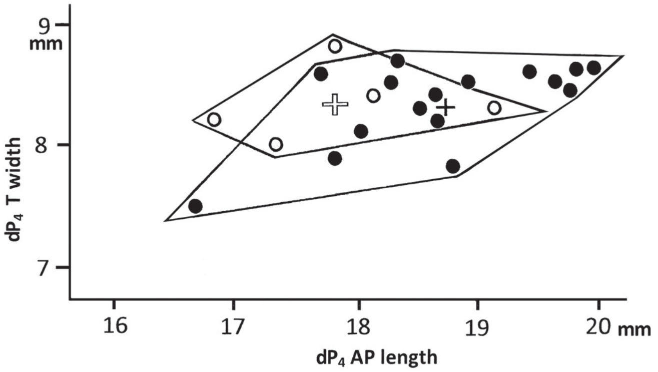

FIGURE 9. Scatter diagram, transverse width versus anteroposterior length of dP_4 of *Bretzia* (open circles and cross) and *Odocoileus hemionus* (solid circles and cross). Crosses indicate intersection of means of both measurements.

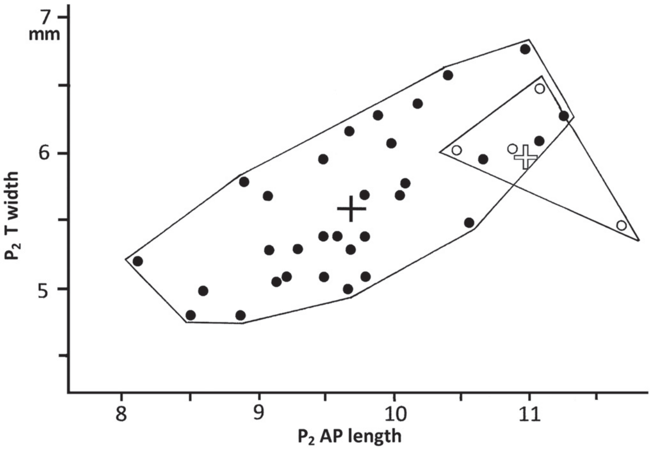

FIGURE 10. Scatter diagram, transverse width versus anteroposterior length, P_2. Open circles and open cross are *Bretzia pseudalces*; solid circles and solid cross are *Odocoileus hemionus*. Crosses indicate intersection of means of both measurements.

procumbent incisors, an incisiform lower canine, three premolars (P_1 and P_1 are absent) and three molars. The presence or absence of an upper canine is unknown.

A single incisor is referred to *Bretzia* (SDSM 22214), probably L I_1. The tooth is unworn, spatulate, with a slightly raised lateral and medial border and a longitudinal ridge about two-thirds of the distance from the medial side to the lateral side. The anterolateral corner is chipped off. In size and form it resembles the I_1 of *Odocoileus hemionus;* crown length = 11.5 mm, crown width =7.8 mm.

One L incisiform canine is available. It is only slightly worn. The crown is long and narrow, curved laterally, with a median dorsal ridge, and raised lateral edges. The crown length = 10.2 mm, width = 2.9 mm. The relative proportions of the median incisor and the canine are more like those of *Odocoileus virginianus* or *Mazama americana*, in which the canine is relatively narrow (reduced), and not like *O. hemionus* in which the canine is relatively large.

The degree of hypsodonty in *Bretzia* is similar to that of *Odocoileus*; premolars are essentially brachyodont (though see descriptions below), the first molar is shorter-crowned than $M_{2\text{-}3}$, and the 2^{nd} and 3^{rd} lower molars are modestly hypsodont.

The outer surface of the enamel is often strongly crenulated (Fig. 8A, Fig 11), though this surface texture tends to wear smooth as the tooth wears down.

Groves and Grubb (1987) describe a general tendency for premolars of many cervids to become more molariform. They generally mean by "molariform," that the premolars become more selenodont, or with crescentic cusps similar to cervid molars. A prior molarization stage also occurs in the premolars of most cervids by the formation of an anterior triangle and posterior basin; the trigonid-talonid or tritubercular form which is characteristic of many primitive mammalian molars, though not of their premolars (Osborn, 1907). This form is visible in P_2, it becomes the predominant form in P_3, and it is variably transformed towards selenodonty in P_4. Molarization is greatly advanced in *Rangifer* and at an extreme in *Alces*, in which P_4 is very similar to the molars. Also in *Alces*, P_3 has many characteristics of P_4 in other cervids, and P_2 resembles P_3 of other cervids. *Bretzia* premolars are generally similar to *Odocoileus* in the degree of molarization. A summary of measurements is given in Table 2.

Deciduous lower dentition—Five examples of the deciduous p_4 are available (Plate 1; Table 1). The other deciduous lower premolars have not been recognized. Deciduous premolars for both extant and extinct cervids or for that matter, artiodactyls in general have seldom been described in detail. For terminology specific to deciduous premolars I use Loring and Wood (1969). The dP_4 of *Bretzia*, as with other selenodont artiodactyls, resembles a lower first or second molar except that, instead of having two pairs of crescentic cusps, it has three. The anterior cusps are termed the lingual and buccal anteroconids. For the rest of the tooth the terminology is as for the molars. The crowns of these deciduous teeth are much shorter than those of the molars. There are three roots; the anterior and posterior roots are the larger, and a smaller central root supports the protoconid. Two ectostylids are present, the posterior one being slightly the larger. The anteroconids together form a U-shaped structure (connected at the anterior margin) which is separated from the rest of the tooth in early wear but becomes connected (that is, the exposed dentine becomes connected) later (Plate 1E). Also with wear the protoconid becomes connected diagonally with the entoconid (Plate 1C) and in the last stages before the tooth is shed,

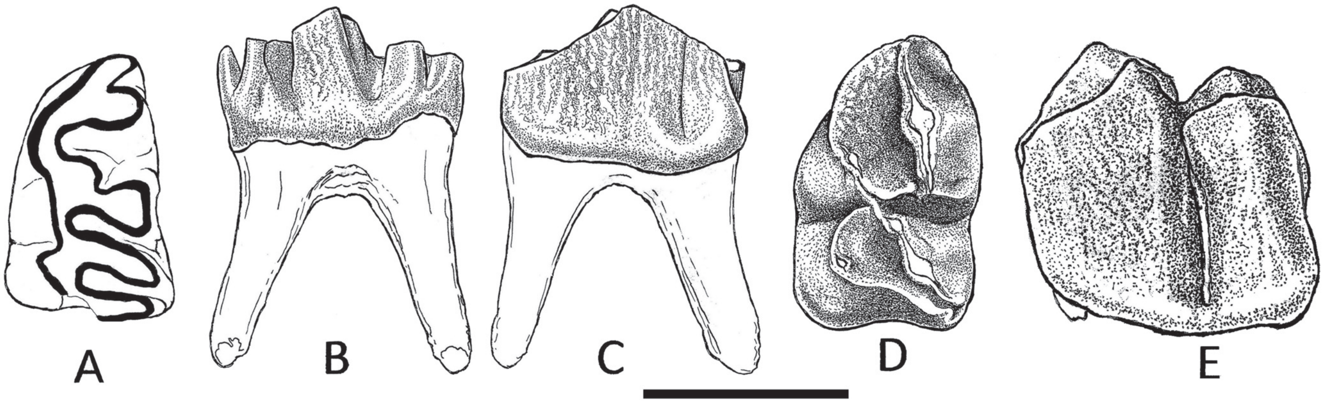

FIGURE 11. *Bretzia pseudalces*, A-C, UWBM 95599, LP_3, A, occlusal, B, lingual, and C, labial views. D-E, UWBM 50402, LP_4, unworn tooth. D, occlusal view, E, labial view. Scale bar equals 1 cm.

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the metaconid and hypoconid connect with the other cusps (Plate 1A).

Comparing *Bretzia* with my sample of *O. hemionus* (Fig. 9; N = 16), the mean transverse width is almost the same as in the *Odocoileus* sample but the mean length is somewhat smaller. The anterior surface of the anteroconids in *Bretzia* tends to be rounded; in the *Odocoileus* sample the anterior side of the lingual anteroconid is usually strongly concave until a very late wear stage is reached. The fossettids, especially the anterior and medial fossettids, tend to disappear with wear more quickly in *Odocoileus*. The pattern of cusp connections with wear is similar in both.

P_2 description—Four examples are available (Figs. 7, 8C, Plate 2F, K, M, and P). In occlusal view the P_2 is a rounded triangle. Interdental wear (by contact with upper premolar) is restricted to the posterior part of the tooth, behind the protoconid. The anterior part of the tooth is composed of an anteroposterior ridge (preprotocristid) which curls anteromedially to a small round or comma-shaped paraconid. There is a distinct notch isolating the paraconid. The protoconid is the tallest part of the tooth and is triangular, with a flattened and worn posterior facet; the posterolingual corner may be slightly extended as a minor ridge. The posterior third of the tooth is composed of two transverse crests (entocristid and entostylid) connected on the labial side by the hypoconulid, forming a U-shaped structure (posterior valley) open on the lingual side. Exposed dentine on the posterior face of the protoconid connects to anterolabial corner of the entocristid. There is no cingulid.

Compared to *O. hemionus*, the P_2 of *Bretzia* tends to fall within or just above the upper range in size of *Odocoileus*, particularly in AP length (Fig. 10). In *O. hemionus* the paraconid tends to be less distinct, the entostylid tends to wear away more quickly, and the ridge on the posterolingual corner of the protoconid is frequently more robust, even forming a distinct cusp (metaconid) on 6 out of 34 examples.

Variation in most features of P_2 in modern *Odocoileus hemionus* is substantial. This tooth ranges from a relatively narrow, simple bladelike tooth with very subdued accessory crests to a relatively complex tooth with a three-cusped trigonid and strong posterior crests. The *Bretzia* sample is too small to provide a good representation of the probable range of variation in cusp structure.

P_3 description—Nine examples are available (Figs. 7, 8C, 11, Plate 2). The P_3 also resembles a primitive mammalian lower molar in having a more-or-less triangular anterior section (trigonid) and a smaller posterior section (talonid). As with P_4 and molars, the enamel ridges and cusps quickly wear off to expose the hard edges of the enamel layer and the softer dentine, as in the typical grinding occlusal surface of brachyodont and hypsodont mammals. The anterior wing of the protoconid splits into a y-shaped structure composed of paraconid and (slightly smaller) parastylid; a paraflexid separates them but gradually reduces with wear. The tall protoconid connects via a ridge to the equally tall metaconid. A deep, open trigonid valley separates the metaconid from the paraconid. A second ridge, on the posterolabial side of the protoconid, extends posteriorly to the hypoconid. In primitive ruminant molars a fold on the posterior side of the protoconid (and associated ridge) in this position is called a *Paleomeryx* fold. The lower posterior (talonid) portion of the tooth is composed of a hypoconid which connects the labial ends of the entoconid and entostylid ridges. The metaconid is separated from the entoconid ridge by a central valley, open lingually; likewise the entoconid and entoconulid ridges are separated by a posterior valley open lingually. The surface of P_3 in less-worn stages is covered with numerous vertical crenulations, as are seen in most little-worn cheek teeth (Fig. 11).

Compared to the sample of *O. hemionus* (Fig. 12),

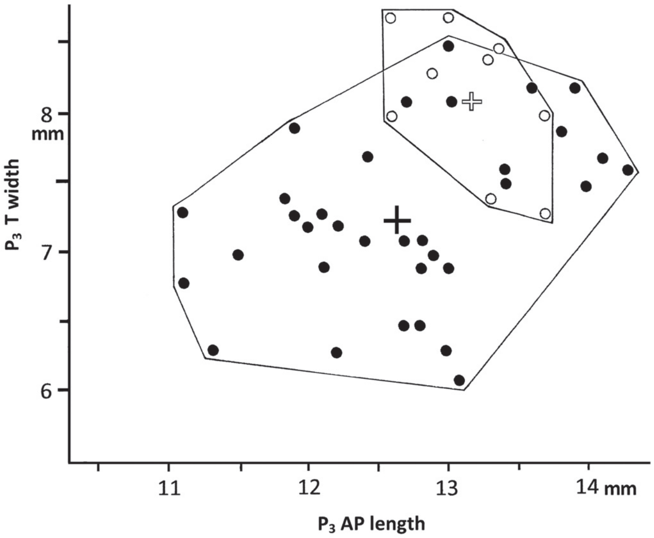

FIGURE 12. Scatter diagram, Transverse width versus anteroposterior length, P_3. Open circles and open cross are *Bretzia pseudalces*; solid circles and solid cross are *Odocoileus hemionus*. Crosses indicate intersection of means of both measurements.

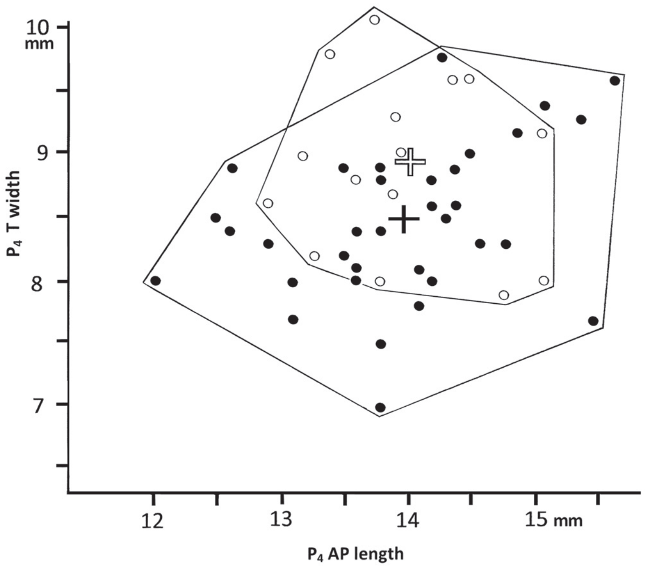

FIGURE 13. Scatter diagram, Transverse width versus anteroposterior length, P_4. Open circles and open cross are *Bretzia pseudalces*; solid circles and solid cross are *Odocoileus hemionus*. Crosses indicate intersection of means of both measurements

the available examples of *Bretzia* P_3 fall within or just outside the upper range of modern *Odocoileus*, with means of both measurements being substantially higher in *Bretzia*. The *Odocoileus hemionus* sample differs from *Bretzia* in the following features; in *Odocoileus* the entoconid is usually not connected to the hypoconid and forms a short ridge at about a 45 degree angle to the AP axis of the tooth; the paraflexid is frequently shallower; with wear the metaconid and entoconid tend to connect; the distinction between protoconid and metaconid tends to be lost; the posterior valley tends to be closed by a lingual connection between entoconid and entoconulid.

P_4 description—Fifteen examples are available. The P_4 is considerably higher-crowned (more hypsodont) than P_3. Protoconid and hypoconid are strongly crescentic; protoconid and metaconid are the tallest cusps; metaconid is straight and anteroposteriorly oriented; entoconid is straight, and is angled at about a 40 degree angle from the midline of the tooth. Protoconid connects to entoconid via the equivalent of a *Paleomeryx* fold at some stage of some teeth (i.e., Fig. 11, Plate 2A, F, H). The *Paleomeryx* fold is present frequently even when the protoconid-entoconid connection does not occur (Plate 2C, D, E, G). Groves and Grubb (1987) state that the protoconid-entoconid connection is commonly seen in *Odocoileus* (they call it "very characteristic"). My sample of *O. hemionus* from Oregon shows this to be a minority feature, at least in this population. The hypoconid stays isolated from the other cusps until late in wear in the *Bretzia* sample (Plate 2, L-P). An anterior cingulid is usually present but small.

The presence of the *Paleomeryx* fold here (in P_4) is interesting, because this feature is characteristic of molars of many primitive (Oligocene and Miocene) pecorans, including Miocene deer, but it disappears from molars in later deer (Groves and Grubb, 1987). In these deer premolars it can be traced from a ridge connecting the posterior side of the protoconid to the trigonid in P_2 and P_3, and forming a major part of the long labial anteroposterior grinding surface in P_3. As the cusps become more selenodont in P_4 this connection becomes obsolete and the fold is lost in the completely selenodont molars. The pattern of molarization here in the fourth premolar is repeating an earlier feature of the molars, which has been otherwise lost.

Compared to my sample of *O. hemionus* this sample of *Bretzia* P_4s is well within the size range of modern mule deer in AP length, with a nearly identical mean (Fig. 13), but the *Bretzia* P_4 average is slightly wider.

The premolars of *Bretzia* are relatively large compared to the length of the lower cheek tooth row (Fig. 14). In New World deer and other genera of the capreoline clade (telemetacarpal deer) the premolars tend to be 40% of the total cheek tooth dimensions or more. Old World deer tend to have relatively shorter premolars. Croitor and Stefaniak (2009) point out the relatively long premolars of *Procapreolus moldavicus* (ranging from 38.5% to 41.4%) as a character relating this taxon to the Capreolinae. That range is very similar to the range in my sample of *Odocoileus hemionus*, where with sufficient

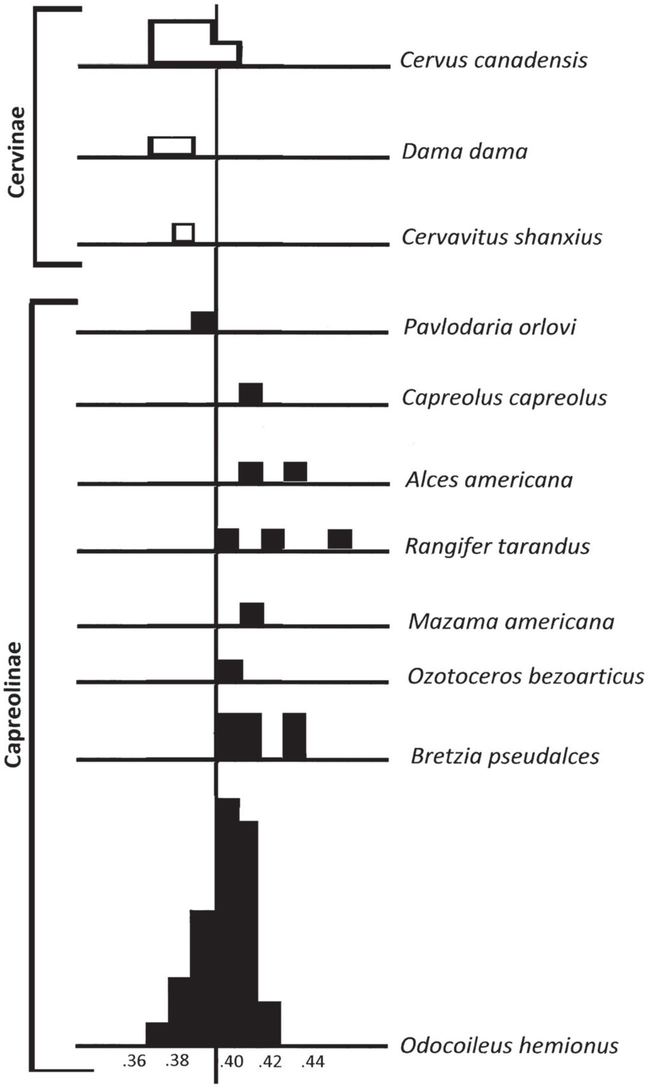

FIGURE 14. Ratio of premolar length to total lower cheek-tooth length in various cervids; Capreolinae tend to average 40% or more, Cervinae average less than 40%. *Bretzia* falls with the Capreolinae.

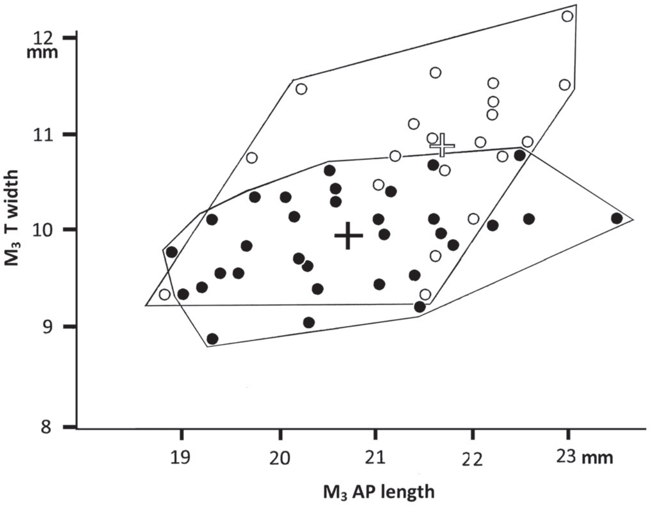

FIGURE 15. Scatter diagram, Transverse width versus anteroposterior length, M_3. Open circles and open cross are *Bretzia pseudalces*; solid circles and solid cross are *Odocoileus hemionus*. Crosses indicate intersection of means of both measurements.

sample size the measurement ratios begin to show a normal distribution. Except for *O. hemionus,* Fig. 14 is based on very few specimens, but there appears to be a clear trend, in which Capreolinae have relatively long lower premolars. *Bretzia* falls with the Capreolinae in this ratio.

Lower molars—First and second molars (Figs 7, 8, Plates 1, 2) are mutually similar in many ways but isolated teeth can be distinguished. I have sorted isolated molars by making a bivariate scatter plot of measurements of those teeth which could definitely be identified by tooth position, then adding the isolated teeth onto the plot. The result was a clear separation of the first from second molars. In addition to larger AP and T dimensions, first molars were consistently more worn or lower-crowned than second molars. Twenty-two first and 28 second molars are known.

Bretzia molars, like other cervid molars, tend to be rather invariant. They are tall-brachyodont to short–hypsodont (Hypsodonty Index = 1.1), four-cusped, with selenodont cuspids, especially the labial cuspids. The lingual cuspids have a much less-crescentic shape, often affected by a strong rib on the metaconid and entoconid. A strong anterior cingulum is usually present, sometimes forming a visible cingulum extending around the entire labial side of the molar. An ectostylid is present on all examples of $M_{1\text{-}2}$ and is often rather prominent. There is no trace of a *Paleomeryx* fold on the molars.

Connection of the dentine between protoconid and entoconid is sometimes present, which can isolate the hypoconid. This connection seems to develop with wear earliest on M_1, later on M_2, rarely on M_3; it does not form a strong linear feature.

Compared to the sample of *O. hemionus*, the molars of *Bretzia* are slightly less hypsodont, have a stronger cingulum (a feature often absent or nearly absent in *Odocoileus*), and have a consistent ectostylid (which is often completely absent in in *Odocoileus*).

The sample of *Bretzia* includes 23 third lower molars. Except for the presence of the posterior "lobe" made up of hypoconulid, entoconulid, and back fossettid, the M_3 resembles the first two molars. In dimensions (Fig. 15), the *Bretzia* M_3 is almost identical in range of AP length to the sample of *Odocoileus hemionus*. However, the transverse width of M_3 averages considerably wider, enough so that the T mean for *Bretzia* falls outside the range of this sample of *Odocoileus.*

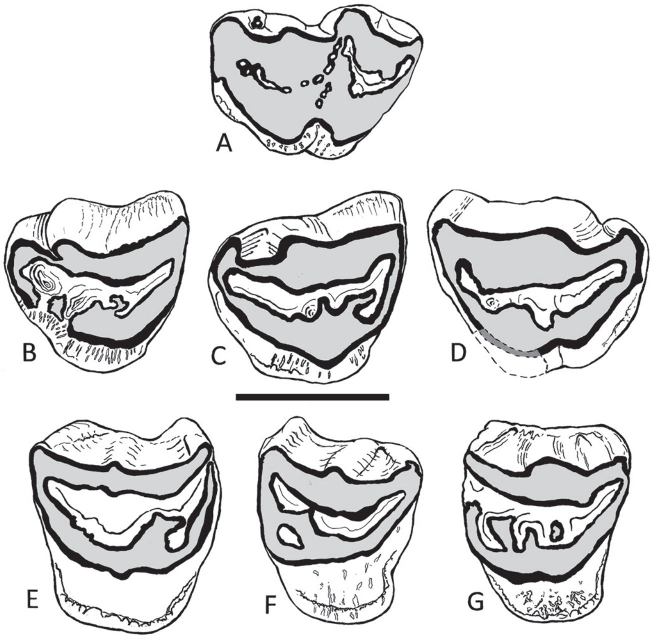

FIGURE 16. *Bretzia pseudalces*, upper premolars. A, LdP^3, SDSM 22196, occlusal view, anterior to left. B-D, upper P^2, occlusal views. B. UWBM 42222, LP^2, C. LACM 154775. LP^2, D, LACM 154780, RP^2; E, UWBM 95600, LP^4; F. SDSM 22197, RP^3; G. SDSM 22198, RP^3? Scale bar equals 1 cm.

Deciduous Upper Dentition—A single upper deciduous tooth has been identified as *Bretzia pseudalces* (Fig. 16A). The tooth is heavily worn but retains a shape typical of cervid dP^3. It had four crescentic cusps, as in dP^4 and molars in other cervids, but the anterior portion is longer and narrower than in the molars or in the dP^4. In comparison to this tooth in *O. hemionus*, the Ringold tooth is not easily distinguishable. Both are similar in overall shape and size. It is also very similar to the dP^3 of *Capreolus*, though larger than the latter. The available examples of dP^3 of *O. hemionus* tend to have more prominent paracone rib and metacone rib, and the anterior lingual side of the hypocone tends to have a cingulum which is not present on the single tooth of *Bretzia*. The *Bretzia* tooth has a small separate cusp on the labial side of the paracone and a small cingulum on the anterior side of the protocone.

The dP^3 of *Bretzia* is easily distinguished from that of *Cervus canadensis*. The latter has these distinguishing features: larger size and more molariform shape, larger paracone and metacone ribs, and a greatly enlarged anterior cingulum. The dP^3 of *Dama dama*, another cervine, has the anterior portion (protocone and paracone) reduced relative to either *Bretzia* or *Odocoileus* and much reduced relative to *Cervus.*

Permanent Upper Dentition—A summary of measurements is given in Table 3.

P^2 description—Three examples are available (Fig. 16). They are strongly asymmetrical, with the metastyle much larger than the parastyle. The metastyle forms an acute angle, similar to *Odocoileus*, *Hippocamelus*, *Capreolus*, *Dama*, and *Cervus*; the metastyle tends to be reduced in *Alces*. The paracone rib is prominent, angled to the anterior, adjacent to the parastyle. The anterior crista of the protocone may be incomplete, as in UWBM 42222. One example of *Alces* in the LACM is very similar. A medial crista is present, sometimes doubled or more complexly folded. A lingual cingulum is present (but not prominent) on all three teeth. An entoflexus, an infolding of enamel on the lingual side, is variable, weak to prominent, and when prominent begins the incipient division of the protocone into two distinct cusps (LACM 154780). This division of the lingual cusp into two in P^2 is a common and highly variable feature of advanced cervids. Many Cervini (e.g., *Cervus, Dama*) consistently divide this cusp, but most examples of New World deer do not. I have one individual of *O. hemionus* and another of *Mazama americana* in each of which P^2 on one side has a strong entoflexus and the other side shows little sign of it. *Capreolus capreolus* frequently has two distinct cusps but the entoflexus does not completely separate the cusps, with a dentine tract connecting them. The style of variation in P^2 of *Bretzia* is very similar to that seen in *Odocoileus*.

P^3-P^4 description—The P^3 and P^4 of *Bretzia* are very similar. A total of eight of these teeth are known, and most can be assigned a position with the exception of SDSM 22198. Both are much more symmetrical than P^2. The parastyle tends to be slightly larger than the metastyle in both teeth. The fourth premolar is slightly larger than P^3. The paracone rib is usually slightly more anterior on P^3; it is central on P^4. The protocone is undivided, with no entoflexus, or only the slight hint of one. On both P^3 and P^4 there is a prominent medial crista occupying the posterior part of the fossette. In SDSM 22198 the medial crista is doubled, and a small cuspule occupies the central fossette. In other examples the crista extends toward the posterior crista of the protocone, and in later wear, contacts it, leaving a small isolated enamel lake (Fig. 16F). The basal-lingual side of these teeth in *Bretzia* has a strong bulge surrounded with a distinct cingulum. In *Odocoileus* this bulge is present but usually less well-developed and rarely has a continuous cingulum.

The P^3 of *Cervus* and *Dama* tends to be more intermediate in form between P^2 and P^4, unlike *Odocoileus*, *Mazama, Alces*, *Capreolus*, and *Bretzia* in which P^3 and P^4 are more similar to each other than to P^2. The P^3 of both *Cervus* and *Dama* usually has a well-developed entoflexus, unlike the capreolines.

M$^{1-2}$ description—The first and second upper molars of *Bretzia pseudalces* (Fig. 17, 18) are selenodont brachyodont teeth very typical of Cervidae in general. The M^2

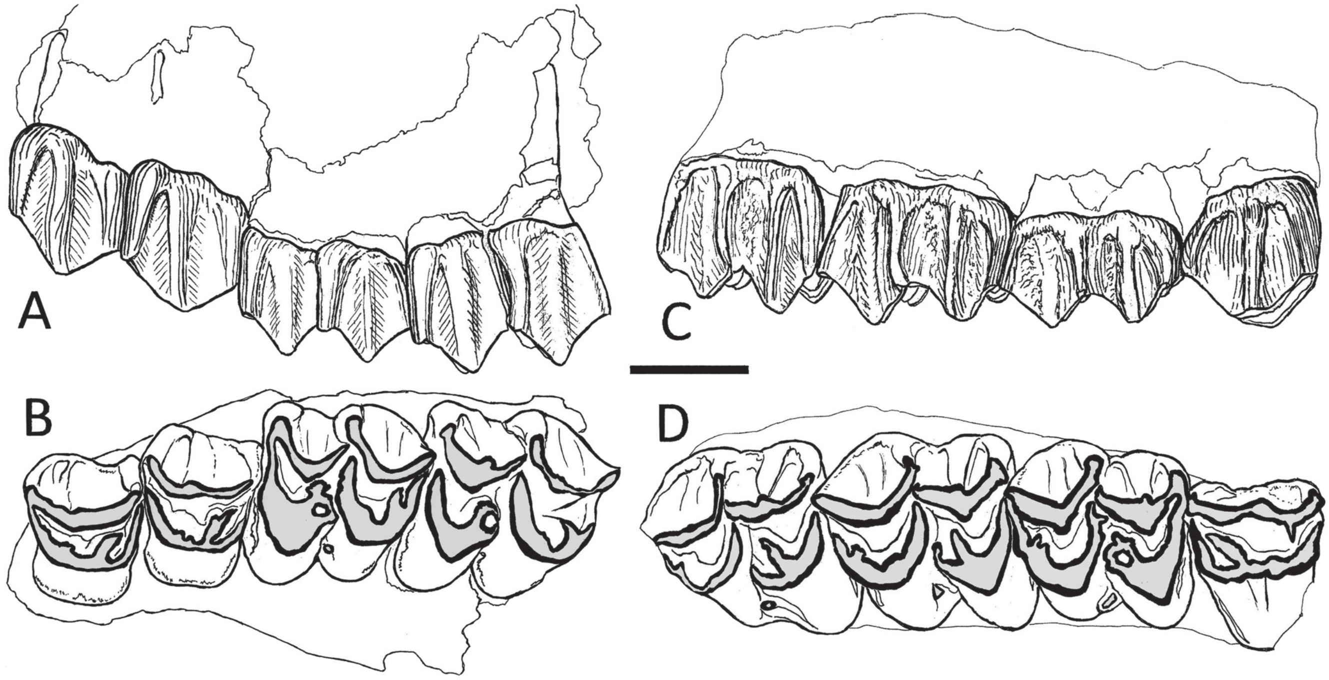

FIGURE 17. A-B, *Bretzia pseudalces*, maxillary dentition, UWBM 52677, L P^3-M^2. A, lateral view; B, occlusal view. C-D, LACM 120169, RP^4-M^3. C, lateral view; D, occlusal view. Scale bar equals 1 cm.

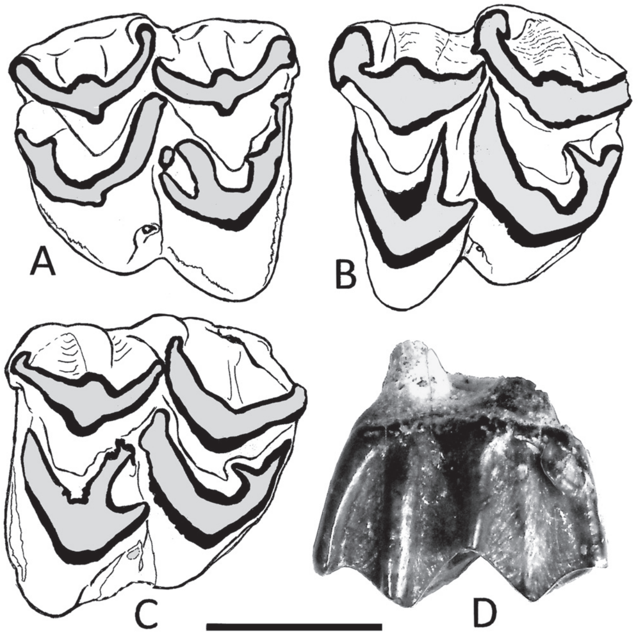

FIGURE 18. *Bretzia pseudalces,* A, SDSM 22199, RM^2; B, UWBM 95062, LM^2. C-D, LACM 118598, LM^3; C, occlusal view; D, labial view. Scale bar equals 1 cm.

is slightly larger than M^1. There are four main cusps and prominent parastyle, mesostyle, and metastyle. The paracone rib is more prominent than the metacone rib. An entostyle is present on all examples, generally larger in M^1 than in M^2. The posterior protoconal crest is always bifid, divided by a protoconal fold which becomes an enamel island in later wear stages. A spur is present on the posterior crest of the metaconule. Anterior, medial, and posterior cingula are usually present.

In almost all details the M^1-M^2 of *Bretzia pseudalces* are indistinguishable from the molars of *Odocoileus hemionus*. The latter are similar in size, shape, and prominence of styles and presence of protoconal fold and metaconule spur. The protoconal fold and metaconule spur are present on *Mazama americana* and *Capreolus capreolus*, occasionally present on *Alces*, but reduced or absent on *Ozotoceros, Dama*, and *Cervus*.

M^3 description—Nine examples of the M^3 are in the collections (Fig. 17, 18, 19). The anterior half of M^3 is similar to that of M^2. The posterior half is narrower; the metaconule is smaller than on M^2, giving

M^3 a distinctive posterad taper. The entostyle is very small on several examples. The most distinctive feature on M^3 is the strong metastyle, particularly the basal portion, which, instead of becoming smaller, even indistinct towards the base as on M^1-M^2, becomes larger, often turning anterad into a ridge or cuspule at the base. As a result the base of the metacone rib runs into a depressed

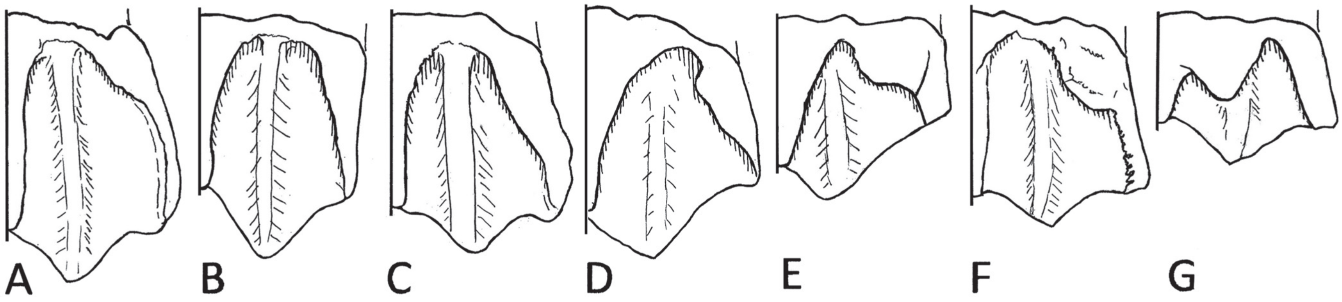

FIGURE 19. Variation in basal metastyles on posterior labial M_3 of *Bretzia pseudalces,* anterior to left. All depicted as left M3. A. LACM 120169, B. UWBM 92883, C. UWBM 47397, D. UWBM 46832, E. UWBM 42987, F. LACM 118598, G. SDSM 22200.

area or pocket formed posteriorly by the base of the metastyle. This feature is quite variable (Fig. 19). A similar feature is seen in alcine deer (*Alces* and *Cervalces*), in which it has been called an "additional fold" (Fig. 20A, B; see Breda, 2008, Fig. 6). In modern *Odocoileus* the basal metastyle on M^3 almost always becomes smaller and less distinct near the base. Only one example of *Odocoileus hemionus* in my collection has a basal metastyle strong enough to form a similar pocket (Fig. 20D). This "additional fold" or metastyle pocket is also present on some examples of *Hippocamelus antisensis* (Fig. 20C) and *Rangifer tarandus* (Fig. 20E) and has been reported in *Hydropotes* (C. Dailey, 2013, personal communication).

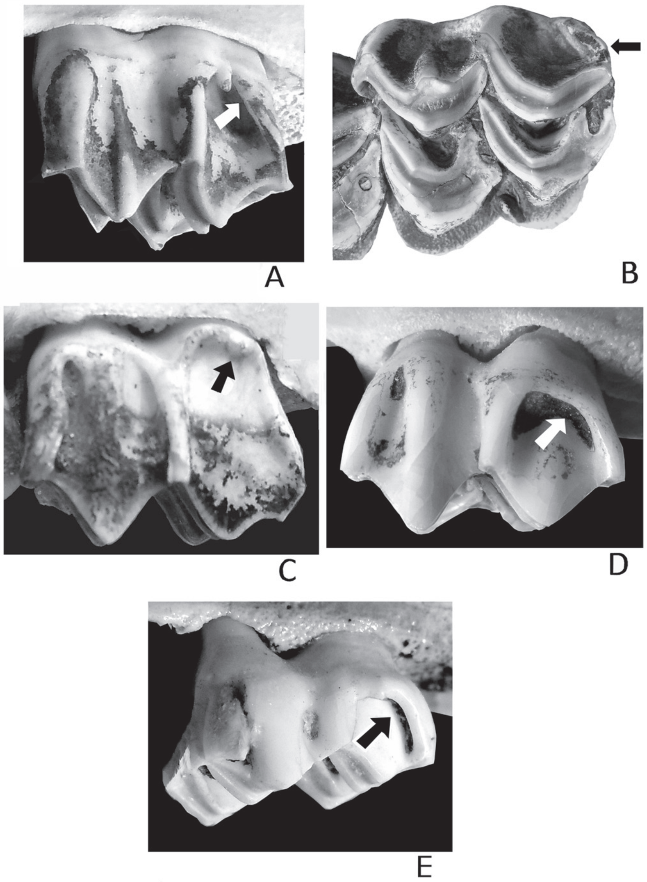

FIGURE 20. Variation in basal metastyle in modern Capreolinae, showing pocketed forms. "Additional fold" or metastyle pocket indicated by arrows. A-B, *Alces americana,* LM^3 (2 individuals), A, labial view, B, occlusal view. C, *Hippocamelus antisensis* LM^3 (AMNH 21595, from Chile), labial view. D, *Odocoileus hemionus* from Oregon, LM^3, labial view, with enlarged basal metastyle (arrow) forming a pocket, here filled with dark food debris. E, *Rangifer tarandus*, from Alaska, LM^3, with metastyle pocket.

Skull—Several partial skulls are here assigned to *Bretzia* (Figs. 21, 22, and 23, measurements in Table 4). Most are male frontals with pedicles; a few fragments of pedicles remain attached to antlers (Figs. 23, 31, 32, Plate 4E-F). One fragmentary female partial cranium is preserved (UOMNH F-322030), sufficient to demonstrate a lack of antlers, as in most other female cervids.

The most prominent features of the surviving male skull fragments are the pedicles. These are nearly cylindrical at their distal ends, where antlers were attached. Natural abscission caused the antler to drop off and left a porous bone surface, rough, and frequently with a central round depression (antler detachment surface, Fig. 21D-E). This detachment surface, flattened but often irregular, forms an angle of about 45 degrees to 50 degrees with the sagittal plane of the skull and is tilted inward from the vertical by about 30 degrees. The preferential preservation of this part of the skull is accounted for by the presence of dense bone in the pedicle and attached reinforced frontal bone, needed to support the antler. On the ventral side of the pedicle is a flattened area, the ventral table, which allowed clearance for the passage of the coronoid process of the dentary.

Three specimens with part of the frontal are considered juveniles because of their small size (Fig. 23). One had shed the antler, but the on other two the base of the antler, including the burr, remains attached. The juvenile pedicle is longer relative to its diameter compared to the adults. The preserved antler base is similar to shed

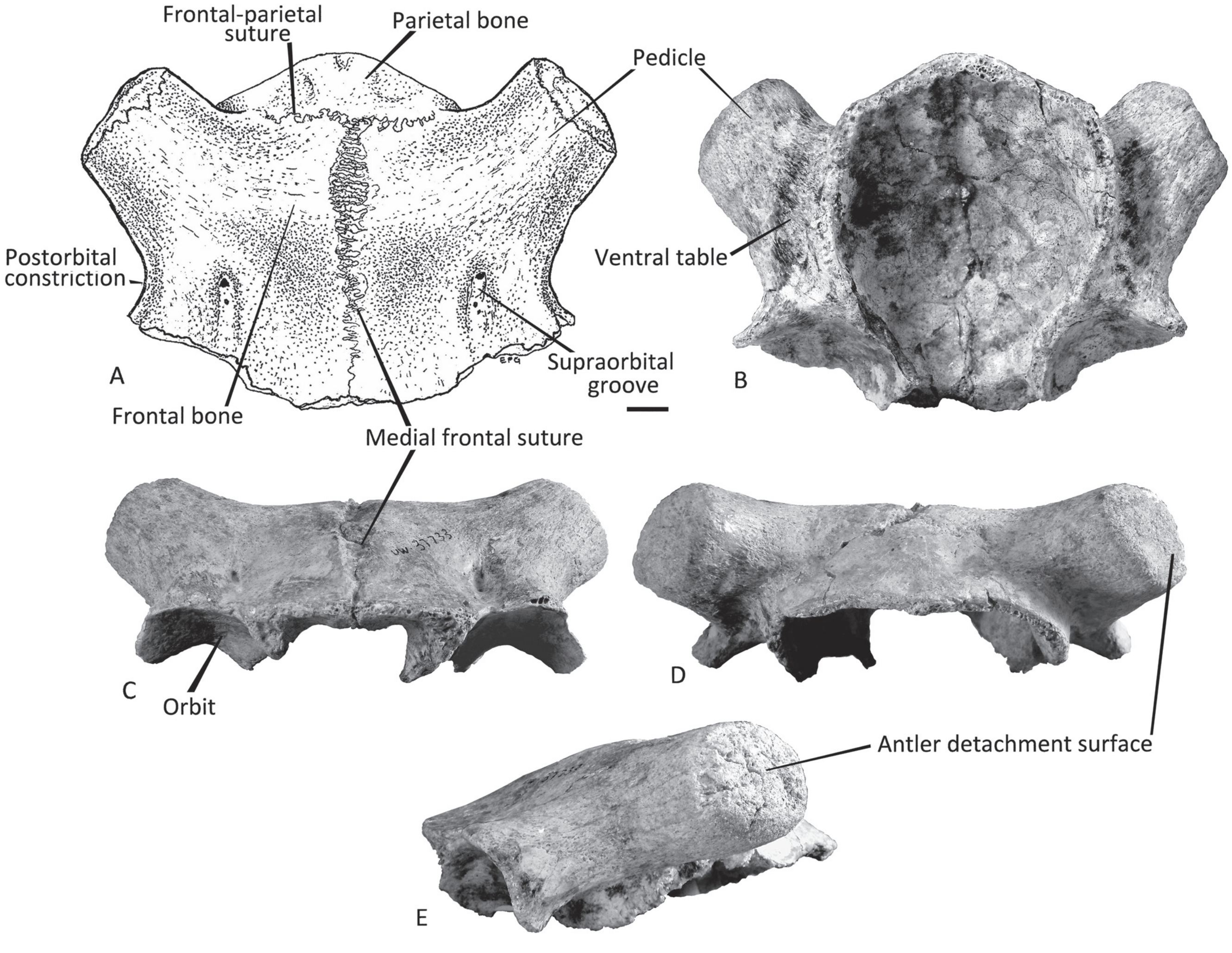

FIGURE 21. *Bretzia pseudalces*, skullcap. UWBM 37733, paratype of *Bretzia pseudalces*, partial male skull. A, dorsal view, anterior at bottom; B. ventral view; C. anterior view; D. posterior view; E left lateral view. Scale bar equals 1 cm.

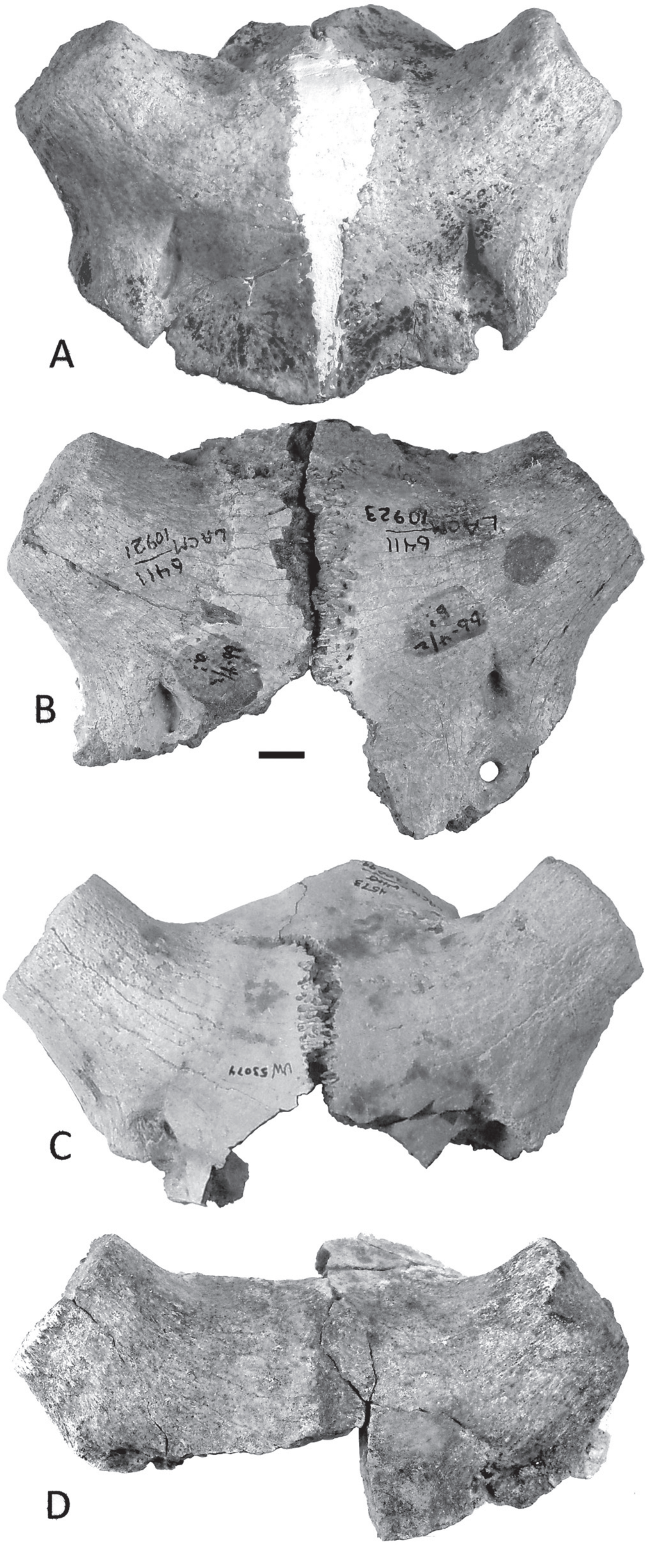

FIGURE 22. Adult male *Bretzia pseudalces* skull fragments, all frontal view. A. UWBM 95606; B. LACM 10921 and LACM 10923; C. UWBM 53074 and LACM 120099; D. SDSM 22203. Scale bar equals 1 cm.

antlers also classed as juveniles (Fig. 27).

The attitude of the pedicles is one of the most obvious distinguishing features of the skull of *Bretzia*. From the side, the pedicles are slightly depressed from the plane of the forehead (Fig. 21E). In frontal view, the angle between the pedicles is 90 degrees or slightly larger (Figs. 21, 22, 24). This is a larger angle than is commonly seen in any of the Rangiferini or Cervini (Fig. 24) and is only exceeded among the modern Capreolinae by the 180 degree angle between the pedicles of *Alces* and *Cervalces* (Figs. 25B, 39A-B). The modern extremes in this character are both seen in non-rangiferine Capreolinae, the lowest angle being in *Capreolus capreolus* (pedicles slightly convergent posteriorly; Fig. 25A), and highest in *Alces* (each pedicle at 90 degrees to the sagittal plane of the skull, or even angled slightly forward, Fig. 25B). The angle between the pedicles also is low (most commonly 10 degrees-20 degrees) in smaller New World deer, such as *Mazama* and *Pudu* (Fig. 25C; see also Hershkovitz 1982, Fig. 15).

Early fossil Capreolinae (*Pavlodaria, Eocoileus*) seem to vary in this angle between 25 degrees and 60 degrees (my measurements). The same is true in larger South American deer (*Blastocerus*, *Ozotoceros*, *Hippocamelus*). Some individuals of *Odocoileus* have the angle between the pedicles approximately at 90 degrees. This is at the high end of the range in *Odocoileus*, in which it is quite variable. Variation in the pedicle shape and angles of *Odocoileus hemionus* is illustrated by Plate 3, showing two bucks, a younger and older individual, both of which had shed their antlers. In the younger buck, the pedicles are relatively more prominent but are narrower, with a smaller detachment surface directed more to the rear. In the older, larger individual, the pedicle is shorter relative to its width; the detachment area is relatively large and more visible from the dorsal view. In *Bretzia*, little of the detachment surface is visible in dorsal view (Figs. 21, 22).

The outline of the dorsolateral margin of the skull of *Bretzia* is distinctive. The pedicle is large and extends laterally to or beyond the orbit. Cervids vary greatly in the relative prominence or protuberance of the orbit. The extremes of variation among cervids are shown in Fig. 25C-D, between *Pudu*, which has a large orbit which nevertheless fits smoothly into the lateral contours of the skull, and *Rangifer*, in which the orbit is enclosed in a conical protrusion. The orbits of *Odocoileus* are intermediate, though the orbits of *O. virginianus* are usually less protuberant than those of *O. hemionus*. The orbits of *Bretzia* appear to have had an outline much like those of *O. hemionus* (compare Figs. 21 and 22 with Plate 3). Behind the orbit is a narrow postorbital constriction, behind which is the pedicle, which extends laterally much further than in *Odocoileus*.

As in other cervids, *Bretzia* has supraorbital grooves

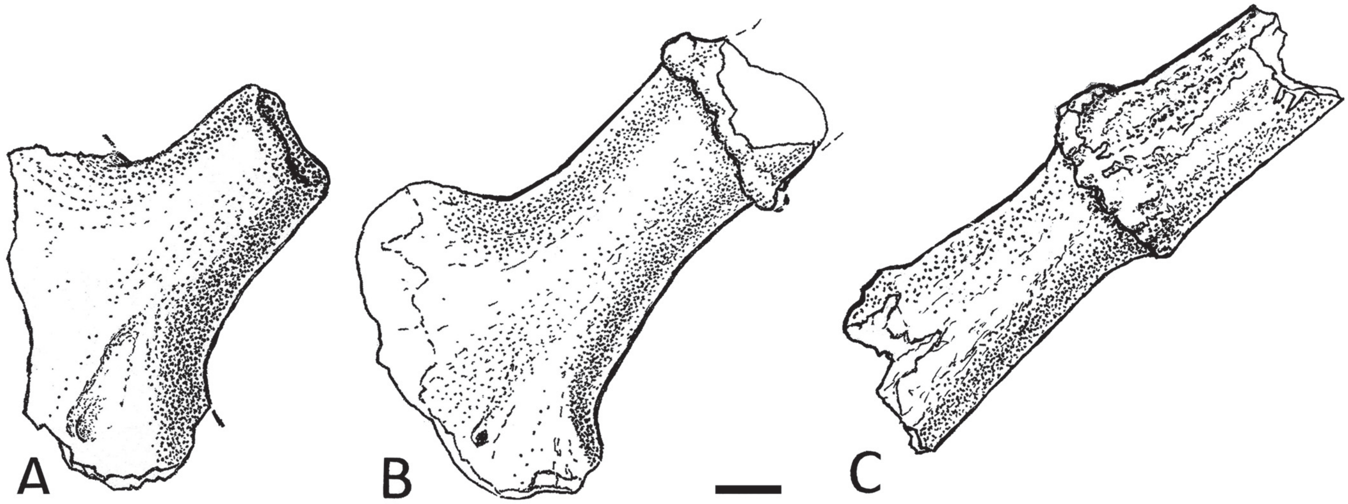

FIGURE 23. Juvenile *Bretzia* skull fragments, all in dorsal view, anterior at bottom. A. SDSM 22204, partial L frontal with pedicle; antler naturally shed; B. UWBM 41478, partial L frontal, antler not shed but broken off just above burr; C. UWBM 45016, partial L frontal (pedicle) with base of antler attached. Scale bar equals 1 cm.

(Fig. 21A) containing several foramina. Only the posterior parts of the groove are preserved in the fossils, except for one (Fig. 22B. left side). It is well separated from the orbital margin as in *Odocoileus*, *Blastocerus*, and others, and more so than in *Pudu* and *Dama*. The frontal tended to break at the level of the largest anterior foramen. This feature (the groove) is highly variable in modern *Odocoileus.* In the *Bretzia* skull fragments the posterior end of the groove is pocketed, with one or two small foramina at or near the posterior end. The lateral wall has a sharp margin in three of the skull fragments (Fig. 22A, B, C), on two others both walls are rounded. The central part of the groove becomes shallower, at the primary foramen, but the anterior end in missing in all specimens. In most specimens of *O. hemionus* the supraorbital groove tends to be deeper than in *Bretzia* and to have sharp-edged margins, though the size and distribution of foramina are similar.

In the several specimens of *Bretzia* the medial frontal suture runs posteriorly past the highest point of the skull between the pedicles. Just behind that high point, it meets the frontal-parietal suture at close to a right angle. The latter suture runs about half-way to the pedicle on each side, where it abruptly turns posteriad, continues for a short distance, then curves sharply laterally to run along the posterior margin of the pedicle. This is a similar pattern to *Odocoileus,* except that in *Odocoileus* the join between the medial frontal and frontal-parietal sutures is slightly more anterior, at the high point of the ridge crossing the skull between the pedicles. In *O. hemionus*, also, the area of that join tends to form a knob or boss which is not seen in *Bretzia*. As in all medium-to-large antlered cervids, the medial frontal suture, beginning at a point between the orbits, forms a complex interdigitation which strengthens the structure of the antler-supporting part of the skull. The complexity of the suture increases to the posterior end, where it meets the frontal-parietal suture, which is likewise complexly interdigitated. Despite the complexity of these sutures in the several specimens of *Bretzia*, they

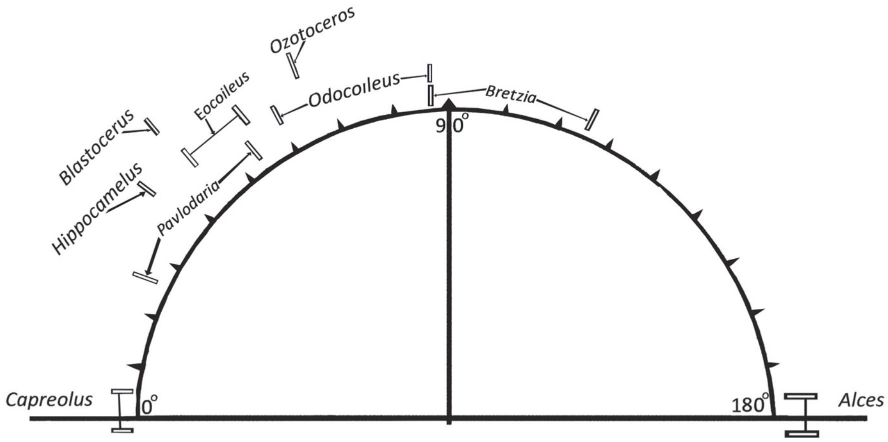

FIGURE 24. Angles of divergence of adult pedicles in various medium- and large-sized Capreolinae. Based on small samples; *Capreolus* N=4, *Pavlodaria* N=2, *Eocoileus* N=3, *Hippocamelus, Blastocerus* and *Ozotoceros* N=1 each, *Odocoileus* N=10 (8 *O. hemionus*, 2 *O. virginianus*), *Bretzia* N=5, *Alces* N=3.

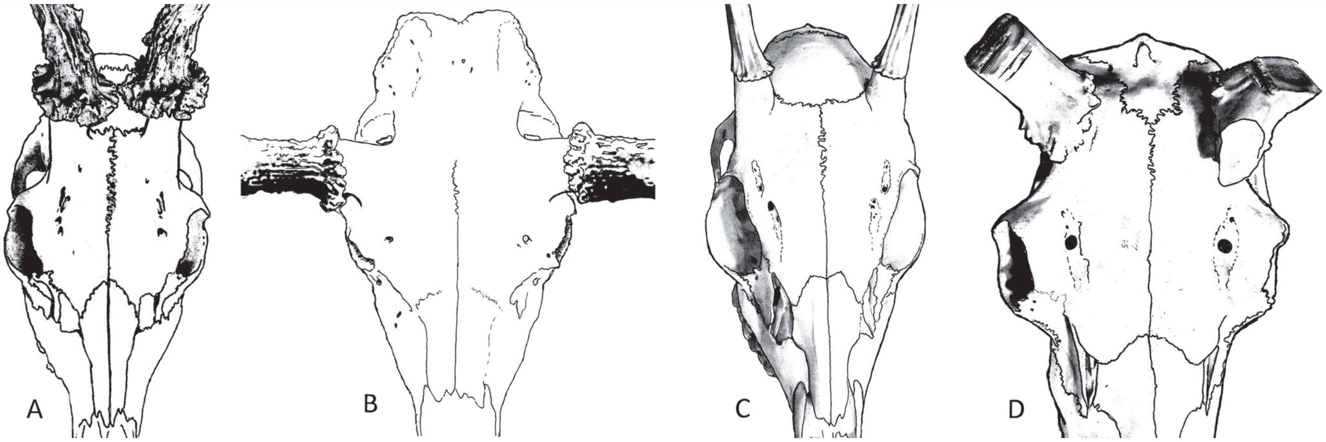

FIGURE 25. A-B, Skulls of *Alces* and *Capreolus*, frontal view. In Capreolus (A) the angle of divergence is near zero, with pedicles parallel or even slightly convergent. In *Alces* (B) the pedicles form a near 180-degree angle. C-D, Skulls of *Pudu* (C) and *Rangifer* (D), frontal view, showing differing degrees of protrusion of orbits.

are considerably less complex in *Bretzia* than in most specimens of *O. hemionus*.

Antlers—The antlers (or pieces of them) are the most common remains of *Bretzia*. They were presumably developed only on males. All evidence suggests that antler development and yearly replacement followed patterns common among modern temperate-climate deer. Variation in antler size and shape tends to be extreme in medium to large-sized deer. An earlier description of antler characters in *Bretzia* (Gustafson, 1985a) is supplemented here with additional characters listed below. Descriptive terminology follows Gustafson (1985a) and Bubenik (1990), with minor modifications. A summary of measurements is given in Table 5.

The general characters of the antlers of *Bretzia pseudalces* are these (modified from Gustafson, 1985a, see Figs. 26-34, this paper, and Fig. 28 for terminology):

1. Antlers are spread laterally, in part because the pedicles form a wider angle with the skull axis than in cervids other than *Alces*;
2. Anterior tine rises nearly vertically above forehead; base of tine is at 45 degrees-80 degrees from horizontal;
3. The plane of the burr is at a low angle, nearly a right angle, to the axis of the adjacent shaft;
4. The shaft just distal to the burr frequently bends downward or forward slightly, increasing the width of the antler spread;
5. The first branching point occurs distal to a variable (moderate to long) shaft or basal section;
6. Distal to the first branching point, the posterior branch (beam) is dominant (thicker than the anterior branch);
7. The dominant posterior branch (beam) is flattened or spread into a vertically-oriented palmate shape in mature individuals;
8. Tines on the palm are restricted to the corners and distal edge; they may range in number up to six or more;
9. There is no basal tine (variously called snag, sub-basal snag, prong, brow tine, eye-guard, etc.) as in *Odocoileus* (Fig. 38C-D);
10. Rugosity/pearling usually absent to moderate; small adventitious points ("sprouts") are not seen;
11. Small dorsal branch is sometimes present on the anterior tine (Plate 4A).

Description of antlers—Descriptions presented here are in two series; first, describing characters and variations based on parts of the antlers, namely the base, anterior tine, and palm which naturally break apart (Fig. 26, Plate 4, using less complete specimens), and second, describing variations during stages of development during the lifetime of the animal (Figs. 27-34 and Plates 5-8, using the more complete antlers).

Base of antlers—The base of the antler (Fig. 26 and others) is frequently all that remains, being the densest bone of the overall structure. Most of the antler bases are from naturally-dropped antlers, a process which in modern temperate-climate deer usually occurs after the end of a seasonal mating period. Dense bone forms a plug which separates the antler from the pedicle when the antler completes growth, and then sometime later a thin layer of bone is removed across the pedicle just below the burr, causing the antler to drop off (Bubenik, 1990, Fig. 31). The surface of the antler which was connected to the pedicle is convex in all examples of *Bretzia*, and may sometimes have a central bump. As seen from the pedicle end, the stump of the antler is close to circular.

The burr is a narrow ridge surrounding the antler base (Figs. 28, 32). It forms during the yearly growth of a new

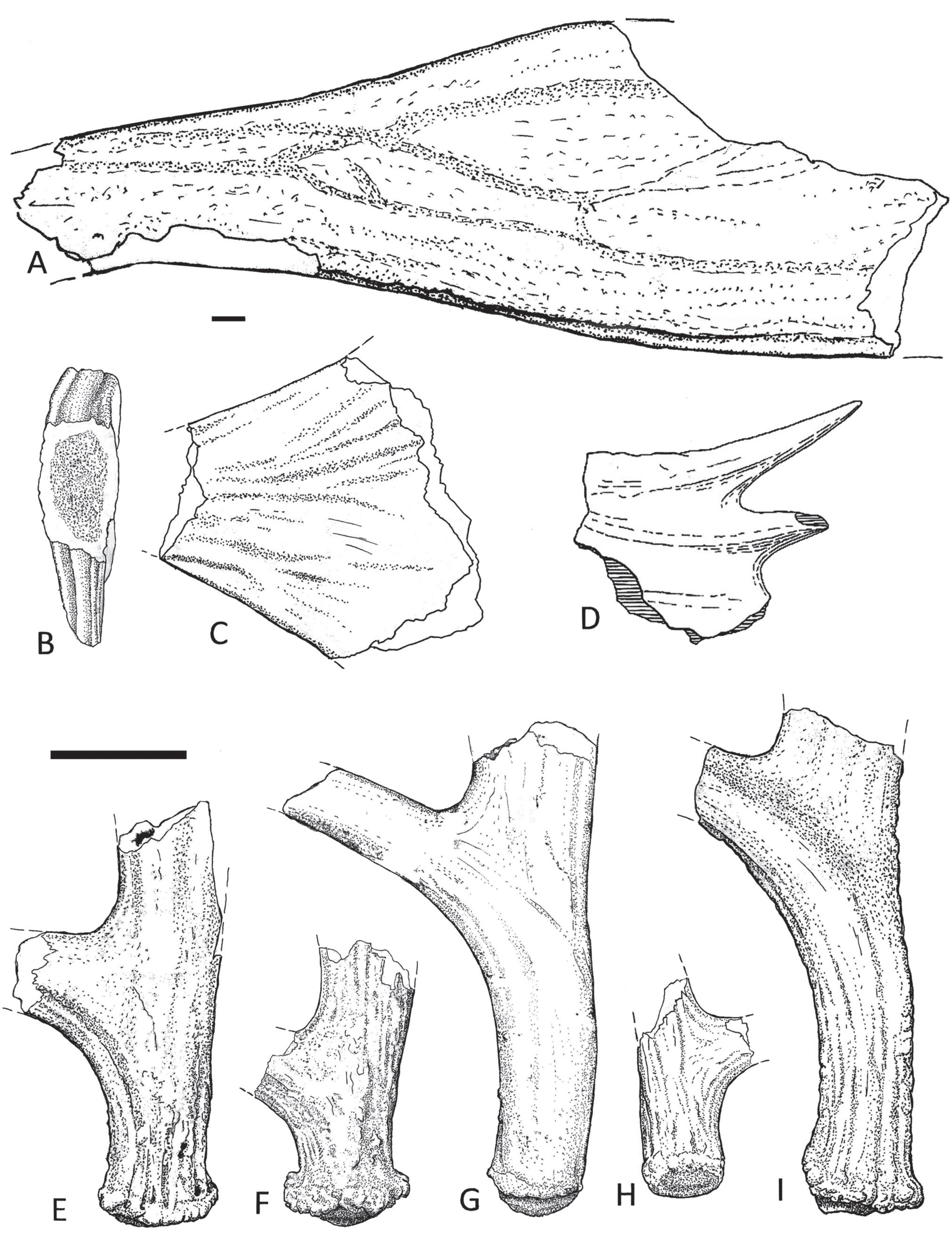

FIGURE 26. Antler fragments. A-D, Partial palms, medial view. A, WHC 0014, palm of left antler; B, UWBM 45032; C, D, UWBM 49478. E-I, Antler bases, E-G and I, medial view; D, lateral view. E. LACM 120163; F. LACM 11379; G. LACM 120168; H. UWBM (no number); I. LACM 11378. Scale bar equals 5 cm.

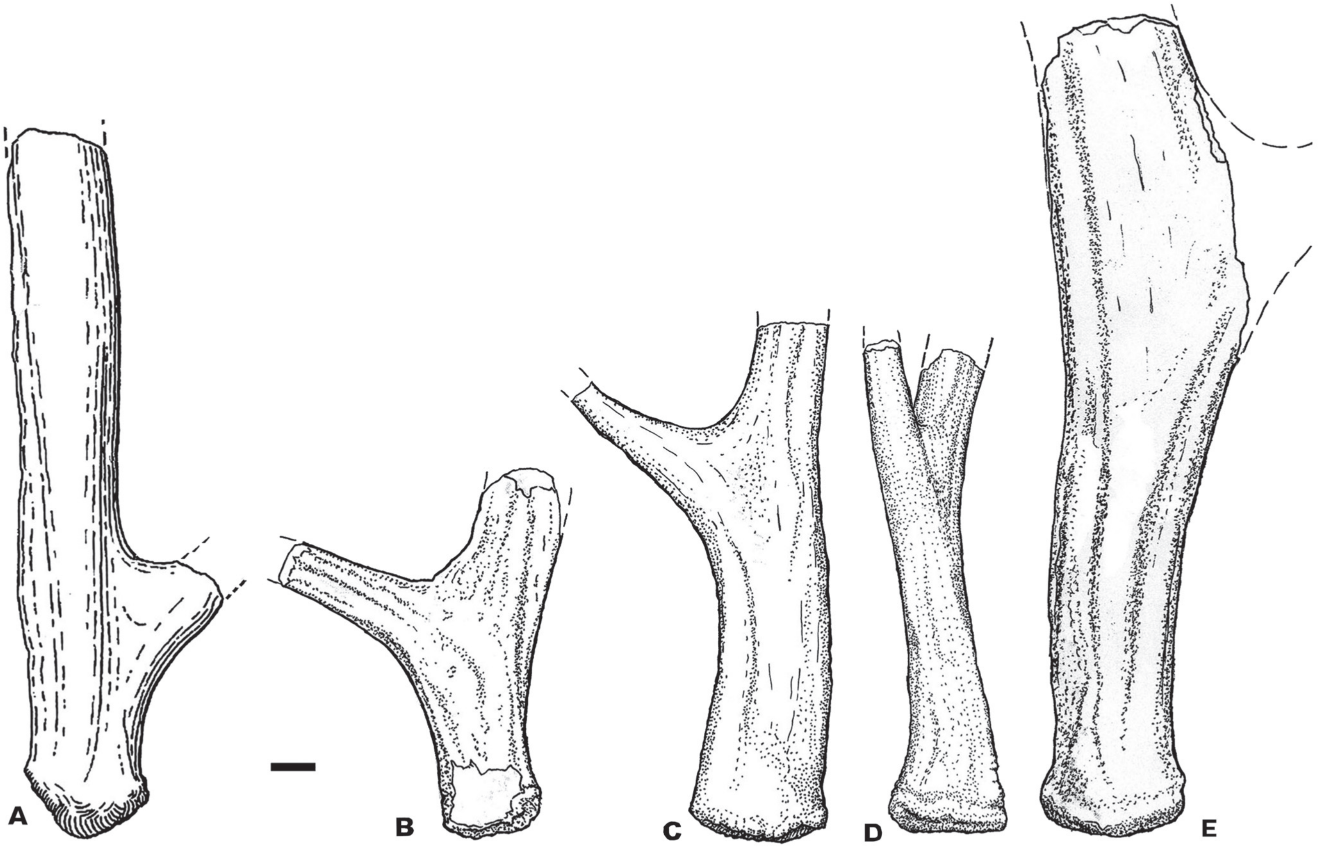

FIGURE 27. Juvenile (yearling) antlers. A, L antler, UWBM 45031; B, R antler, UWBM (Shawver, no number); C, D, R antler, LACM 11375; (C, medial view, D, anterior view); E, L antler, UWBM 51755. Scale bar equals 1 cm.

antler, visually separating antler from pedicle, which otherwise is continuous (compare Fig. 31, an antler attached to the pedicle, on which the burr has not yet formed, with Fig. 32, a mature antler which has a fully-developed burr). The bony ridge is commonly divided into sections by passageways for the blood vessels which feed the velvet skin-covering of the growing antler. In many examples the route of the blood vessels past the burr can be followed along grooves up the shaft and on to the anterior tine or beam, then on to the palm or to marginal tines. Development of the burr, especially in the more strongly beaded or pearled individuals (Fig. 26F and I, Plate 4A, E and F, Plate 6D) which appear to be from mature animals, may be correlated with physiological vigor. Some other examples (Fig. 26G, Plate 5A and B) have a poorly-developed burr. Variable development of the burr and associated rugosity seems to be in the lower range of variation seen in modern *Odocoileus hemionus* based on examination of the comparative material cited above; isolated small rounded growths above the burr ("pearls") are rare in *Bretzia,* though common in *Odocoileus*. The ring formed by the burr is not precisely concentric with the antler shaft above it, but commonly is at a slight angle (Fig. 26H) which suggests that the axis of the antler shaft was often not quite parallel to the axis of the pedicle. In one juvenile example (Fig. 23C) the antler bends slightly forward; this appears to be the case with other examples of *Bretzia* and is seen in other deer, including *Eocoileus* (Fig. 37C-D) and *Hippocamelus* (Fig. 40C-D).

Above the burr is a more-or-less cylindrical shaft. Shaft length varies from less than its own diameter (Fig. 26F, Plate 6A) to three or four times its own diameter, with most examples falling somewhere in between. Curvature of this section is common and variable in degree, though less so in direction. Curvature is generally concave towards the lateral-ventral side. It is most obvious on some apparently adolescent antlers (Plate 5A and D).

Anterior tine—A single large tine branches from the dorsal or anterior-dorsal surface of the shaft in all examples which preserve more than the very base of the shaft. In a few examples this anterior tine is at an angle of less than 90 degrees to the shaft; that is, it is depressed towards the front (Plate 4B). In some cases the anterior tine forms nearly a right angle with the shaft (Plates 4A, 6B, 7B). In a majority this angle is considerably more than a right angle, up to 130–140 degrees. The angle tends to be higher in those examples in which the division begins farther up the shaft, especially in examples identified as adolescent antlers (Plate 5).

The relative thickness, length, and curvature of the anterior tine are also notably variable. Several specimens preserve the anterior tine complete or nearly complete (Plate 4A-F, Plate 5B, D, E, F, Plate 6A-D, Plate 7A, B). The extremes in thickness relative to the shaft are shown in Plate 4D (small) and in Plate 4A and B (large). Specimen LACM 120168 has an especially long inwardly curved anterior tine (Plate 4F). The anterior tine on UWBM 42973 is almost perfectly straight (Plate 6A). In two examples the anterior tine had a secondary small tine on its posterior side (Plates 4A, 7B).

The nature of the branch between shaft and anterior tine in *Bretzia* is also interesting for what it suggests about the evolution of the antlers of *Odocoileus*, which evolved about the same time and from ancestry similar to that of *Bretzia.* The beam, or posterior branch past the first fork, is larger in diameter than the anterior tine in most capreoline deer (Gustafson, 1985), as in *Bretzia*. In *Odocoileus* the reverse is true; the anterior tine is dominant and the first fork is moved farther up the shaft, or the shaft elongates, so the first true fork is further from the burr. In *Bretzia* some individuals (including the type) have the anterior tine and beam of almost identical thickness. In those individuals of *Bretzia* in which the first fork is furthest from the burr, the shaft, and anterior tine tend to form a continuous curve, which approaches the helical curve usually seen in *Odocoileus* (Gustafson, 1985a). With an antler orientation like *Odocoileus* (antler held more vertically) and a slightly smaller beam, the antlers of *Bretzia* would appear much more similar to *Odocoileus* than they do in the reconstructions presented here. The additional fork seen on two anterior tines would be positioned as the second vertical tine seen in most *Odocoileus* (Fig. 38D) In other words the morphologies of both genera suggest the development of diversity in antlers from the same primitive form, which could have been similar to that of *Eocoileus.* In Figs. 36-40 I have numbered the tines of several varieties of cervids to show my interpretation of tine homology. The anterior tine is marked A (1), the equivalent of the anterior marginal tine of the palm is marked 2, and the posterior extension of the beam is marked 3.

Palm—Distal to the first fork in *Bretzia* antlers, the beam flattens and in adult bucks the flattened area forms a large palmate structure (Figs. 26, 28, 29, Plates 6-8). According to the evidence presented here (below), the palm was held in a nearly vertical position as in *Dama*, and not in the mostly horizontal position seen in *Alces.* By analogy to other cervids (Bubenik, 1990, fig. 34) the palm developed by the formation of a web of bone between preexisting tines. Palmation is not unusual in other cervids (e.g., *Alces*, *Rangifer*, and *Dama*) and is seen in others in which it is not the normal form. In *Odocoileus* when palmation occurs, it frequently forms a partial web from which the normal points protrude. In *Eocoileus* as in *Ozotoceros*, (Fig. 37, 40) the beam normally divides into two tines; this is presumably similar to the primitive form for *Bretzia*. Formation of a bony web between these two tines, then later elaboration including addition of additional tines along the distal edge (but not other edges) would account for the observed morphology in *Bretzia*. The distal edge was relatively thin and fragile, so other than in the type antler, distal tines are found as isolated fragments (Fig. 26D). Partial palms (Fig. 26A-C) preserve the thickest portions and on the broken edges, they show the internal structure. The dense bone on the surfaces is relatively thick, with a core of cancellous bone (Fig. 26B). In two individuals the palm is relatively narrow and long (Fig. 26A, 29), but otherwise the palm characteristics are similar to the other examples. Most of the specimens show a groove on the anterior-dorsal edge of the palm and the posterior-ventral edge is more tapered toward the margin. All specimens show a pattern of ridges and grooves showing the positions of blood vessels in the velvet as the antler grew. One distal fragment (Fig. 26D) clearly shows the marks of blood vessels reaching to near the tip of each point.

The shape of the combined beam and the anterior and posterior margins of the palm has the posterior margin being in-line with the beam (or at a slight angle) and the anterior margin being at a much sharper angle on the anterior-dorsal side. This shape is reminiscent of the relative attitudes of the tines on the beam of antlers of *Eocoileus* and *Ozotoceros* (Figs. 37D, 40B). It is less similar to the pattern in the antlers of *Capreolus* or *Alces*, in both of which, at the first fork the beam angles backwards from the shaft (Figs. 38B, 39A-B).

ANTLER MORPHOLOGY BY DEVELOPMENTAL STAGE

Juvenile antlers—Antlers classed as juvenile are small in diameter and length, and have a small anterior tine (Fig. 27). These were presumably first-year (yearling) antlers, which probably began growth during the animal's first spring season. All known examples are forked and flattened to some degree. They vary considerably in size and shape, as do first-year antlers of most living cervids depending on a combination of heredity, health, and nutrition.

Adolescent antlers—Antlers in the White Bluffs cervid sample which are larger, often with a basal diameter approaching average adult size, with a large anterior tine but without an adult palm are here considered "adolescent" (Plate 5). This designation is analogous to the developmental pattern seen in *Alces*, in which the antlers of young individuals are often "cervicorn" (Fig. 39A), that is, deer-like or without any trace of a palm. *Alces americana* from Canada often have a cervicorn antler in

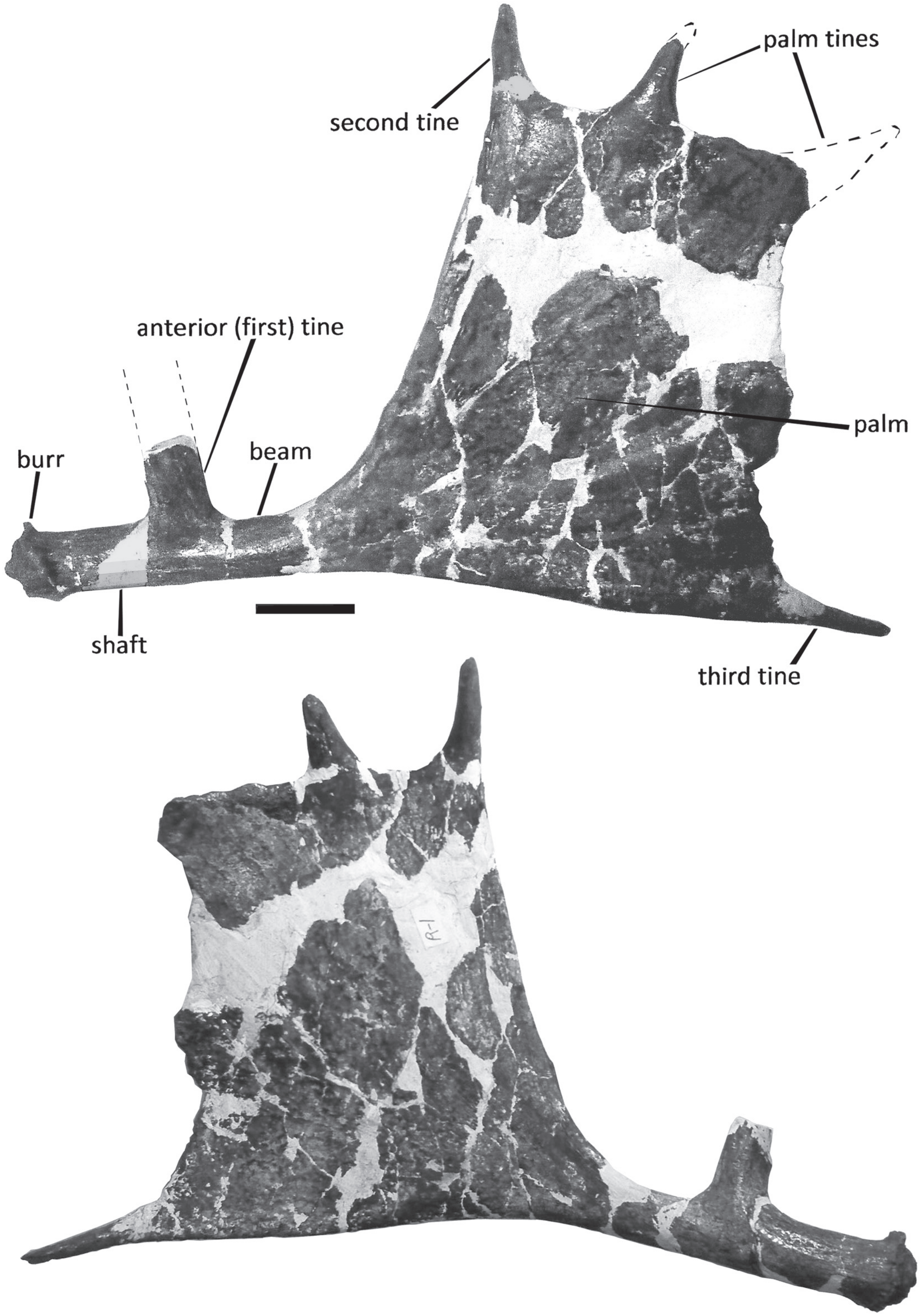

FIGURE 28. Mature antler. UWBM 42971, holotype left antler, lateral view (top) illustrating terminology, and medial view (bottom). Scale bar is 5 cm.

FIGURE 29. *Bretzia pseudalces* adult antler WHC 0009, right antler, medial (top) and anterior (bottom) views. Scale bar equals 5 cm.

the first and second year (Child et al., 2010); in European *Alces alces* this form of antler may persist even longer. The cervicorn form may have a forked beam, a beam with a single point, or even both on a single individual (Fig. 39A). In *Bretzia* the posterior tine in adolescents may be flattened and widened, but not palmate.

Mature antlers—This group includes fully developed antlers with consistent size, a large anterior tine which is straight to broadly curved, and sometimes forked (i.e., with a smaller dorsal tine), and a posterior branch widened into palm with distal points (Figs. 28, 29, Plates 6-8). The palm may be fairly narrow, or triangular, or kite-shaped. It usually has an anterior groove. Added tines seem to be developed only on the distal end or edge of the palm. Pearling is rarely observed, though in some individuals the surfaces, especially near the base, can be quite rugose (Plate 6D). Curvature of the anterior tine and palm, concave toward the midline, is usually moderate, ranging from nearly flat (Plate 6A) to strongly curved (Fig. 29).

Senescent antlers—A single antler (LACM 11392) has characteristics commonly found in modern deer which have lived well past prime breeding age. This antler (Fig. 30) has a large base and well-developed burr. The anterior tine is relatively short and flattened, almost blade-like, and is curved forward. The beam above the fork is considerably smaller than the shaft below it, suggesting that the distal palm may have been reduced. The large diameter at the base, odd shape and reduced distal antler are all often seen in old males of other cervid species.

Antler in velvet—A single specimen (Fig. 31) has the characteristics of an antler in velvet (in the process of growth). LACM 154803 is a partial antler attached to its pedicle and part of the frontal. The burr is represented by a low circumferential ridge; nutrient channels are not well- developed. The distal incomplete ends of both the anterior tine and palm are worn in a rounded fashion

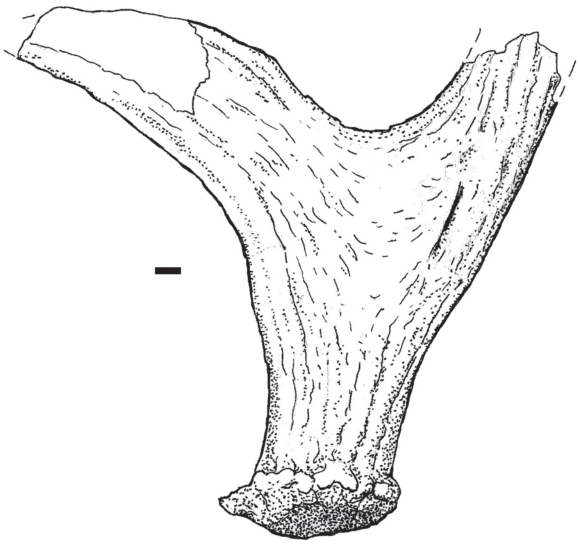

FIGURE 30. Senescent antler, medial view. LACM 11392, right antler. Scale bar is 1 cm.

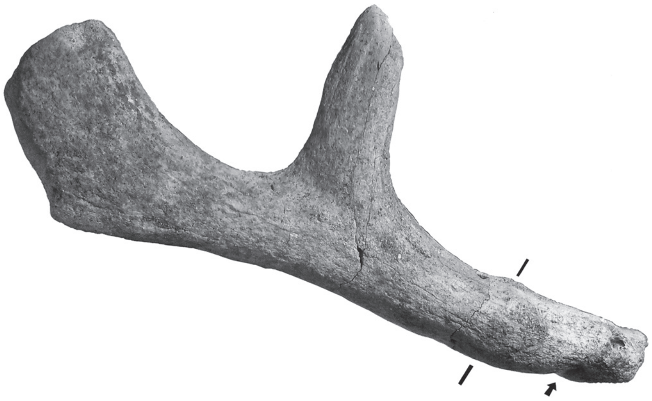

FIGURE 31. Right antler which appears to have been in velvet growth stage, lateral view, LACM 154803. Position of burr indicated by lines; arrow indicates ventral table of pedicle.

which is seen in the poorly mineralized ends of growing tines of antlers in modern deer. This animal died at a growth stage which in *Odocoileus* would have been reached in early to mid-summer.

ANTLER RECONSTRUCTIONS

Attitude at which the antlers were held— No indication was seen in the type or paratype series which would accurately indicate the proper attitude of the anterior tine and the palm. Thus the previous reconstruction (Gustafson, 1978) erroneously showed the antlers rotated 45 degrees or more from the orientation shown by further specimens.

Several antler specimens are preserved attached to the pedicle, particularly LACM 154803 and LACM 120168 (Figs. 31 and 32). Features of the pedicle allow interpretation of orientation of the anterior tine and palm relative to the skull. This is due to the presence of a ventral flattening (here called the ventral table) necessary to allow space for the coronoid process to move freely alongside the cranium.

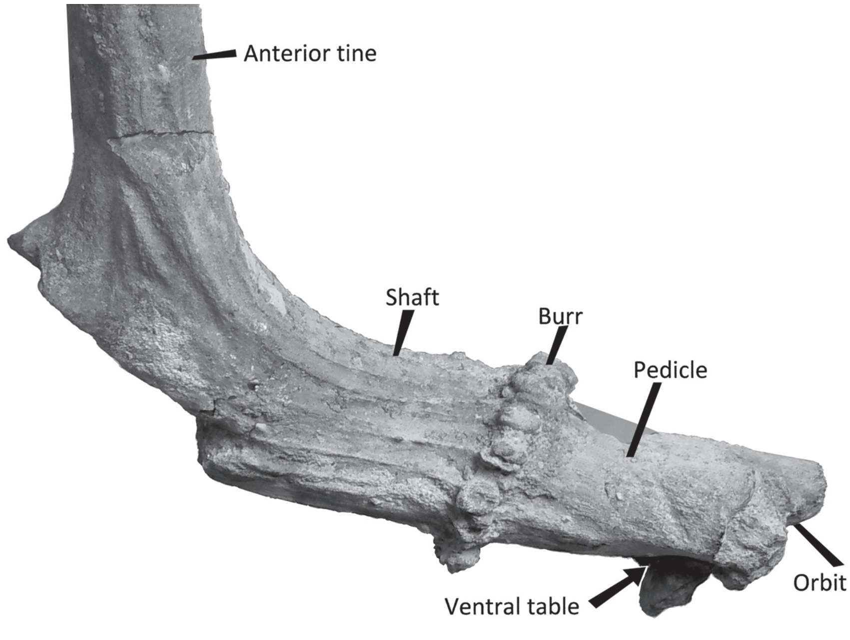

FIGURE 32. Feature used to determine attitude of antlers in life. Base of right antler LACM 120168 attached to pedicle and fragment of frontal bone. Arrow indicates position of ventral table, the flattened area on the ventral side of the pedicle.

In *Bretzia* the ventral table tilts downward to the anterior at about an angle of 20 degrees to 30 degrees when the head is horizontal. In all examples of the pedicle in *Bretzia pseudalces,* including juveniles, this feature is pronounced. The specimens which have both the pedicle and the anterior tine have the ventral table rotated at about a 45 degree to 80 degree angle from the surface from which the anterior tine arises; hence the anterior tine rises nearly vertically above the face, as shown in the new restorations presented here (Figs. 33, 34, Plate 8). The actual orientation resembles the orientation of the antlers in *Dama dama* (Fig. 35).

Cervids which have antlers placed high on the head (e.g., *Capreolus* and *Pudu*) have no ventral table. Their pedicles are basically round. In *Rangifer* the pedicle rises more vertically from the frontal and does not interfere

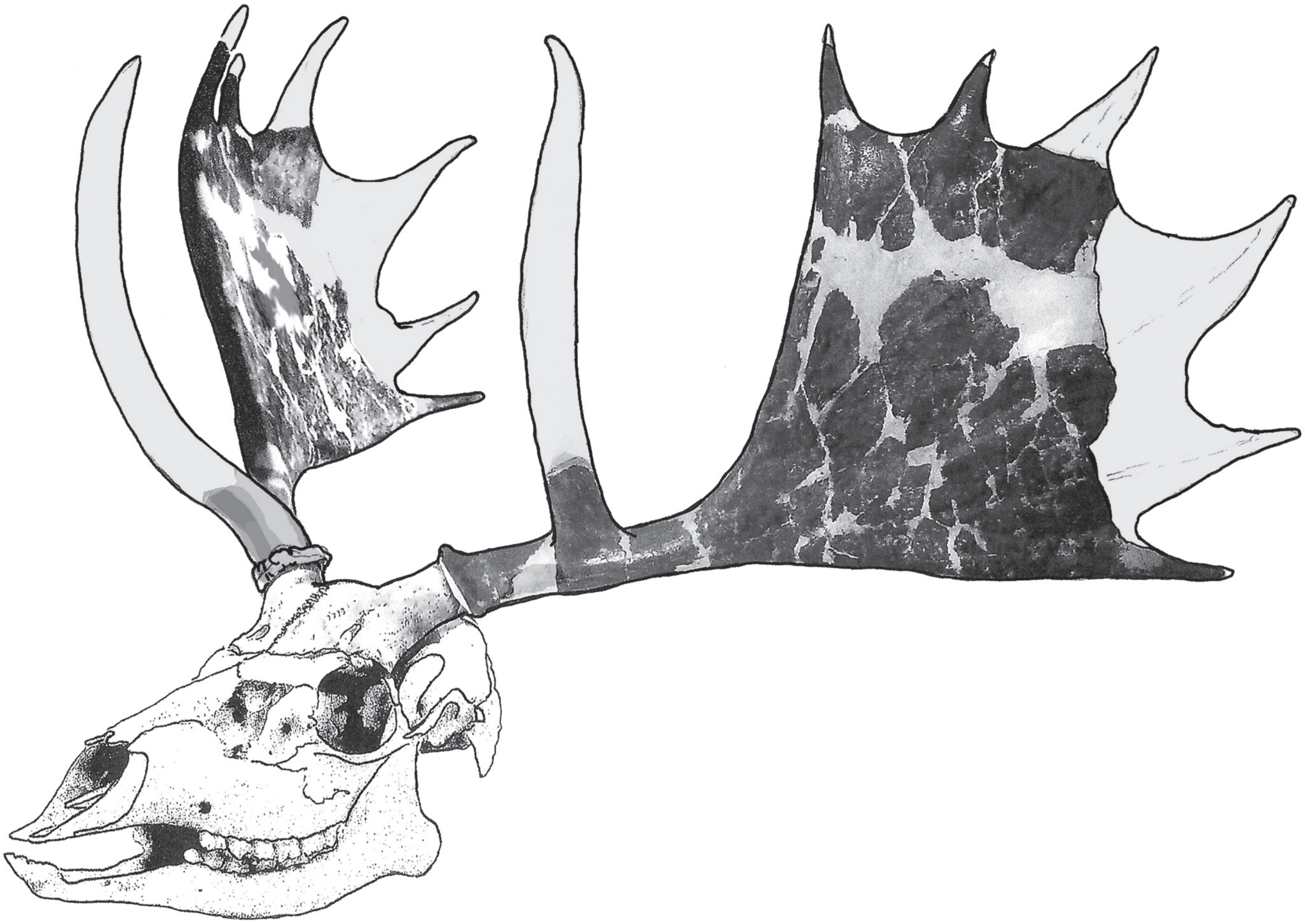

FIGURE 33. Reconstruction of skull and antlers of *Bretzia pseudalces* using UWBM 42971 (holotype antler) UWBM 42972 (paratype antler) and skull fragment (paratype, UWBM 37733) with antlers in correct position (mounted on skull of male *O. hemionus*).

FIGURE 34. *Bretzia pseudalces*, reconstruction based on WHC 0009, UWBM 37733, mounted on skull of *O. hemionus*, front and left lateral views.

FIGURE 35. Head and antlers of *Dama dama*, captive individual at Wildlife Safari, Oregon

with the coronoid process, so it also lacks a ventral table. Cervids with larger, more laterally-held antlers have a variably expressed ventral table. In *Odocoileus* it is present generally, even in yearling bucks with relatively small antlers.

The reconstructions presented here were produced by mounting the paratype skullcap (UWBM 37733) on the skull of a young mature *Odocoileus hemionus* buck of the same size, then photographing each of several antlers in as close as possible to life position. The antlers were assumed to be symmetrical. The skull of *Odocoileus* was used to provide a sense of scale and orientation. The preserved jaws indicate that its proportions are similar to those of *Bretzia*.

Five antler specimens were used to show something of the variation which would have existed in *Bretzia* in life. The holotype antler, UWBM 42971 (Fig. 28), is the largest available specimen, with a large and well-preserved palm. It has almost the same dimensions as a paratype, UWBM 42972, from the same locality, which preserves the anterior tine nearly complete. These two specimens, with the paratype skull fragment UWBM 37733, were used to complete the first reconstruction (Fig. 33). An adolescent antler, LACM 154802, (Plate 8A) shows the probable appearance of the cervicorn (non-palmate) antlers in anterior and three-quarter views. A relatively small antler (paratype UWBM 42974, Plate 8B, also two views) is probably a more average individual in adult antler development. Another example (paratype UWBM 42975, Plate 8 C) is an individual which had developed a forked anterior tine. The final restoration (Fig. 34) is based on WHC-0009, an adult antler with a narrower and more curved palm than most examples. Distal ends of tines and palms are somewhat conjectural.

COMPARISONS TO ANTLERS OF OTHER CERVIDAE

Understanding the antler patterns of *Bretzia pseudalces* requires some direct detailed comparisons to other cervids, both those of the same approximate age of appearance (late Miocene-early Pliocene) and those of similar ancestry. Deer of similar age (sufficiently well-known) include *Procapreolus* from Eastern Europe and Asia, *Cervavitus* and *Pavlodaria* from Asia, and *Eocoileus* and *Odocoileus* from North America. Of these only *Odocoileus* survives. *Bretzia* will also be compared to the living Capreolinae with multi-tined antlers, including *Capreolus*, *Alces*, *Rangifer*, *Ozotoceros*, *Blastocerus,* and *Hippocamelus*. The order in which these taxa are listed is informed by the branching pattern of cervid phylogeny suggested by the work of Duarte et al. (2008; Fig. 49 here). Deer from the late Miocene and early Pliocene most frequently have antlers of the three-point pattern of Geist (1971).

Late Miocene-early Pliocene deer: Cervavitus shanxius—The "pliocervine" deer *Cervavitus shanxius* (Fig. 36) is common in the late Miocene of north-central China (Zdansky, 1925; Dong, 2011). Most of those specimens appear to be older than the White Bluffs l.f. *Bretzia pseudalces*, dating probably to about 7-6 Ma (Baodean). Variation in antlers of *Cervavitus shanxius* has been partly illustrated (Zdansky, 1925, as *Cervocerus novorossae*) but many more recently collected specimens have not been described in detail. The pedicles are longer than in *Bretzia*; this is usually considered a primitive character. The basic adult antler is a three-point pattern. The first branching occurs a short but variable distance from the burr. The anterior tine is smaller than the beam. The beam divides, usually into two subequal tines, but sometimes there is an additional tine or a small palm (Fig. 36D). The orientation of the antler in *Cervavitus* is not always clear. In a mounted specimen on display at AMNH, the antlers appear to be rotated outward from life position (Fig. 36A). In Zdansky's (1925) other examples the anterior tine is much more vertical.

The most significant differences between antlers of *Cervavitus* and *Bretzia* are these: the default pattern for the beam in *Cervavitus* is a subequal fork, only occasionally a small palm; the anterior tine forms a more acute

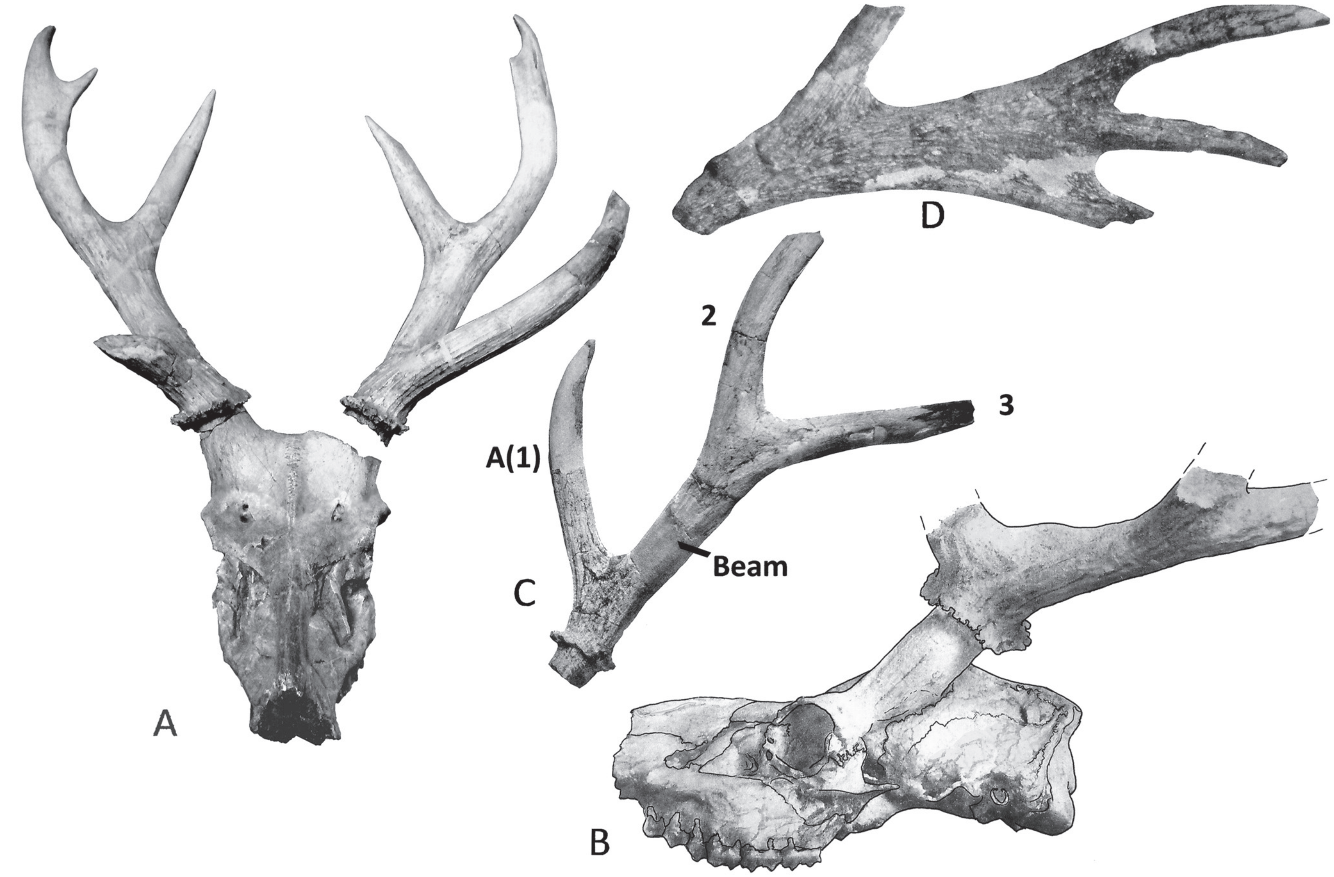

FIGURE 36. Skull and antlers of *Cervavitus shanxius*; A, frontal view, AMNH specimen; B, lateral view of skull with partial antler, C, antler, D, palmate antler. B, C, D, after Zdansky, 1925. Tines numbered to show interpretation of equivalence to tines in *Bretzia* (Fig. 28).

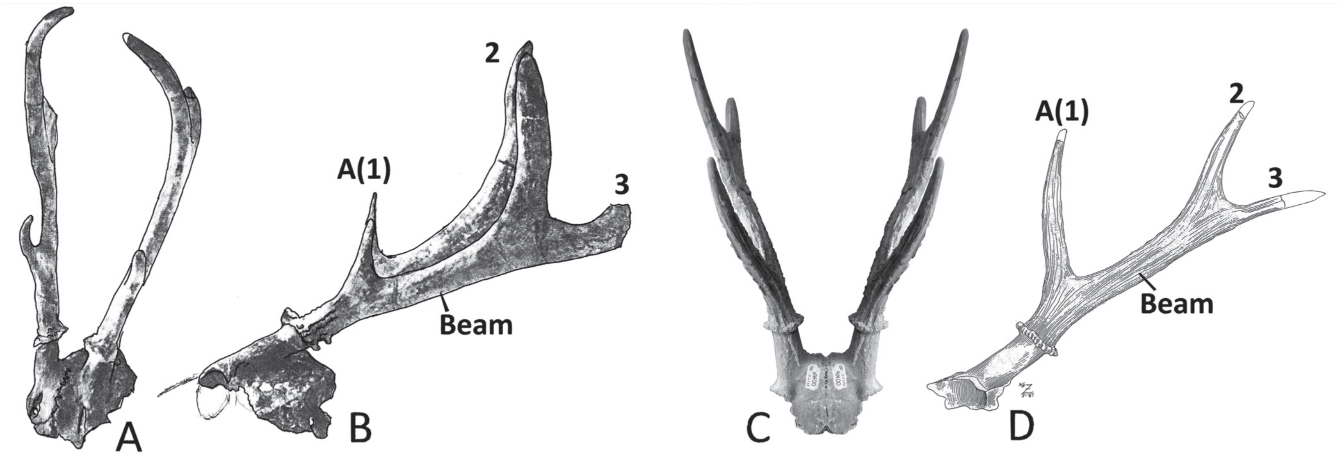

FIGURE 37. A-B, Skull and antlers of *Pavlodaria*, after Vislobokova, 1990. C-D, Partial skull and antlers of *Eocoileus gentryorum*. C, antlers and frontal, reconstructed from UF 90400, paratype antler and partial skull, anterior view; D, lateral view drawing from Webb, 2000. Tines numbered to show interpretation of equivalence to tines in *Bretzia* (Fig. 28).

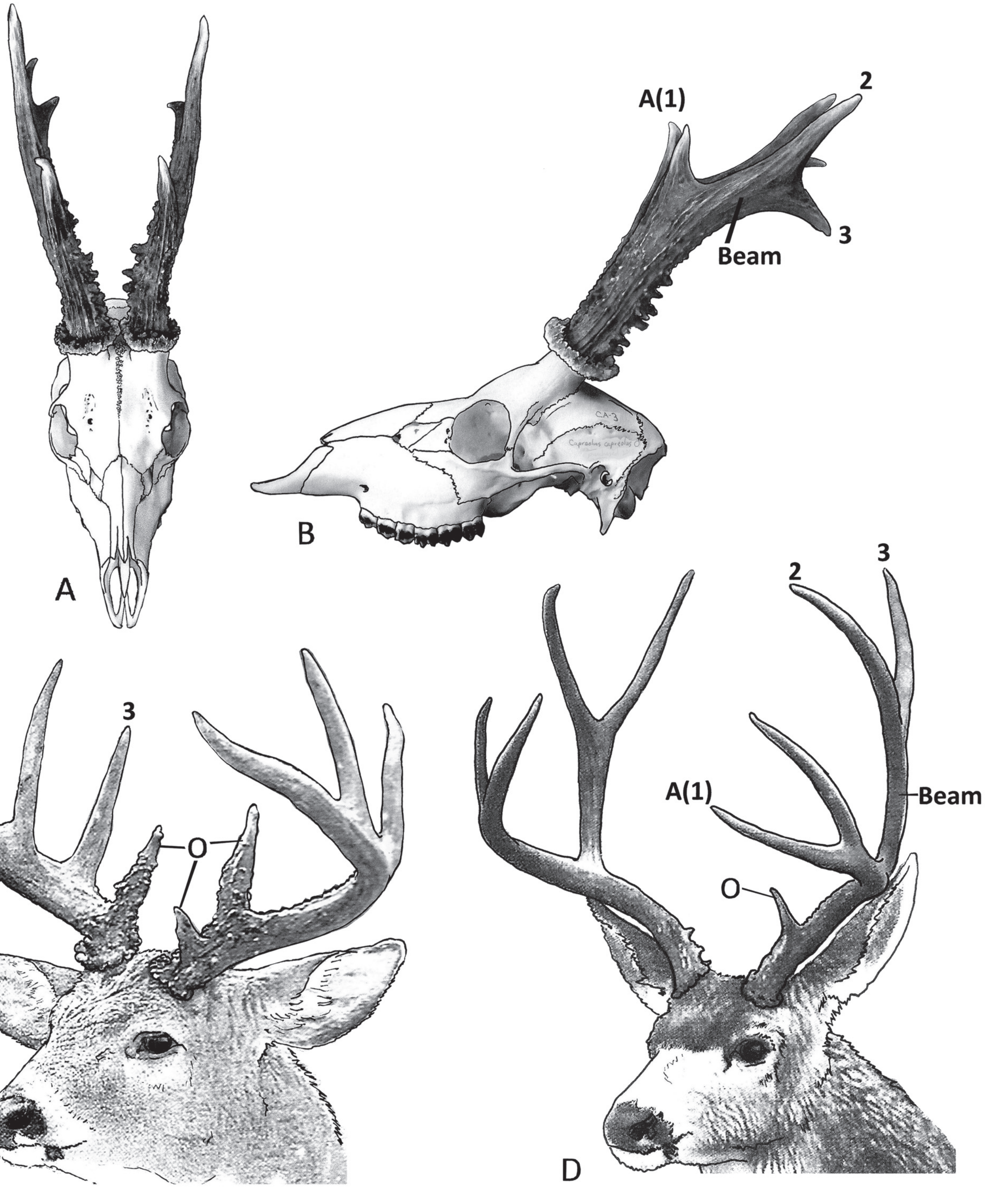

FIGURE 38. A-B, Skull and antlers of European roe deer *Capreolus capreolus,* A, frontal and B, left lateral views.. C, Head and antlers of *Odocoileus virginianus; D, O. hemionus*, C and D from photos of wild individuals. Tines numbered to show interpretation of equivalence to tines in *Bretzia* (Fig. 28). O indicates accessory tines (snags) characteristic to *Odocoileus*. Note variation, with two snags on the left antler in C and none on the right antler in D. The snags are usually larger in individuals of *O. virginianus* than in *O. hemionus.*

angle with the beam; the three tines of *Cervavitus* do not fall in a single plane; and the posterior-most tine (third tine) bends downward at the second fork.

Pavlodaria orlovi—The central Asian species *Pavlodaria orlovi* occupies a special place in cervid history as the oldest known rangiferine cervid; that is, the posterior choanae were apparently divided by the vomer (Vislobokova, 1980). It is said to be early Pliocene, suggesting near-contemporaneity with *Bretzia pseudalces*. The antlers of *Pavlodaria* (Fig. 37A-B) were of the three-point plan, held on pedicles which were similar in position and angles to *Eocoileus*, *Ozotoceros*, and *Blastoceros*, therefore held more vertically and closer together than in *Bretzia*. The burr is at a considerable angle to the axis of the shaft. The shaft is long and remains straight, in line with the beam and the posterior-most tine (third tine), similar in this form to *Bretzia* and *Eocoileus*. The anterior tine is relatively small and forms a 50-degree angle with the beam. The fairly long beam divides into two subequal tines; the second tine arises from the anterior/dorsal side of the beam and curves strongly inward toward the median. The third tine also curves inward. The distal parts of the antler tend to be flattened, blade-like, and sometimes are almost palmate. The antlers of *Pavlodaria* tend to be smooth, though they have a beaded burr. Vislobokova (1980) remarked that "in structure they remotely resemble the early stages in development of reindeer antlers" (compare with Fig. 39D). The resemblance is especially in that both start from a three-point form, are relatively smooth and flattened, and tine 2 tends to be larger than tine 3 and is inwardly curved.

Eocoileus gentryorum—*Eocoileus* (Webb, 2000) appears contemporaneously with both *Odocoileus* and *Bretzia*. Specimens of the skull show similarity in proportions and in the arrangement of the pedicles between *Eocoileus* and *Pavlodaria*. Its antlers (Fig. 37C-D) are of a three-point plan, relatively straight and with a posterior margin (through shaft, beam, and third tine) which is straight or only slightly curved, as in both *Pavlodaria* and *Bretzia*. Compared to *Pavlodaria*, the anterior tine in *Eocoileus* is much larger and the second tine is smaller. There is little significant flattening or palmation in the extant specimens, though one specimen (Webb, 2000, Fig. 4.6) shows an anomalous tripartite branch. The antlers of *Eocoileus* are very similar in size and form to those of *Ozotoceros* (Fig. 40A-B), in fact Webb (2000) simply stated "antlers as in *Ozotoceros*, widely separate bases, sloped posterodorsally 60 degrees above parietal surface, open, doubly dichotomous branching, moderate transverse flattening, and no helical rotation." The antlers tend to be smaller than *Bretzia*, much straighter and lack palmation.

Odocoileus hemionus and O. virginianus—Comparisons of antlers of *Bretzia* (and other genera) to *Odocoileus* are complicated by two main factors. First, the precise structure of the earliest specimens of *Odocoileus* sp. from the Miocene-Pliocene boundary deposits of Florida has not been studied, so the form of the earliest examples is not clear. Second, the two living *Odocoileus* species, mule and whitetail deer, have substantially different adult antler patterns (Fig. 38C-D), though both start from basically the same juvenile structure (Gustafson, 1985a). Both of these *Odocoileus* species share notable similarities to *Capreolus* in that the first major branching point is a considerable distance above the burr, and the posterior branch (the beam) bends rearward from the shaft. In addition this beam is often forked, especially in *O. hemionus*. The resemblance is masked by the peculiarities of the antlers of *Odocoileus*, namely that the shaft is not straight, but helically curved (Gustafson, 1985a); the beam is smaller than the anterior tine; and both *Odocoileus* species add a new structure, often called a snag, brow tine, or eye-guard , occupying part of the dorsal surface of the shaft. The snag seems to develop from hypertrophied pearling. Major pearling near the base of the antler is also a feature of *Capreolus,* which does not develop the snag. Bubenik (1990) does not consider this a true tine, but rather a secondary structure. It is much more common and usually larger in *O. virginianus* than in *O. hemionus*.

The two *Odocoileus* species differ in several ways. The first vertical tine (see Gustafson, 1985a, and above) appears to be the homologue to the beam of *Bretzia*, *Eocoileus*, and other three-tined deer, based on its position and the tendency to subdivide; regularly in *O. hemionus*, occasionally in *O. virginianus*. The fork in the first vertical tine and its considerable length are plesiomorphic features for *O. hemionus* and the shortness of this tine is derived in *O. virginianus*. The anterior tine develops a secondary dorsal tine in many examples of both species, as it does occasionally in *Bretzia* (Plate 4A). *Odocoileus virginianus* frequently develops a third, fourth or fifth vertical tine; *O. hemionus* rarely adds even the third. Despite these differences, the basic similarities listed above show a commonality not shared by other deer. Thus it appears that the oddly-shaped antlers of both species of *Odocoileus* developed from the same basic pattern, and that pattern was a three-point pattern similar to those of other very early Capreolinae. Genetic tests suggest that the modern species of *Odocoileus* diverged relatively recently (Duarte et al., 2008; Fig. 49).

Capreolus capreolus and C. pygargus—Two species of *Capreolus* are generally recognized (Groves and Grubb, 2011), the European roe (*C. capreolus*) and the Siberian roe deer (*C. pygargus*), which differ in size and details of the antler form. The roe deer lineage is old and has been fairly well-established, beginning perhaps with late Miocene *Procapreolus* (Lister et al., 1998; Valli, 2010). The antler characters of the European roe (Fig. 38A, B) are distinctive, starting with a long straight shaft. At the

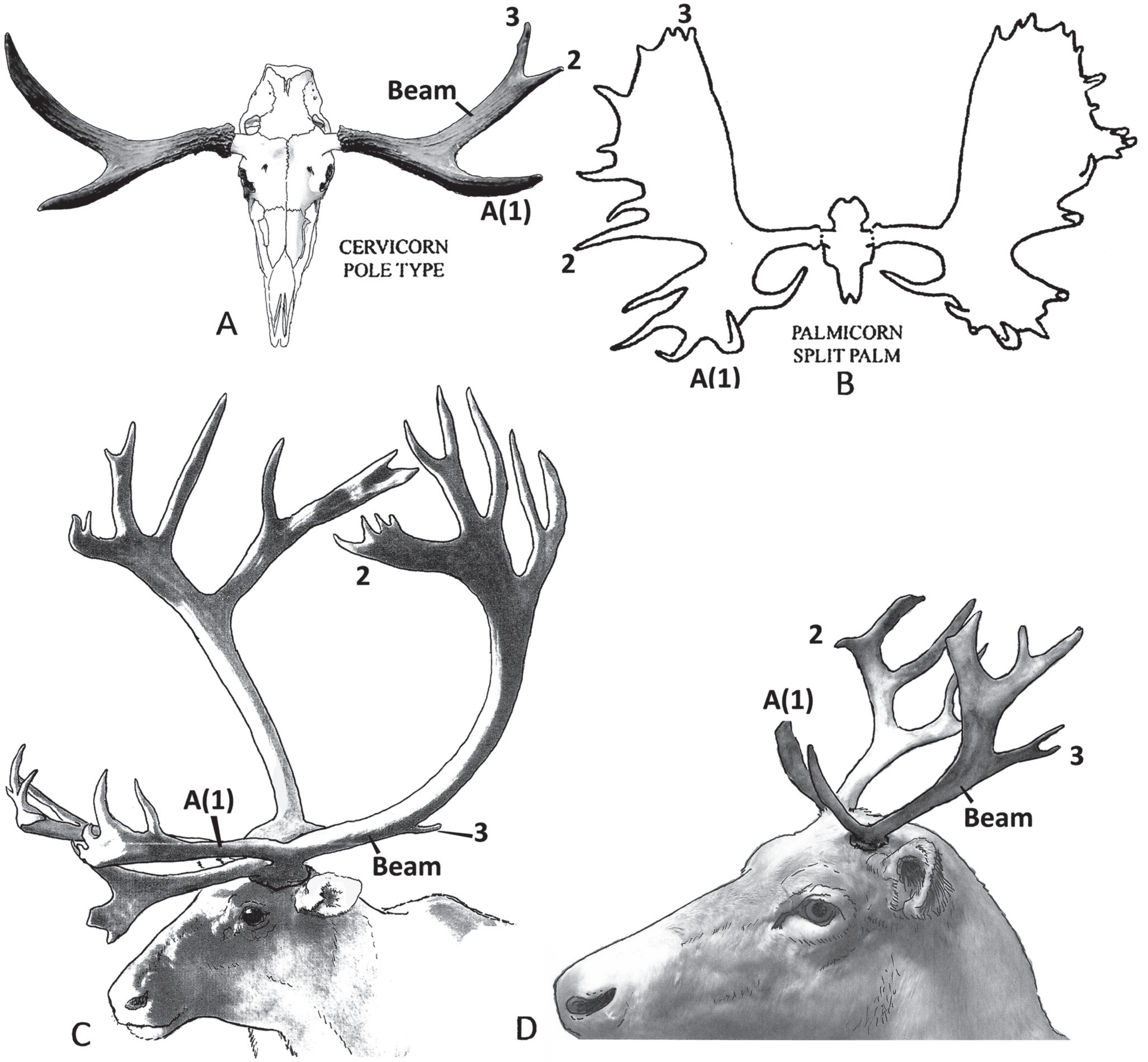

FIGURE 39. A, Adolescent European *Alces alces* with unpalmated antlers, 2- or 3-point pattern; B, mature antler in British Columbia moose, *Alces americana*, from Child et al., 2010. C-D, Head and antlers of caribou, *Rangifer tarandus, C*, male, from photo; D, female, specimen at Philadelphia Academy of Sciences. Tines numbered to show interpretation of equivalence to tines in *Bretzia* (Fig. 28).

first branching the anterior tine is short, the beam angles back, and frequently forks a second time, so that most mature adults have three tines. Variants may have two to four tines. The anterior tine rarely approaches the length of the posterior tine or tines. The pedicles are close together and parallel and the burrs of the antlers are large, often in contact with each other. Some of these features are seen in *Procapreolus*, particularly the long straight shaft and small anterior tine. *Capreolus pygargus* is larger than *C. capreolus*, with relatively longer antlers; the pedicles are not closely appressed, pearling is relatively less pronounced and the posterior tine from the beam tends to bend strongly toward the midline of the skull. In these features *C. pygargus* is more similar to early Pliocene *Procapreolus moldavicus* from Ukraine than to *C. capreolus* (Croitor and Stefaniak, 2009).

Both species of *Capreolus* share the basic, presumably primitive (plesiomorphic for Capreolinae) three-point shape with *Bretzia pseudalces,* though it is masked in *Bretzia* by palmation. Other shared features include a substantial shaft, a beam which is generally thicker at the base than is the anterior tine. Otherwise, antler

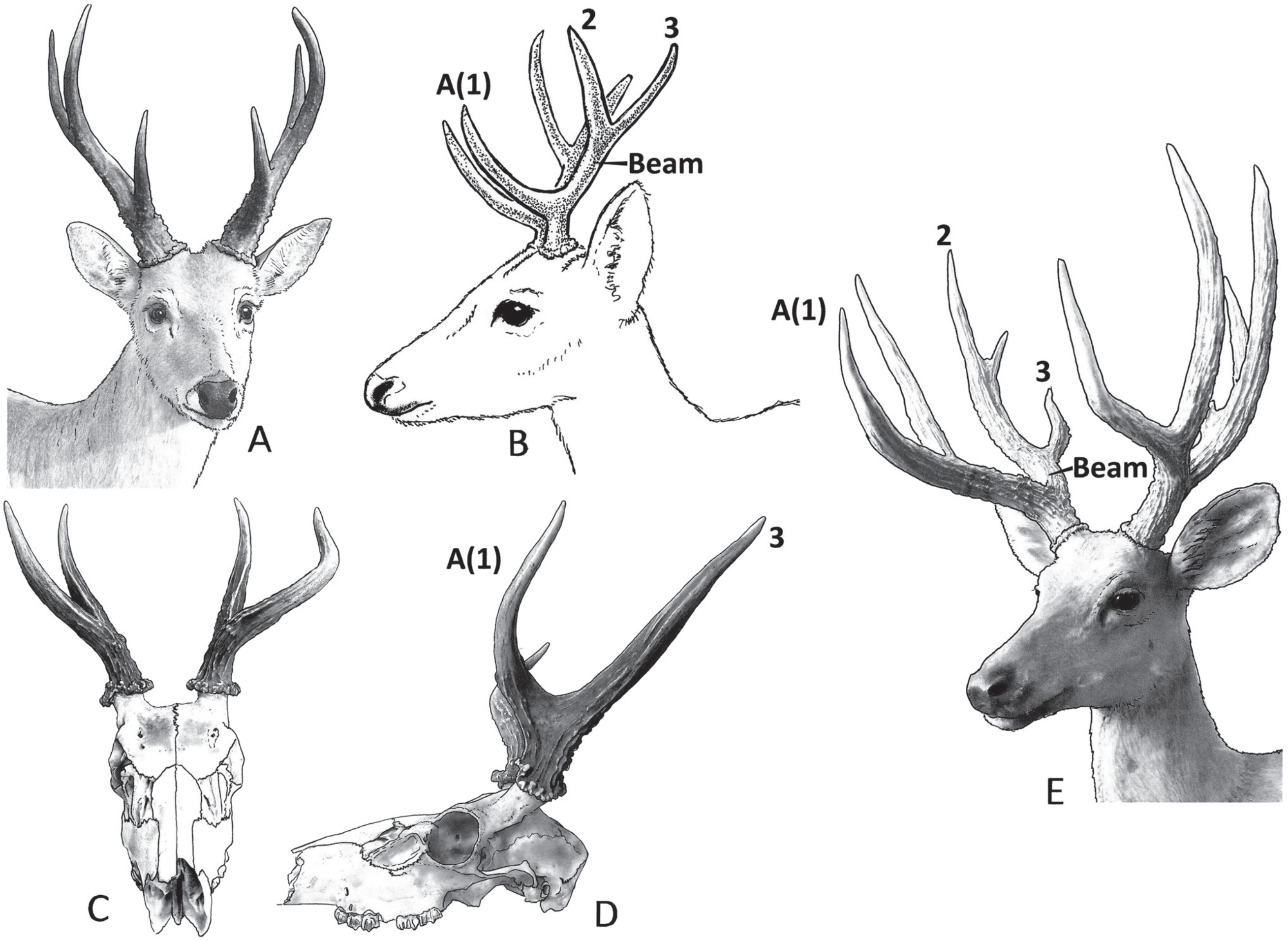

FIGURE 40. A-B, Head and antlers of *Ozotoceros*, from photos of wild individuals. C-D, Skull and antlers of *Hippocamelus antisensis*, the taruca, AMNH specimen. E, Head and antlers of *Blastocerus dichotomus*, the marsh deer. Specimen at the Vienna Museum of Natural History. Tines numbered to show interpretation of equivalence to tines in *Bretzia* (Fig. 28).

morphology in *Bretzia* differs from that of *Capreolus* by the posture of the pedicles, the somewhat shorter shaft, the long anterior tine, the straight posterior margin of the beam and palm, usually stronger curvature, usual adult palmation, and overall larger size.

Alces americana and Alces alces—There is a considerable size difference between *Alces* and *Bretzia*, *Alces* being larger to much larger. *Alces* antlers are held close to a true 90 degrees to central axis, so the shafts are directly opposed; *Bretzia* antlers angle back at 45 degrees or less. Both tend to have one large sometimes forked anterior tine, though sometimes there are multiple tines or a palm (Fig. 39B) in *Alces*. Both have gap between burr and anterior tine, sometimes quite wide, though the minimum gap is smaller in *Bretzia*. The anterior tine in *Alces* is sometimes either absent or melded with a palm. The posterior edge of the palm sweeps backwards in *Alces* (as do the posterior tines in *Capreolus*), from which I suggest that the back of the palm probably developed from a posterior distal tine (third tine) which bent backwards. In *Bretzia* the posterior edge tends to be straight or only slightly curved. I suggest that this edge in *Bretzia* developed from a straight single posterior (third) tine which had a forward branch (tine 2), as in *Eocoileus*. Adolescent antlers of *Alces* can be very similar to those of adolescent *Bretzia* (compare Fig. 39A to Plate 8A). Variants among adult antlers of *Alces* can be very similar in shape to adult antlers of *Bretzia*. This superficial similarity is what gave *Bretzia pseudalce*s its trivial name. That said, it is apparent that the antlers of *Bretzia* were held in a position usually very different from those of *Alces*.

Rangifer tarandus—The circumpolar genus *Rangifer* is classified as a single species, *R. tarandus,* despite much variation among populations (see Groves and Grubb, 2011). This is the only cervid in which both males and females have antlers on a regular basis (Fig. 39C-D). The large complex antlers of the males have a number of specializations which obscure the pattern from which they developed. The ancestral pattern appears to have been a three-point form not too distant from antlers of *Pavlodaria* and *Eocoileus* (Fig. 37). This basic pattern can be seen in juvenile males and in the antlers of females, such as the example in Fig. 39D; it was alluded to by Vislobokova (1980) in her discussion of *Pavlodaria*. This female antler has a very short shaft, a branching into an anterior tine and a larger posterior beam, and some distance up, the beam divides into a second large vertical and incurved tine (which subdivides), and a much smaller third or posterior tine. The posterior branch, much smaller, is in the lower middle of the sweeping curve, and it is my interpretation that this, and not a branch further up is the homologue of the third tine in other genera. If so it is much reduced relative to the second tine, which makes up most of the distal antler. This interpretation is compatible with that of Geist (1998, Fig. 12-2). In mature males the antlers may be huge, and they usually add an accessory "forehead tine" which may develop on only one or on both sides, branching from the shaft between the burr and the anterior tine. This accessory tine runs forward not far above the animal's muzzle and is palmate at the end. The anterior tine (which is probably homologous with the anterior tine of other rangiferines) is directed forward and is usually palmate.

Ozotoceros bezoarticus—The antlers of *Ozotoceros* (Fig. 40A, B) have the distinction of being the closest approach among living Rangiferini to the late Miocene deer of the three-point antler plan. *Ozotoceros* survives today in limited areas in South America. As with other rangiferine deer (except *Alces*), the antlers are much more upright than in *Bretzia*. *Ozotoceros* is about the size of European roe deer but generally has larger antlers, with a large anterior tine, long beam, and subequal second and third tines. The beam bends to the posterior a little at the first branching, apparently more than in *Eocoileus* or *Bretzia*. There are seldom any accessory tines or palmation.

Blastocerus dichotomus—The marsh deer *Blastocerus* is the largest of the South American deer (Fig. 40E). Its antlers have considerable resemblance to those of *Odocoileus hemionus*, in that the beam and anterior tine are of similar size and each is commonly forked. *Blastoceros* lacks the additional snag which is common in *Odocoileus*, and the beam or posterior branch in the marsh deer frequently has multiple tines growing from its posterior side. Carette (1922) illustrates variations in which either the anterior tine or the beam is larger. The anterior tine does not form as smooth a helical curve with the shaft as in *Odocoileus*. Some examples have the anterior tine branching from the straight shaft and beam at nearly a right angle, as in frequent in *Bretzia*. I have not seen any examples of *Blastocerus* with palmation.

Hippocamelus antisensis and H. bisulcus—The genus *Hippocamelus* has two nominal species which may not be closely related (Duarte et al., 2006). These are the taruca, *H. antisensis* (Fig. 40C-D), and the heuemul, *H. bisulcus,* both of which occupy portions of the Andes Mountains. Both are endangered and poorly understood. They appear to have been forced to survive in perhaps marginal habitat in mountainous terrain. Both species typically have antlers with only two tines, though in the past, the huemul, at least, has produced antlers with as many as five tines (Flueck and Smith-Flueck, 2011) and some populations still produce antlers with three or four tines in as many as 40% of the males. When an additional tine forms in the huemul, it appears on the anterior face of the beam, in much the same position as the equivalent tine in *Ozotoceros* (Carrette, 1922). These two species both have upright antlers, a short to moderate shaft, a large anterior tine and a beam which may support additional tines. No palmation has been reported in either taruca or huemul.

POSTCRANIAL SKELETON

The preserved postcranial skeleton of *Bretzia pseudalces* is made up of a series of referred isolated bones. This presents some obvious problems for the taxonomist, most importantly, which specimens to include in the species concept. I only include postcranial specimens here which show adequate cervid characteristics. Some badly-eroded specimens which may be *Bretzia* have been excluded. Morejohn and Dailey (2004, p. 46) selected several specimens, mostly postcranial, from the LACM Ringold collections for which they suggested a close relationship with *Pavlodaria*. By implication they would not be included in *B. pseudalces*. I conclude in this paper that there is no evidence of *Pavlodaria* in the White Bluffs local fauna.

Vertebrae—Only three vertebrae can be listed here, an axis, another cervical, and a posterior thoracic. The thoracic vertebra is badly eroded and one cervical (possibly C3) preserves only the centrum. The axis vertebra however is largely complete except for dorsal and lateral processes (Fig. 41). Size is as a male *O. hemionus* in length, though it appears less wide in the centrum. The anterior articular surfaces are well-preserved. The dens is a broad spout-shaped process as in other cervids. The dorsolateral processes of the dens do not extend as far dorsally as they do in *Odocoileus*. The articular surface forms a broad flange, though not as broad as in *Odocoileus*, and a distinct ventral notch in this flange which is prominent in *Odocoileus* is only slightly expressed in the *Bretzia* vertebra. Total length = 81 mm; anterior width = 47 mm.

Scapula—One scapula fragment (Plate 9A) is assigned to *Bretzia pseudalces*. It preserves the glenoid cavity, a few centimeters of both borders and the base of the scap-

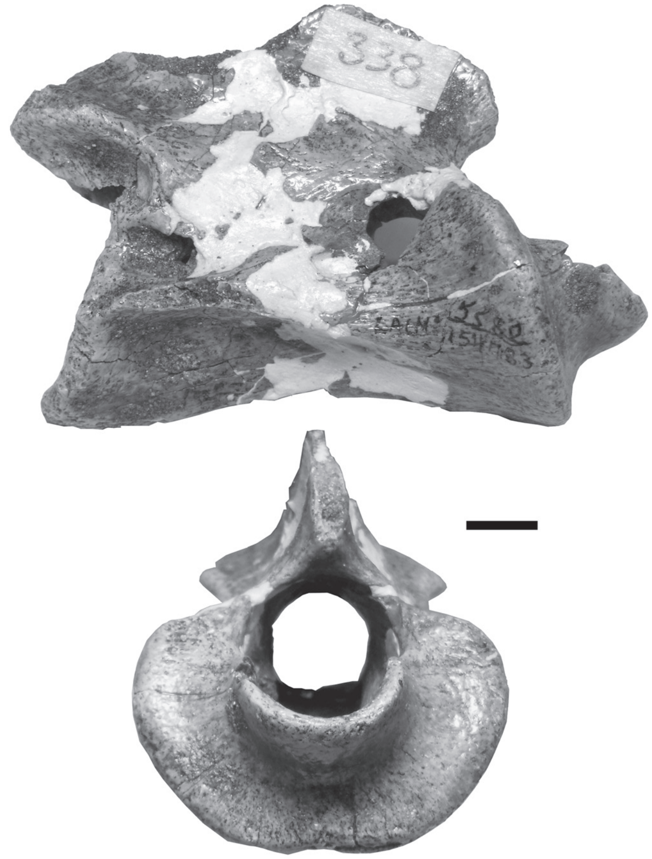

FIGURE 41.-Axis vertebra, LACM154783. Top, right lateral view; bottom, anterior view. Scale bar equals 1 cm.

ular spine. It is about the size of the scapula of a male *O. hemionus*, although the neck just above the glenoid articulation is somewhat thicker (width = 29 mm) and the overall impression is of greater bone mass. The glenoid articulation measures 40 mm in the anteroposterior dimension. The scapular tuberosity on the anterolateral margin of the glenoid fossa is more robust than that on the mule deer. The coracoid process is broken off. The infra-articular tuberosity is rough and well-marked but not raised above the posterior margin.

Humerus—One distal right humerus is assigned to *Bretzia pseudalces* (Plate9B-F). It is the size of the humerus of a small female *O. hemionus*, and has some damage from weathering. It retains the distal point of the deltoid tuberosity near the break. The lateral epicondylar crest is relatively narrow and high. The proximal end of the olecranon fossa is not well demarcated, In *O. hemionus* this depression tends to have a proximal rim, but in the *Bretzia* specimen it merges smoothly with the posterior side of the shaft. The carina on the articular surface is less distinct, less prominent in the *Bretzia* humerus, though this may largely be due to abrasive damage. In other morphology this specimen closely resembles *Odocoileus hemionus*. Width of shaft at narrowest point = 16.5 mm; distal width = 35.5 mm.

Radius—Two fragments of the radius of *Bretzia* are available, one proximal and one distal (Plate 9I-M). The proximal fragment is abraded around the margins of the broadly oval articular surface. It came from an individual about the same size as for the humerus (small female *O. hemionus*) and would articulate smoothly with it except that the radius is from the left side. Proximal width = 32.7 mm minimum; width of shaft at break = 25.1 mm. It articulates well with an appropriate-sized female *O. hemionus* humerus and ulna. The notch and adjacent processes for the articulation of the ulna are less pronounced on the *Bretzia* radius than on those of *O. hemionus*. Compared to a radius of *O. hemionus* of the same proximal width, the shaft of the *Bretzia* radius is slightly wider and does not flare out to the lateral tuberosity as rapidly.

The distal radius fragment, also from the left side, is from a slightly larger individual, though still well within the size range of female *O. hemionus*. On the anterior surface the groove for the ligaments for the extensor muscles forms a flattened area with raised borders. The distal articular surface is complex, with three major articular areas separated by ridges; the medial scaphoid articulation, a central and lateral lunar articulation which extends diagonally across most of the distal end, and in the posterolateral corner, the articulations for the distal ulna and triquetrum. These articulations are essentially similar to those of *Odocoileus*. The shaft of the radius near the distal end, like that near the proximal end, appears to have been slightly broader relative to the distal articular width than in *Odocoileus*. Distal width = 34 mm.

Ulna—One proximal fragment of an ulna in available (Plate 9G-H). The olecranon process was deep as on *Odocoileus* and other closely related cervids, not shallow as in *Cervus* (Morejohn and Dailey, 2004). Size is well within the range of *O. hemionus*. Height = 40 mm, width = 21 mm.

Metacarpals—Two complete cervid fused metacarpals III and IV are present in the White Bluffs collections and are assigned to *Bretzia pseudalces* (Fig. 42, 43, Plate 10, Table 6). Lateral metacarpals (II and V) have not been identified in these collections. In length, proximal and distal width, both metacarpals III-IV fall well within the range of variation of my sample of *Odocoileus hemionus*. In overall proportions they are about 15% to 20% thicker (minimum shaft width) than an *O. hemionus* metacarpal with the same distal width and similar length. The metacarpals of *Bretzia* do not flare from a narrow shaft to the wider articular surfaces as much as do the *O. hemionus* specimens.

The proximal ends show several significant characteristics. Most important in a taxonomic sense is a lack of any evidence for the presence or retention of the prox-

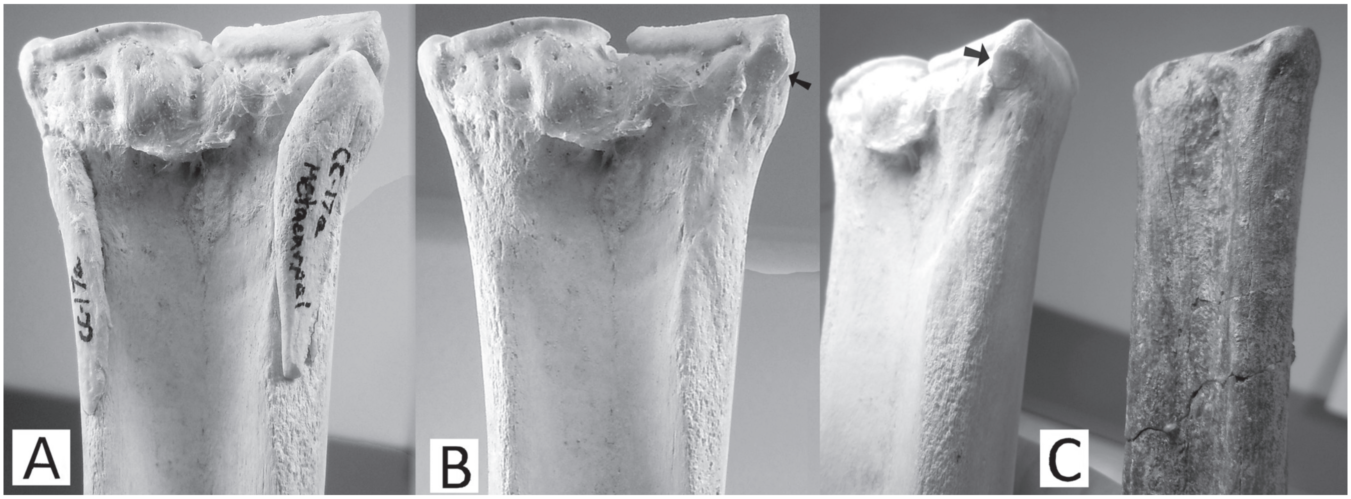

FIGURE 42. Proximal right metacarpals of *Cervus* and *Bretzia,* posterior view. A. Proximal metacarpals of a plesiometacarpal deer, *Cervus canadensis,* with fused metacarpals III and IV, and proximal remnants of lateral metacarpals II and V in life position; B. Same without the proximal metacarpal remnants, showing the areas of attachment of the lateral remnants and the articular facet (arrows) for metacarpal V; C, comparison of metacarpals of *Cervus* (left) and *Bretzia* (right), showing condition of upper right posterior side. The lack of an articular facet and flattened area for metacarpal V in *Bretzia* is typical of telemetacarpal deer.

imal ends of metacarpals II and V. In the modern plesiometacarpal cervine *Cervus canadensis* evidence in two forms is present of the existence of reduced remnants of metacarpals II and V (Fig. 42). There is a roughened and flattened area on the posteromedial side of metacarpal III for the proximal remnant of metacarpal II, and a similar but larger roughened facet on the posterolateral corner of metacarpal IV for the remnant of metacarpal V. Second, the remnant of metacarpal V articulates with the posterolateral corner of metacarpal IV by way of a small but distinct articular facet. This facet is on the underside of a slight overhang at the posterolateral corner of the proximal articular surface for the unciform in *C. canadensis*. Without similar evidence for the articulation of lateral metacarpals in the White Bluffs specimens, it is reasonable to infer that this animal was telemetacarpaline (lacking the proximal end of the lateral metacarpals), hence also a member of the Capreolinae.

The proximal articular surface also shows significant features (Fig. 43). Morejohn and Dailey (2004) showed that the shape of this surface differs between *Cervus* and the capreoline deer, in that the anterior outline in *Cervus* is more semicircular and this outline in *Odocoileus* and its close relatives (e.g., *Mazama americana*) is flattened on the anterolateral face, giving it a more triangular outline. Some care needs to be taken with these features, as detailed shapes of intercarpal articulation facets are quite variable. In the two examples of *Bretzia* the surface is dominated, as is usual in cervids, by the articulation facets for the fused trapezoid/magnum bone and the somewhat smaller unciform. The anterior outline is somewhat intermediate, not as rounded as *Cervus* but not as triangular as *Odocoileus* or *Mazama.* The posterolateral corner of the unciform facet does not have the overhanging projection (over the metacarpal V remnant) seen in *Cervus* (Fig. 43B). The central area between the two main articular facets has an opening by which blood vessels and nerves pass into the central axis of the bone. In *Cervus* this is usually a single, fairly large, vertically elongated opening, widest anteriorly, rather unlike *Odocoileus* and *Mazama*, in which a bony shelf frequently closes it off, with distinct perforations (often two to four) for the passages. The two examples assigned to *Bretzia* have an opening more similar to that of *Cervus*, though more pinched in appearance. More distinctively, in the *Bretzia* specimens the gap which usually separates the posterior surfaces of the trapezium/magnum facet from the unciform facet is closed (Fig. 43 E-F). I have not seen another cervid in which this gap is not distinctly open.

At the distal end, the intertrochlear notch was not completely fused, much as in modern *Odocoileus*, *Hippocamelus* and *Cervus* but unlike *Rangifer* and *Alces*, in which this is completely fused (Morejohn and Dailey, 2004). The shape of the trochlear surfaces resembles that of *Odocoileus* except that the outer trochlear articular surfaces are not as prominent in *Bretzia. O*n the posterior end of the trochlear surfaces (i.e., on the palmar surface) the articulation ends in distinct pits in *Odocoileus*, which presumably allow more digital flexion. Those pits are small or absent in *Bretzia*, which may not have been able to flex its digits as far as *Odocoileus* can.

Pelvis—One partial pelvis is assigned to *B. pseudalces* (Plate 11A-B). The specimen preserves most of the acetabulum and part of the ilium and ischium, but lacks

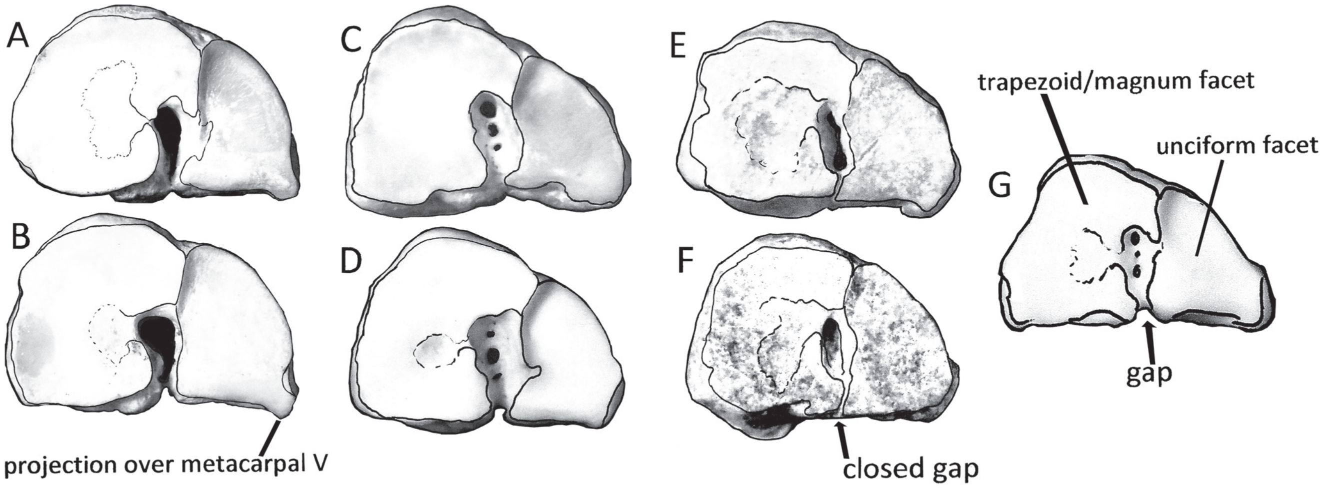

FIGURE 43. Proximal surface, fused metacarpals III-IV, A, B. *Cervus canadensis*, C, D. *Odocoileus hemionus*, E,F. *Bretzia pseudalces*, G. *Mazama americana*, all drawn to the same width. Actual widths are, A. 52mm, B. 45mm, C. 34mm, D. 28mm, E. 31mm, F. 31mm, G. 16mm.

the pubis. Fusion of the bones is complete. The individual was the size of a large male *O. hemionus*. The articular surface for attachment of the ilium to the sacrum is well-marked. In the studied examples of *O. hemionus* the sacral articulation extends forward and down to the anterior margin of the ilium, but on the *Bretzia* exemplar there is a ventral margin of about 16 mm unscarred by that articulation. The flattened body of the ilium is considerably broader than in any of the examples of *O. hemionus*. The lunate surface of the acetabulum is well-preserved, with a thickened lip on the posterior rim but not the anterior or lateral rims. A deep depression on the ventral ilium just anterior to the acetabulum is much shallower on the *Bretzia* pelvis than on the mule deer pelvis. On *Odocoileus* and *Mazama* this depression is bounded by two equal strong ridges which brace the acetabulum against the ilium, but on the *Bretzia* example the lateral of the two is much smaller and is bifurcated. Proportions of the ischium appear to be similar to *Odocoileus*.

Femur—The collections hold one proximal and two distal femora assigned to *Bretzia pseudalces* (Plate 11C-J). The proximal specimen is missing most of the greater trochanter. It generally resembles the same bone in *Odocoileus hemionus*. Morejohn and Dailey (2004) identified features which distinguish the proximal femur of *Odocoileus* from *Cervus*, *Rangifer*, and *Alces*, particularly the angle between the femoral head and the greater trochanter as seen from the posterior side, and between the femoral head and the lesser trochanter as seen from the proximal end. In each of these features the proximal femur of *Bretzia* resembles *Odocoileus* (and also *Mazama americana*) and does not match these other genera.

The distal femoral fragments are somewhat abraded, but adequately preserved. I find no features which distinguish these fossils from *Odocoileus*. Distal width = 47 mm and 45 mm.

Tibia—The tibia is relatively well-represented, with three complete, one partial proximal and seven partial distal examples (Plate 12, Table 6).The length of each of the complete examples is well within the range in length of this bone in the studied sample of *Odocoileus hemionus*, particularly of the females. All three are shorter than the male examples. Minimum transverse diameter of the shaft is also within the range of variation of *O. hemionus*. The proximal condyles and intercondylar eminence are much as in other cervids. The anterolateral muscular sulcus is shallower than in *Odocoileus*, *Mazama* and *Cervus*, and not as sharp-edged. The tibial tuberosity is not distinctive. In cervids the proximal epiphysis of the tibia does not fuse or ossify thoroughly at its anterodistal surface, leaving an area of weak bone where the epiphysis attaches to the anterior crest, even in mature animals. *Bretzia* is typical of cervids in this feature. The anterior tibial crest in *Odocoileus, Mazama*, and *Cervus*, in outline, often have a distinct angle, or break in slope as the distal portion of this crest descends to the level of the shaft. The tibial crest in *Bretzia* descends smoothly, with no abrupt increase in slope (Plate 12E).

On the posterior side of the proximal tibia, there is a moderately open, V-shaped popliteal notch in the *Bretzia* tibiae, partly closed by a shelf-like popliteal tuberosity on the medial side. This tuberosity, apparently for the attachment of the cruciate ligaments which reinforce the knee joint, is larger in *Odocoileus*, and in *Mazama* it is much larger, so that it completely closes off the popli-

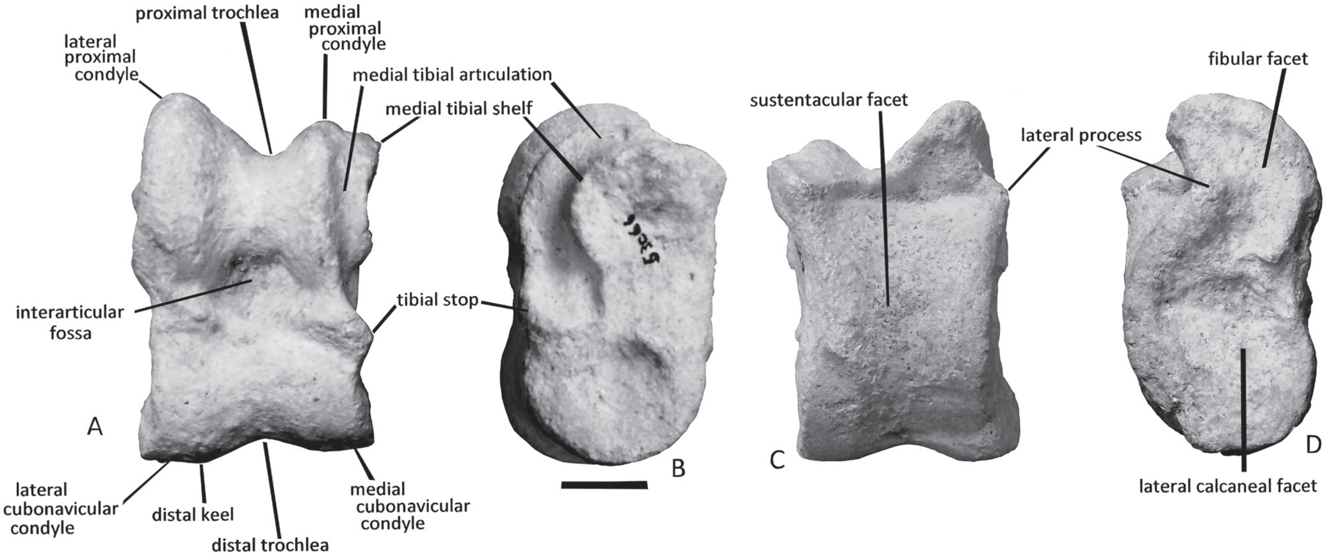

FIGURE 44. *Bretzia pseudalces* astragalus. UWBM 53066. A. anterior view, B. medial view, C. posterior view, D. lateral view. Scale bar equals 1 cm.

teal notch. In *Cervus* this tuberosity is a strong isolated prominence in the center of the popliteal notch, looking very different from that structure in the other genera. On the posterior face of the tibia the intermuscular ridges are prominent.

The distal end of the tibia includes the grooves for the articulation of the proximal astragalus. The best-preserved *Brertzia* astragalus (from the right side) fits neatly into the distal tibial articulation of the four right distal tibias and rotates correctly, while an equivalent-length example of the astragalus of *O. hemionus* is too wide to fit properly. The articular portion of the distal tibia does not increase in width from the shaft as abruptly in *Bretzia* as in *Odocoileus*, in part because the fibular articulations are not as prominent, and in part because the astragalus and its proximal condyles are not as wide. The groove on the posteromedial side of the distal tibia for the flexor digitalis tendon faces somewhat more to the posterior than in *Odocoileus*, *Mazama*, and *Cervus.* In seven of the eight examples of *Bretzia* which preserve both, the anteromedial distal process is equal in length to or longer than the mesial malleolus, but in *Odocoileus* the mesial malleolus is consistently the longer.

Astragalus—Five examples of the astragalus are available, but only one is well-preserved (Fig. 44). The others show substantial wear from a period of being transported as sedimentary particles. The astragalus has a double-trochlear ("double pulley") shape typical of cervids and artiodactyls in general. The fossil examples are narrower than an astragalus of the same length of *Odocoileus*. To some extent this appearance seems to be caused by the erosion of the edges and processes of the fossils. However, the one well-preserved fossil shows that the narrowness of the proximal end is real, the trochlear groove is narrower than in *Odocoileus* and the medial and lateral condyles are closer together than in *O. hemionus*. The proximal end of the *Bretzia* astragalus is about as wide as in a similar-length astragalus of *Odocoileus*, largely because the medial tibial shelf – the medial extension of the articulation with the tibia-is more prominent than in *O. hemionus*. The medial condyle in *Bretzia* is also less prominent, and the posterior end of the medial tibial articulation extends posteriorly past the end of that condyle. In this feature the *Bretzia* astragalus is much like the astragalus of *Mazama*, in which this extension is very obvious. *Odocoileus* also has a posterior extension of the medial tibial articulation, though less pronounced, but *Cervus canadensis* does not have this feature. In *Alces* the medial tibial articulation extends beyond the medial condyle to form a prominent and substantial flange. The tibial stop, a process which prevents flexion of the astragalus on the tibia at a certain point, is closer to the distal end of the astragalus than in *O. hemionus*. The interarticular fossa is large, as in *Odocoileus*, and larger relatively than in *Cervus*. The lateral process on the proximal corner of the sustentacular facet is prominent, much like that in *Odocoileus* and *Mazama*, but not like the relatively small lateral process in *C. canadensis*. The distal (cubonavicular) articulation is much like that of *Odocoileus*, except that the distal keel on the lateral condyle is closer to the lateral side, and the trochlea is a little shallower. The proximal edge of the sustentacular facet is straight and at a right angle to the long axis of the bone, as in *Odocoileus lucasi* (Morejohn and Dailey,

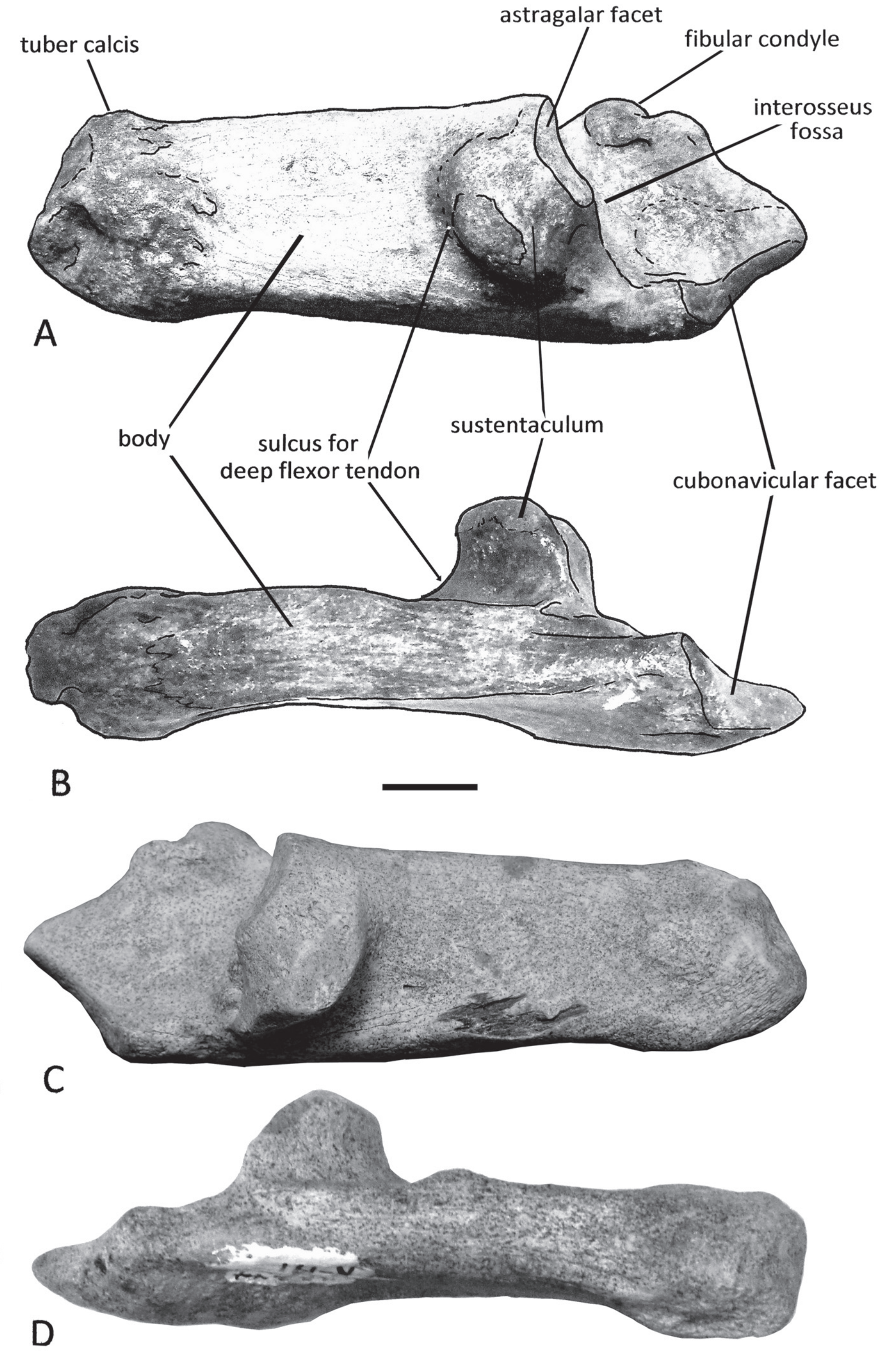

FIGURE 45. *Bretzia pseudalces* calcanea. A, B, WHC 0002, right calcaneum, medial (A) and posterior (B) views; C, D, SDSM 22244, left calcaneum, medial (C) and posterior (D) views. Scale bar equals 1 cm.

2004) and in *Mazama americana*. Overall, the astragalus of *Bretzia pseudalces* shows a number of features which align it more closely to rangiferines than to cervines. Proximal width = 29 mm; lateral length = 44.8 mm.

Calcaneum—Two complete and two partial calcanea are in the collections from the White Bluffs. Size of these specimens falls within the range of my sample of *Odocoileus hemionus*; the two complete calcanea are slightly smaller than male examples but slightly larger than several female examples of the modern species. Overall proportions (Fig. 45, Plate 13D-E) are similar to other medium-to-small North American cervids (*Odocoileus* and *Mazama*) in relative thickness of the body, relative size of the sustentaculum, and less pronounced fibular condyles. The body is less arched (i.e., convex on the dorsal margin and concave on the ventral margin) than in most examples of *Odocoileus*. The dorsal and ventral margins of the body in *Bretzia* are almost parallel but in *Odocoileus* they taper much more posteriorly. The sulcus for the deep flexor tendon is well-developed, less than in *Odocoileus*, but more as in *Cervus* in which the posterior face of the sustentaculum frequently forms an obtuse angle with the medial side of the body (Morejohn and Dailey, 2004). The medial end of the sustentaculum is strongly convex, with a slightly flattened spot on the ventrolateral surface. This area in *Odocoileus* is usually concave with a median ridge. The lateral margins of the astragalar facet and of the sulcus for the deep flexor tendon on the sustentaculum are less sharp than in *Odocoileus*, or for any of the other cervids I observed. This may perhaps be partly attributed to postmortem abrasion of the bones. The astragalar facet is shaped much as in *Odocoileus*, but differs from that of *Cervus* in having (in common with *Odocoileus* and *Mazama*) an invagination into the central lower smooth surface of that facet. The fibular condyle, which has an S-shaped surface in most cervids, is narrower and slightly smaller than in *Odocoileus*. It is much more similar to that of *Odocoileus* than to *Cervus,* or to *Alces* in which the shape is quite different. There is a small shelf between the fibular condyle and the interosseus fossa in the *Bretzia* specimens, similar to that in *Odocoileus* but much smaller than that in *Cervus*, in which a prominent overhang develops (Morejohn and Dailey, 2004, their Fig. 18). The cubonavicular facet faces more to the distal face of the calcaneum in *Bretzia*, so

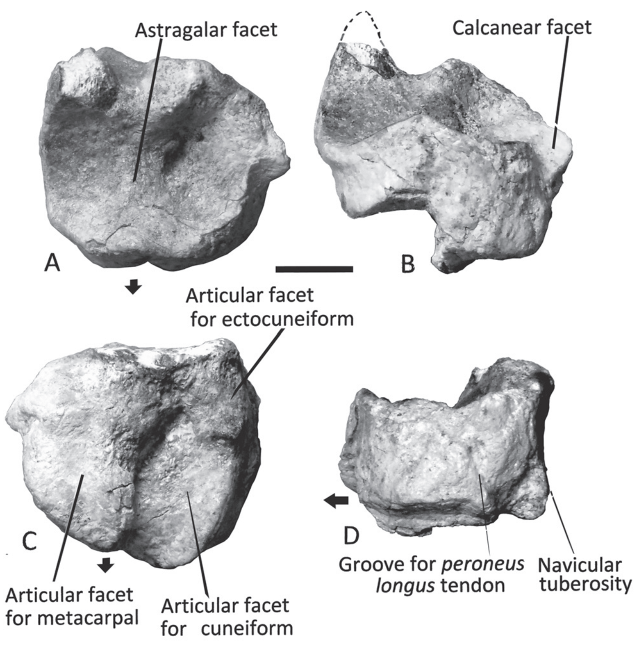

FIGURE 46. *Bretzia pseudalces*, SDSM 22245, L cubonavicular bone. A. proximal view, B. anterior view, C. distal view. D. lateral view. Arrows indicate anterior direction. Scale bar equals 1 cm.

it is less visible from the medial view than this facet in *Odocoileus*, *Cervus* or *Alces*. In this it closely resemble the calcaneum of *Mazama*. The triangular distal projection of the calcaneum is similar in *Mazama*, *Bretzia*, and *Odocoileus*. Overall, despite the disparity in size, the calcaneum of *Bretzia* resembles that of *Mazama* more than it resembles the other North American cervids.

Cubonavicular—Only one cubonavicular (SDSM 22245, left side) can be assigned to *Bretzia pseudalces* (Fig. 46). The surface of the bone shows signs of weathering which has obscured some of the articular surfaces. Nevertheless, the bone is well-fused and typical of cervids. Size is similar to a male example of *O. hemionus*. Shapes of the margins of articular facets and grooves for passage of ligaments, nerves, and blood vessels are all highly variable in the tarsal bones, including the cubonavicular. The calcanear facet appears to be relatively small on the Ringold fossil cubonavicular compared to *Odocoileus*, and much smaller when compared to *Cervus*. The front rim of the astragalar facet tends to have two peaks in *Odocoileus* and *Cervus*, one central in line with the astragalar trochlea and a second at the lateral corner. There is only the central one in the Ringold fossil, though there is damage to the part of the bone where the second peak would be (Fig. 46A). Morejohn and Dailey (2004) pointed out two features of the cubonavicular which may differentiate rangiferines and cervines. A groove for the peroneus longus tendon occurs on the lateral side below the calcanear facet. They observed that in *Odocoileus lucasi* and other *Odocoileus*, this groove is deep and cuts across the lower end of the calcaneal facet, whereas in *Cervus* it is shallow and terminates at the level of the facet. The cubonavicular assigned to *Bretzia* has a shallow peroneal groove. In the studied sample of *O. hemionus* I find examples with both conditions and intermediates, so I would not consider this distinction reliable. They also point out that the distal end of the navicular tuberosity in rangiferines extends distal to the posterior edge of the articular facet for the ectocuneiform; it is not so in cervines. In a sample of *O. hemionus* (n = 11), 10 had the suggested rangiferine condition and one had the condition more similar to *Cervus*. The *Bretzia* cubonavicular has the rangiferine morphology.

Metatarsals III and IV—Among the collections are four complete metatarsals, two proximal, and six distal partials (Plate 14, Table 6). The fused metatarsals III and IV have a range in length similar to my *O. hemionus* sample, although the longest *Bretzia* metatarsals are shorter than the longest male *Odocoileus* example and the shortest *Bretzia* specimen is shorter than the shortest female *Odocoileus* in this Oregon population sample. Matched to *Odocoileus* metatarsals of the same length, the *Bretzia* metatarsals are consistently thicker and more robust.

The proximal articulation is characterized by the presence of the articular facets for the cuneiform and ectocuneiform, and by two articular facets (anterior and posterior) for the cubonavicular. The ectocuneiform facet is small, oval, slightly tilted medially, frequently with a raised lateral margin. It forms a pointed projection on the posteromedial corner of the articular face of the bone, usually projecting farther posterior than in *Odocoileus*. The cuneiform facet (the main articulation to metatarsal III) in outline is an inclined rounded rectangle which projects ahead of the other facets. Details of its shape are highly variable in both *Bretzia* and *Odocoileus*. The anterior cubonavicular facet is slightly smaller than the cuneiform facet and is more rounded on the lateral edge. That anterolateral margin is slightly indented by a groove on the anterolateral face of metatarsal IV for the passage of extensor ligaments. The posterior cubonavicular facet extends transversely across the posterior side of the articular surface. Its shape varies from an almond-like pointed oval, with the point on the medial side next to the ectocuneiform facet, to an elongated parallel-sided strap, still pointed at the medial end. Variation in these features in *Bretzia* is similar to variation in *Odocoileus*. In *Cervus* this articulation is larger and tends to obscure the view of the central posterior indentation more than in either *Odocoileus* or *Bretzia*. On the posterior side of metatarsal IV just distal to the articular surface is a substantial tuberosity, which tends to be relatively larger in *Odocoileus* than in *Bretzia*.

The groove on the posterior side of the metatarsals is relatively shallow, as in *Odocoileus*, not deep as in

Rangifer. The lateral margin (posterior side of metatarsal IV) is more prominent than the medial margin. On the anterior face, a central narrow groove extends distally to a point above the distal end which is equal to or just a little less than the distal width of the bone, at which point it is covered by a bony bridge as in other cervids.

At the distal end the metatarsals III and IV fail to fuse completely, just as in the metacarpals.

The gap between the distal articular surfaces is slightly greater in all *Bretzia* specimens than in equivalent-length *Odocoileus* metatarsals, so that the central condylar ridges for articulation with the proximal phalanges were farther apart. *Bretzia* had a slightly wider foot than *Odocoileus*. Otherwise the shapes of the trochlear surfaces are similar between these two genera.

Summary of postcranial skeleton—Overall the appendicular skeleton of *Bretzia pseudalces* suggests an animal of similar size and proportions to *Odocoileus hemionus* from eastern Oregon, but with slightly more robust limbs and wider feet. The following features are more like *Odocoileus* (and usually other Capreoline deer) than like *Cervus*: deep olecranon process on ulna; lack of metacarpal V articulation facet; shape of proximal metacarpal; shape of proximal end of femur; shape of popliteal notch and popliteal tuberosity on tibia; presence of a posterior extension of the medial tibial articulation on the astragalus; lateral process on the sustentacular facet on the astragalus is prominent; astragalar facet on calcaneum has an invagination into the lower smooth surface; shape of the fibular condyle; distal end of navicular tuberosity extends distal to the posterior edge of the articular facet for the ectocuneiform; shape of the posterior ectocuneiform facet on metatarsals. Some bones (e.g., distal femur and radius) show few features which might distinguish *Bretzia* from *Odocoileus*. Features which serve to separate these genera are: tendency for long bones to be more robust in *Bretzia*; posterior gap between the proximal articular facets on metacarpals is closed in *Bretzia*; the anteromedial distal process of the tibia is equal to or longer than the mesial malleolus in *Bretzia*; the astragalus is relatively narrower in *Bretzia*.

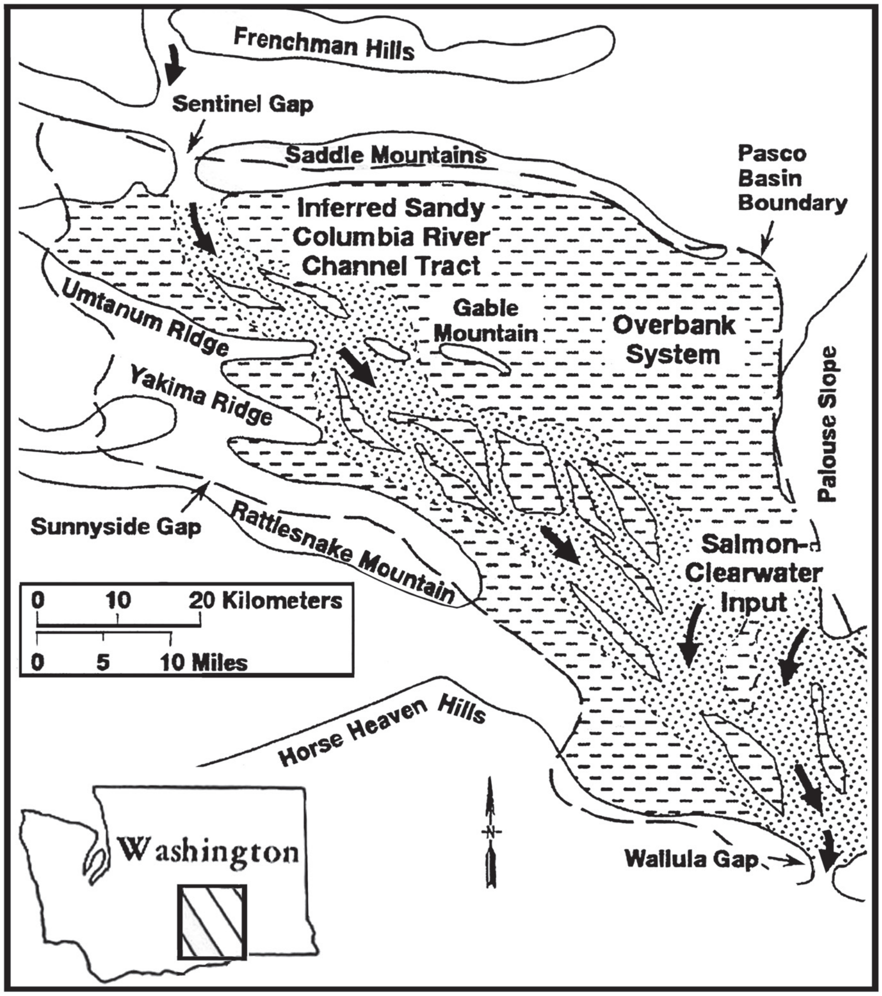

FIGURE 47. Paleogeographic interpretation of the member of Taylor Flat, ca. 4.9 Ma, modified from Lindsey, 1996. Compare with modern map, Fig.3.

DEPOSITIONAL AND CLIMATIC ENVIRONMENT

PALEOGEOGRAPHIC RECONSTRUCTION

Lindsey (1996) reconstructed the probable paleogeographic and depositional environment of the Pasco Basin during the deposition of his “member of Taylor Flat.” With the beginning of deformation of the formerly flat-lying flows of the Columbia River Basalts, the river began entrenching itself through the crests of anticlines which crossed its path, though for some time it flowed southwest from the northern Pasco Basin, across what is now the Yakima Valley.

The rapid rise of the western Horse Heaven Hills and other ridges in the late Miocene, combined with depression of the central Pasco Basin apparently set the river on a new course southeast from Sentinel Gap to a low point in the hills at Wallula Gap (Fig. 47). The new course allowed the river system to wander and deposit sediments over a potential flood plain of up to 90 km in width, with a potential area of over 5000 km^2 of fertile and well-watered land. At its southeast corner, the ancestral Salmon-Clearwater drainage flowed into the basin (Smith et al., 2000). During deposition of sediments containing the White Bluffs local fauna in the early Pliocene, the river carried large volumes of sand and gravel across the central basin, depositing finer sediments in the overbank system of the distal floodplain. Larger floods moved coarse gravels away from the main channel allowing lateral channels to accumulate gravel of grain sizes too large for them to normally carry. Lag deposits of these coarse gravels incorporate bone and teeth, providing the source of the larger members of the fossil fauna, including *Bretzia*.

At the end of deposition of the middle Ringold “member of Taylor Flat,” still in the early Pliocene, sediment sizes deposited in the Pasco Basin abruptly diminish from sand to clay and diatomite, indicating a change in flow regime from an active through-flowing stream to the slack water of a large lake.

PALEOCLIMATE AND ENVIRONMENT

Gustafson (1978) proposed that the local climate during the deposition of the middle Ringold (“member of Taylor Flat”) was somewhat less dry than at present. Modern yearly rainfall in the Pasco Basin averages about 200-250 mm. The large variety of mammals in the fossil fauna, including drought-sensitive forms such as *Scapanus* along with numerous browsers (including *Bretzia*) could have been supported by riparian gallery forest near the main river channels. Much of the lowland surrounding the more dense vegetation would have been grassland or sagebrush steppe. A rainfall of about 375 mm yearly was proposed.

Retallack (2009) has reported paleosols from a middle Ringold site which would have been on the floodplain where silty overbank flood deposits accumulated. Silty beds show soil features (his pedotypes Cil and Cilpa) which have a crumbly, relatively fine-grained structure over a deeper calcareous nodular level. He suggests the presence of tall grassland, either a sod-forming grass or longstem bunchgrass. The calcareous nature of these soils suggests a relatively dry climate with yearly rainfall around 400 mm (plus or minus 100 mm), similar to the earlier estimate.

Leopold and Denton (1987) record a pollen profile taken from two well cores drilled into a finer-grained portion of the “member of Wooded Island.” These pollen records are from within the Hemphillian portion of the lower Ringold deposits, of an age close to 6.8 to 6.6 Ma (Lindsey, 1996; Gustafson, 2012; Fig. 3). Pollen counts record abundant Taxodiaceae, probably from the swamp cypress *Taxodium*, which is abundant as silicified wood in the underlying interbasalt floras of the Columbia River Basalts. *Taxodium* requires fairly wet conditions, probably including abundant summer precipitation. The abundance of *Taxodium* pollen decreases upward; at the same levels the abundance of *Pinus* and cedar (*Juniperus*) pollen increases. This shift in abundances is interpreted to suggest a climatic trend from a higher–precipitation summer-wet condition to a dryer, summer-dry condition during the deposition of the lower Ringold Formation. This agrees well with the climatic trends suggested by Smiley (1963) on the basis of leaf floras in the Ellensburg Formation to the west of the Pasco Basin. The drying trend is generally correlated with the uplift of the Cascade Mountains during the later Miocene and development of an increasingly effective rain shadow. The reduction of moderating effect of the marine air masses would also result in a more continental, more seasonal climate.

Leopold and Dentons’ data suggest that when the yearly rainfall dipped below about 500 mm of precipitation per year, conditions would become suitable for the widespread development of grassland and sagebrush steppe. They further conclude that steppe in the Columbia Basin probably did not develop as a major vegetation unit until after the Hemphillian, that is, after about 5 Ma.

Smith et al. (2000) described the Pliocene climate of the Pasco Basin on the basis of the fish fauna of the Ringold sediments. They noted the absence of cold water fishes such as salmonids and the abundance of warm water fishes such as catfish and sunfish. Absence of trout, salmon, whitefish and sculpins in the Ringold faunas indicates normal daily temperatures exceeding 27 degrees C (80 degrees F) during the warmest month, with at least 30 days in which the temperatures exceeded 32 degrees C (88 degrees F) in warm seasons. If Pliocene climates in the Pasco Basin were cyclic during the deposition of the Ringold Formation, then winter periods were essentially frost-free at least during long warm periods in the cycle.

Smith et al. (2000) also note that the presence of muskellunge (*Esox*) is correlated with areas that receive at least 50 mm of rainfall each month and 750-1000 mm per year, an estimate, substantially greater than other local rainfall estimates. They note that white sturgeon also require large-stream habitat which requires that streamflow remains high throughout the year.

In the Columbia River system today runoff is distributed over months with little precipitation by delayed snowmelt. Flow in the Columbia today is at a maximum in late May and June, when little rain falls in the Pasco Basin (Waichler et al., 2005). The ancestral rivers may have had similar flow regimes to those of today, which depend largely on snowfall at higher elevations. Warmer conditions than today in the early Pliocene could have meant earlier maximum stream flow, perhaps in April and May.

Overlying this regional pattern (of increasing drying and seasonal variation) is another set of conditions of more global effect. After a period of high temperatures in the middle Miocene, many climatic areas cooled gradually towards the end of the Miocene, moderating again after the start of the Pliocene at about 5 Ma (Retallack, 2007). In Antarctica glaciation had been underway for several million years (Davies et al., 2012). The first major West Antarctica ice sheet grew in the period of 6 to 5 Ma, just at the end of the Miocene. This in turn affected sea levels, lowering them significantly, with low stands at about 5.7 and 4.9 Ma. The broad shallow seas between modern Alaska and Siberia were present intermittently during the late Miocene and Pliocene, from about 5.5-5.4 Ma (Gladenkov et al., 2002), sometimes withdrawing and leaving a dry land connection in the area known as Beringia. The existence of Beringia allowed dispersals between Asia and North America, and it appears to have controlled the timing of the immigration of capreoline deer and other taxa into North America (Repenning, 1987, 2003).

BIOLOGY OF *BRETZIA*

Body mass—Estimates of adult body mass in extinct mammals are necessarily approximate, given the many variables of age, sexual dimorphism, and nutrition. Most of the bones of *Bretzia*, including limb bones such as tibiae and metatarsals, have a range of variation which is compatible with a species which has considerable sexual dimorphism. The comparisons with the Oregon population of *Odocoileus hemionus hemionus*, a subspecies and local population with very similar tooth and bone measurements, suggest that *Bretzia* had similar body mass also (my measurements). The growth of body mass seems to decrease substantially between 2.5 and 4 years of age in *O. hemionus*, although large males can add body mass throughout their lives (Anderson, 1981). Growth in linear measurements for most limb bones stops about the same time, in about the third year.

The formula for determining body mass developed by Janis (1990) using lower molar row length gives a range of body mass for *Bretzia pseudalces* from about 48 kg up to about 57 kg. Judging by comparisons to modern deer, the lower estimate of 48 kg may pertain to mature females and the higher estimate of 57 kg may pertain to males; note however that range in body mass as well as absolute size tends to vary more among males, and maximum body mass could be much larger. Modern species with mass similar to the estimates for *Bretzia,* (as listed by Janis, separating males from females) include *Odocoileus virginianus* (M 68 kg/F 45 kg), *Dama dama* (M 67 kg, F 44 kg), *Cervus nippon* (M 64 kg,/F 41 kg), and *Hippocamelus bisulcus* (M 65 kg/F 55 kg). Her mass estimate for *Odocoileus hemionus*, for which measurements came from another population than my sample, is somewhat higher (M 91 kg/F 57 kg) than my estimate for *Bretzia*. A population of *O. hemionus* from northern Colorado reported by by Anderson et al. (1974) had mean bled carcass weights averaging 74 kg for males and 59 kg for females. Anderson (1981) suggests that this population of Rocky Mountain mule deer is among the largest in body mass of this species. Other populations are smaller and would more closely resemble *Bretzia* in size.

Age structure of the White Bluffs cervid sample—Two lines of observation can give some idea of the age structure of the *Bretzia* population. The antlers (discussed above) change through the life of the individual as they are lost and regrown. However, this series of antlers involves only male individuals, and estimating age beyond the four classes described above (juvenile, adolescent, adult, and senescent) is not practical.

Tooth growth, replacement, and wear provide a method which can give an approximation of age at death. In modern *Odocoileus*, juvenile individuals can be aged to within a few months (Connolly, 1981; Rue, 1997). Beyond about two years, the precision of this method becomes less accurate. However, it is possible to sort the fossil sample of 60 numbered dental specimens into age classes, basically wear stages 2 through 5 of Anders et al. (2011) but dividing their adult class into two stages. No very young infants have been found. I have assumed that the similarity in size of *Bretzia* and *Odocoileus* can be extrapolated into a similar dental replacement process and schedule for tooth wear.

1. Juveniles (deciduous premolars present, M_1 or M_2 showing little or no wear, estimated to be 1.5 years old or less), N=16;
2. Adolescents (permanent premolars erupted, light wear on molars, especially M_3, ages estimated as 1.5 to 3 years) N=9;
3. Young adults (P_4 moderately worn, posterior cusps of M_3 distinctly worn, aged about 3 to 6 years) N=15;
4. Mature adults (all teeth well-worn, especially M_1, though parts of the fossettids remain, aged about 5 to 8 years) N=10;
5. Old adults (fossettids of M_1 entirely gone, all teeth heavily worn, aged 7 years or older) N=10.

The largest age class here is juveniles, making up about 27% of the sample. Adolescents make up another 15%. Together, these two classes total nearly 42% of the sample. Young adults are represented by 25%, mature adults and old individuals in equal numbers represent a final 33% of the total sample. Attrition in this population is concentrated in the first three years of life. Upon reaching adulthood, almost 60% of the adult animals survived into late maturity. Individual animals reaching adulthood stood a good chance of living a full life. This is a common and normal pattern in ungulate populations (Voorhies, 1969).

Concentration of antlers and partial skulls—The largest group of *Bretzia* specimens is of naturally shed antlers. Such antlers which were shed in areas other than the local flood plain would stand little chance of survival as fossils. As a concentrated source of minerals, dropped antlers are usually chewed and consumed by a variety of animals, particularly rodents, and not least by the deer themselves. Weathering rapidly destroys any parts which are left. Few of the Ringold fossil antlers show marks of chewing and most are not seriously weathered, so they were likely not exposed on the ground for long. It follows that the bucks were living on the floodplain in the season in which the antlers were dropped. In northern climates, after a fall rut, many species drop their antlers during the winter, that is, largely from late December through March.

The sample of partial skulls of male *Bretzia* are mostly at a stage where they had shed their antlers but had not yet begun to regrow them. This suggests a concentration of males in this area at a single season (presumably winter or early spring), and a concentrated period in which death was more likely. Again, by observation of modern species, this circumstance suggests that the males were concentrated in the lowland forested floodplain, and that the climate was such as to put considerable stress on this concentrated population after the antlers were dropped.

In areas with strong seasonality, as was developing in eastern Washington's intermontane basins, and areas with summer-dry climate, likewise increasingly so in this area, a combination of winter and spring rains and melting snow in the adjacent highlands produces seasonal flooding. The floods are concentrated in winter and spring (Waichler et al., 2005), around the time or just after the time when the bucks would shed their antlers. This period is also when stress from lack of good nutrition helps to increase mortality (Rue, 1997). Scavenging by numerous carnivores would disassociate many skeletal elements. The floods would move bones, teeth and antlers, breaking and abrading them, and concentrating them with the larger gravel as a base load which would only be moved when currents were strongest, that is, during floods (Voorhies, 1969).

Many deer species (e.g., *Odocoileus hemionus, Rangifer tarandus*, and *Cervus canadensis*) seasonally migrate from higher country (or colder country) in the summer to lower terrain in the winter. This allows the animals, particularly bucks, to maximize the period of time in which they have access to fresh growth and high-quality nutrition. Good nutrition is especially needed to optimize antler growth. In some northern species, particularly in *Odocoileus virginianus*, the animals tend to gather in large groups in the winter in lower, warmer, well-sheltered areas. This behavior is known as yarding (Rue, 1997). Although it does produce more competition for food for each individual, the shelter reduces use of calories and the group provides more security. A pattern of yarding behavior would help to explain the abundance of deer in the ancestral Columbia River floodplain deposits.

The likely formation of herds with substantial numbers of individuals, either of same-sex or mixed-sex groups, fits well with the implications suggested by the antler forms. The antlers of *Bretzia*, with their large tines and broad vertical palmate structure, suggest that they were commonly used as visual signaling devices in a complex stratified social structure (Bubenik*,* 1982.) The closest living analogue in antler structure is *Dama*, the fallow deer, an Old-World cervine (Geist, 1987, his Fig.12). The resemblance of *Bretzia* to *Dama* and its relatives with palmate antlers, the megacerines is notable (Geist, 1998, Fig. 7-2). *Dama* is a highly gregarious deer in which males stake out a territory (a lek) to which females may be attracted. *Bretzia* was likely also a highly social cervid with specialized breeding protocols.

Predators in the White Bluffs fauna—Predators capable of utilizing *Bretzia* as a food source are quite varied in the White Bluffs fauna. The smaller carnivores include *Pliotaxidea*, a small badger, *Trigonictis*, a mustelid with some mink-like features, and *Bassariscus* a ringtail similar to those living in the southwest U.S. today. None of these was likely to pose much risk to a fairly large deer, but any might scavenge carcasses. Likewise, *Eucyon*, the coyote-like canid, was smaller than today's coyote and would be unlikely to be a threat except to small fawns or in packs. The bear, *Plionarctos,* is a tremarctine related to the South American spectacled bear. The latter is mainly a forest animal, "said to be one of the most herbivorous of bears," but "have been reported to prey on deer" (Walker, 1975). *Borophagus* (a canid) seems to have occupied a hunting-scavenging niche, having dental adaptations for crushing bones. Judging from behavior of modern equivalents such as hyaenas, they may have been pack hunters preferring large prey. *Chasmoporthetes* (a hyaenid) apparently had long legs and teeth less-specialized for scavenging, and their niche may have been more like modern cheetahs (Kurten and Anderson, 1980). The cats include a saber-tooth (possibly the short-sabered *Homotherium*) and a large lynx-like felid, about the size of a cougar. The saber-tooths appear to have been specialized for the largest prey, such as mastodons. The cougar-size *Felis* was probably a stalk-and-pounce hunter, well-suited for hunting medium-to-large deer in wooded areas, and is thus the most likely carnivore in the fauna to have regularly preyed on *Bretzia.*

PHYLOGENETIC RELATIONSHIPS

Ancestry and evolution of Cervidae—Artiodactyls of the family Cervidae, characterized by the presence of deciduous antlers with distinctive structures (Bubenik, 1990), originated in Eurasia during the Miocene, by 11-

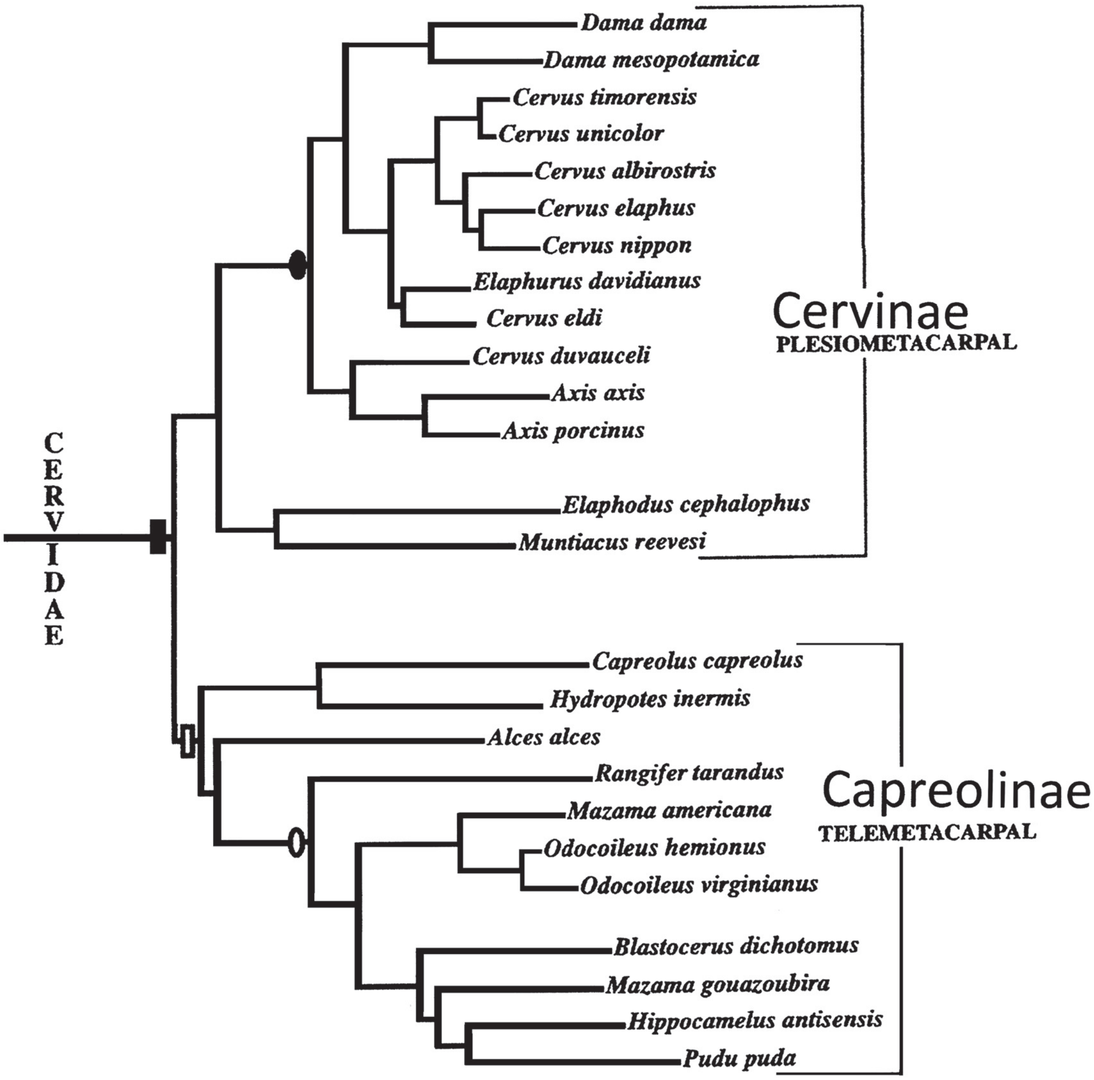

FIGURE 48. Generalized phylogeny of modern Cervidae from genetic evidence, modified from Gilbert et al. (2006). *Bretzia* is telemetacarpal, with its origin near the base of the clade.

10 Ma (Groves and Grubb, 2011; Hassanin et al., 2011). Sometime during the late Miocene the Cervidae divided into two major clades which survive today. These are the plesiometacarpal subfamily Cervinae and the telemetacarpal subfamily Capreolinae. The time of this division has been variously estimated. Pitra et al (2004) placed it at 7.2 Ma but Hassanin et al (2011) calculated a range from 10.0-9.2 Ma. The common ancestor of these two was presumably holometacarpal, (having complete metacarpals II and V). By the last part of the Miocene, ca. 8 to 5.3 Ma, the major modern groups of cervids should have been present (Gilbert et al., 2006; Dong, 2011).

The White Bluffs, at 4.98-4.89 Ma, is just younger than the first appearance of Cervidae in North America, at about 5.0 Ma (Voorhies and Perkins, 1998; Webb, 2000). For correlation with Eurasian taxa which are presumed to include ancestors and close relatives of *Bretzia*, this time period (earliest Blancan in North America) is in the earliest Pliocene (which began at about 5.33 Ma), very early Ruscinian, or European Land Mammal Zone MN 13 (7-4.9 Ma; Lindsay et al., 1988). The period just before this (late Miocene, Turolian in Europe, Baodean in China; Wang et al., 2013) is a period when Cervidae resembling modern taxa in dental and antler morphology were becoming common and increasing in diversity. Among the genera known from these time periods in Eurasia are *Procapreolus*, *Pliocervus*, *Cervavitus*, *Eostylocerus*, *Pavlodaria*, and *Muntiacus* (Zdansky, 1925; Croitor and Stefaniak, 2009, Dong, 2011; Vislobokova, 1980; Zhang, Yue and Cao, 2002, and Zhang et al., 2002). Of these, *Procapreolus* and *Pavlodaria* have been described as capreolines, *Pliocervus* is of uncertain status, perhaps capreoline (Croitor and Stefaniak, 2009), *Cervavitus* was a cervine and *Muntiacus* and *Eostyloceras* were muntiacines. Most are primarily known from antler and some skull materials. Reviewing the material of *Pliocervus* and *Procapreolus*, Croitor and Stefaniak (2009) state that "several lineages of Capreolinae evolved in Northern Eurasia by the Miocene-Pliocene boundary …." Recent publications suggest substantial future taxonomic rearrangement of these genera is likely (Croitor and Stefaniak, 2009; Gentry, 2005). None of these Old World deer is an obvious candidate for ancestry of the New World deer.

The most completely described of the late Miocene Old World deer is *Cervavitus*, particularly *C. shanxius* from China. *Cervavitus shanxius* appears to be a late Miocene representative of the Cervinae, although it is described from excellent fossils of the forefeet as holometacarpal (Zdansky, 1925) and not plesiometacarpal. Close examination of a specimen of *Cervavitus* including complete lateral metacarpals in the Zdansky collection in Uppsala yields the following observations: the lateral metacarpals on this specimen have lost contact with the carpal bones by reduction of the proximal ends of metacarpals II and V; the lateral metacarpals II and V are otherwise complete, though very slender; and metacarpal V appears to retain a contact (including an articular facet) with the posterior side of metacarpal IV, as it still does in the very reduced metacarpal V in modern *Cervus* (Fig. 42). Thus in detail, this structure seems to foreshadow the metacarpal anatomy of later cervines. Data on reduction of lateral metacarpals is still very sparse, and what material is known in the Old World has not been thoroughly studied.

Origin of Rangiferini—Vislobokova (1980) described *Pavlodaria orlovi* (from the late Miocene or early Pliocene of Kazakhstan) as the earliest of the known Rangiferini but describes the forefeet as holometacarpal ("lateral metapodia entire"). She did not illustrate specimens of the metacarpals. The condition of the posterior vomer, which in the Rangiferini divides the posterior choanae into two chambers, is significant in the phylogenetic placement of *Pavlodaria.* Modern Capreolinae which lack this character (Tribe Capreolini) include only the moose, roe deer, and *Hydropotes.* Vislobokova described *Pavlodaria* as unquestionably having a posteriorly extended vomer, which presumably divided the posterior choanae. She bases this observation in *Pavlodaria* on the structure of the basisphenoid, describing this (translated from the original Russian) as "anterior margin (of basisphenoid) abruptly lowering to presphenoid, apparently serving for insertion of vomer" (Vislobokova, 1980, p. 100). Further (p. 106) she states; "vomer, ossified posteriorly, dividing choanal cavity into two. Its anterior margin broken off, but it may be assumed from the relief of the ventral surface of the basisphenoid that the vomer reached it." This posteriorly expanded vomer is restricted in extant deer to the New World deer and to *Rangifer*, which also has divided posterior choanae. Resemblances between antlers of *Pavlodaria* and *Rangifer* have been noted above.

Origin of the New World deer—About 5 Ma, three genera of cervids (*Odocoileus, Eocoileus*, and *Bretzia*) appear in North America, apparently all derived from immigrant Asian ancestry.

The evidence indicates that in the latest Miocene in Asia (ca. 7-5 Ma), the Capreolinae had already divided into at least two clades. One, including the ancestry of *Capreolus* and *Alces*, lacked a posteriorly expanded vomer (Capreolini). The second clade, with expanded vomer (Rangiferini), had already diversified into at least two lines, *Pavlodaria* and the unknown ancestors of *Odocoileus* and *Eocoileus*, which genera had reached southeastern North America by 5 Ma. In *Eocoileus*, morphology of the vomer is unknown, but antler structure suggests relationship to *Ozotoceros* and therefore to the tribe Rangiferini.

Bretzia also reached central North America by 5 Ma, but whether its ancestry is closer to the first clade (Capre-

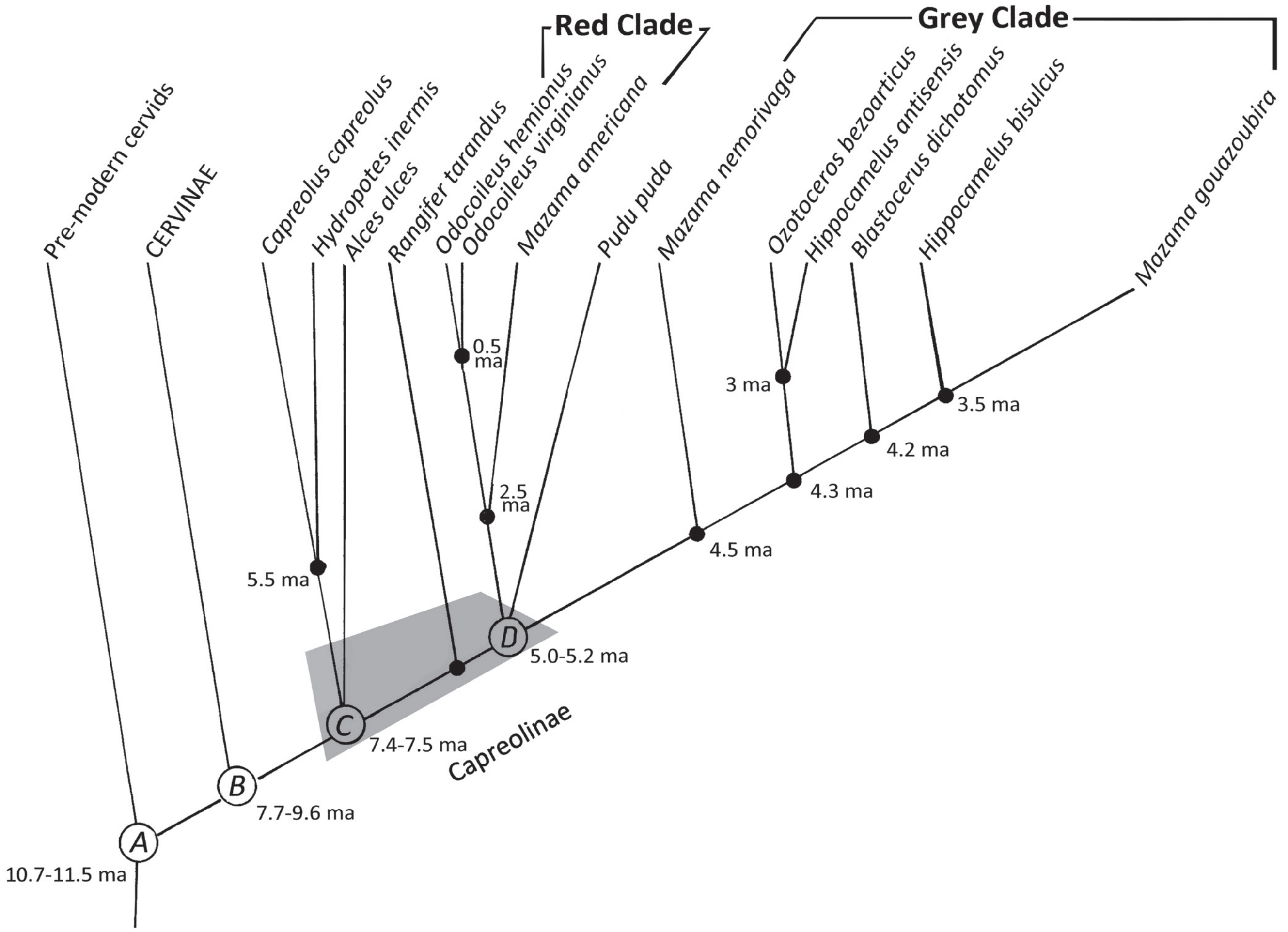

FIGURE 49. Phylogenetic hypothesis; position of *Bretzia* among the New World deer. Shaded area is the window of opportunity for evolution of *Bretzia,* though evidence is inadequate to determine which branch of this group is most closely related to *Bretzia*. Branching pattern from Duarte et al. (2008); dates in millions of years from that work, Pitra et al. (2004), Gilbert et al. (2006), and Hassanin et al. (2011). Character states at branching points are as follows: A, appearance of modern antlers; B, division of telemetacarpal clade (Capreolinae) from plesiometacarpal clade (Cervinae); C, expansion of posterior vomer in Rangiferini separates this group from Alceini and Capreolini; D, emigration to North America and start of New World evolutionary radiation. Branching dates for the "Gray Clade" pre-date the closing of the Isthmus of Panama, suggesting that either the differentiation of South American deer began in North America, or that these dates are too early. This hypothesis is based on DNA of modern species and does not account for known fossil taxa.

olini, roe deer, and moose) or second clade (Rangiferini) is unknown. The metacarpals III-IV assigned here to *Bretzia* lack facets for the articulation of the proximal remnants of the lateral metacarpals. This lack suggests a telemetacarpal condition for *Bretzia,* and assignment to the Capreolinae. This assignment is in agreement with other features of the postcranial skeleton and dentition of *Bretzia*, as described above. A phylogenetic hypothesis indicating where in cervid history *Bretzia* originated, based both on the morphology of the fossils and on the morphology and genetics of modern deer is presented here (Fig. 49). This phylogeny is largely from the work of Gilbert et al. (2006) and Duarte et al. (2008). Dates on the various points of divergence are known only roughly, and those used in this diagram are probably in the correct order. The earliest artiodactyls strongly resembling cervids seem to appear in the fossil record at about 20 Ma (Hassanin, 2011). The latter study put the origin of the Cervidae (presumably the origin of the common ancestor of the modern groups, marked by the appearance of modern deciduous antlers) at 11.5 to 10.7 Ma. Their calculations suggest a split between the two modern subfamilial clades from existing primitive Cervidae sometime between 9.6 and 7.7 Ma. The earliest fossil muntjac, a cervine (Dong et al., 2004) is apparently about 8 Ma, which if accurate would require a date of division older than their later limit (i.e., older than 7.7 Ma).

More significant to the ancestry of *Bretzia* is the calibration of the time of the diversification of the Capreolinae. Gilbert et al. (2006) calculated that the three tribes Alceini, Capreolini, and Rangiferini all diverged from each other within a very short time, at about 7.5 Ma. They estimated that common ancestor of *Alces* and *Capreolus* diverged from the Rangiferini about 100,000 years before it diverged into alceine and capreoline clades. This pattern is supported by the results of Hassanin et al. (2011). The Capreolini (*Procapreolus*) are apparently well-represented in the late Miocene, but the Alceini do not appear in the fossil record until the late Pliocene in Eurasia and Pleistocene in North America.

Among the modern capreoline deer, all are telemetacarpal (Fig.48). Morejohn and Dailey (2004) state that the lateral metacarpals of *Ozotoceros* and *Blastocerus* which they examined do not fit the established pattern of other capreolines, having been reduced to nearly nothing even at the distal end, and they question the retention of these genera in the Capreolinae. They state that “all (specimens) are plesiometacarpaline,” a description which would only pertain if there are substantial retained remnants of the proximal ends of the lateral metacarpals in these deer. I interpret the described condition as the logical consequence of extreme reduction of metacarpals II and V, and continue to include these genera in the Capreolinae as is indicated by the genetic data (Duarte et al., 2008).

Ciccimurri (1999) wrote that *Bretzia* shared sufficient characteristics with *Alces* to be classified as a member of the Alceini. Besides the obvious resemblance of palmate antlers, she cited the presence of the enlarged basal metastyle on M^3 and various characters of the astragalus, calcaneum, cubonavicular, and metatarsals. The antler resemblance is greatly lessened when their correct orientation in *Bretzia* is observed, though the palmation remains a shared character. The enlarged basal metastyle on M^3 is certainly a resemblance, but it can be observed in other genera to some (if lesser) degree. I find little resemblance between the tarsals and metatarsals of *Bretzia* and *Alces*; indeed the resemblance of *Bretzia* to *Mazama americana* is greater. Overall, the details of the osteology place the genus *Bretzia* firmly within the Capreolinae but are ambiguous as to placement between Alceini, Capreolini, and Rangiferini. This ambiguity is to be expected for an early offshoot of the diversification of Capreolinae. The lineage of *Bretzia* can be traced roughly from its earliest appearance in the early Pliocene to the end of the Pleistocene in North America.

There appear to have been three distinct periods of diversification in the Capreolinae (Fig. 49). The first, described above, occurred late in the Miocene (ca. 7.5 Ma) in Eurasia, and probably in the eastern and northern areas, with the division which produced the clades for roe deer, moose, Rangiferini, and perhaps others. The second diversification came about at the time of dispersal of deer into North America (by ca. 5 Ma), with evolution of the three genera *Odocoileus*, *Eocoileus*, *Bretzia*, and perhaps others (Duarte et al., 2008). Development of the Isthmus of Panama (ca. 3 Ma), resulted in the invasion of South America and continued the radiation of multiple lines of cervids (Webb, 2000). This third diversification was probably spread over at least two million years and involved multiple invasions of North American taxa into South America (Duarte, et al., 2008).

For its five-million-year history in North America *Bretzia* coexisted on the continent with a similar-sized relative and potential competitor, *Odocoileus*. Both were successful survivors through the Pliocene and Pleistocene. So far we have little evidence about whether they were direct competitors for the available resources, nor whether the presence of *Bretzia* affected the evolution of the much-more-familiar *Odocoileus*. It will be necessary to work out in much more detail the history of the survivors before their relationships with this extinct group can be understood.

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Illustrations are by the author unless otherwise noted. Drawings in Figs. 26D and 27A, Plates 4B, 5A, 6A and C, and 7B are by Jon Gustafson.

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TABLES

Table 1. *Bretzia pseudalces* lower deciduous tooth measurements (in mm)—dP_4

Specimen	**AP**	**T**
SDSM 22216	18.2	8.4
SDSM 22217	19.2	8.3
SDSM 22223	17.9	8.8
CRCM 58-132	16.9	8.2
UWBM 95595	17.4	8.0

Table 2. *Bretzia pseudalces* lower dentition statistical summary (measurements in mm, *N* = number of measurements, Mean = sum of measurements divided by *N*, *R* = range, *s* = standard deviation, *V* = coefficient of variation)

		N	**Mean**	***R***	***s***	***V***
P_2	AP	5	11.02	10.9-11.7	0.387	3.51
	T	4	6.03	5.5-6.5	0.356	5.90
P_3	AP	9	13.17	12.6-13.7	0.394	2.99
	T	9	8.14	7.3-8.7	0.488	6.00
P_4	AP	15	18.97	12.9-15.1	0.657	4.70
	T	15	8.92	7.9-10.1	0.670	7.51
M_1	AP	22	14.52	13.7-15.7	0.525	3.62
	T	23	10.38	9.5-11.2	0.653	6.29
M_2	AP	30	15.79	14.9-17.4	0.604	3.83
	T	30	11.01	9.4-12.2	0.667	6.06
M_3	AP	21	21.63	18.8-23.0	1.010	4.67
	T	23	10.94	9.4-12.3	0.716	6.54

Table 3. *Bretzia pseudalces* upper dentition statistical summary (measurements in mm, *N* = number of measurements, Mean = sum of measurements divided by N, *R* = range, *s* = standard deviation, *V* = coefficient of variation)

		N	**Mean**	***R***	***s***	***V***
P^2	AP	3	13.30	12.4-14.8	1.31	9.84
	T	3	13.30	12.1-14.0	0.83	6.24
P^3	AP	2	11.25	10.5-12.0	1.06	9.48
	T	2	12.65	12.6-12.7	0.10	0.79
P^4	AP	4	12.18	11.9-12.4	1.15	9.50
	T	4	14.55	13.9-15.4	0.63	4.33
M^1	AP	5	14.80	13.0-16.2	1.32	8.92
	T	6	16.15	15.0-17.0	0.72	4.44
M^2	AP	6	16.72	15.7-17.4	0.62	3.72
	T	6	17.25	15.9-17.9	0.72	4.17
M^3	AP	8	16.06	14.9-17.1	0.77	4.79
	T	8	17.33	16.2-18.7	0.80	4.60

Table 4.- Bretzia pseudalces skullcap measurements (in mm, est=estimated)

Specimen	**total width**	**postorbital width**	**pedicle diameter**	
			L	R
UWBM 37733	134	104	34	33
UWBM 95606	128	106	33	32
UWBM 53074				
LACM 120099	141	105	34	35
LACM 10921	135	107	39	38
SDSM 22203	130	107	38	36
LACM 10922	(166est)	(110est)	37	----
LACM 120161	----	----	----	38
UWBM 45016	----	----	19	----
UWBM 41478	----	----	24	----
SDSM 22204	----	----	22	----

Table 5.—Measurements of antlers (juveniles excluded): (measurements in mm, *N* = number of measurements, Mean = sum of measurements divided by *N, R* = range, *s* = standard deviation, *V* = coefficient of variation)

	N	**mean**	***R***	***s***	***V***
Shaft diameter, AP, 2 cm above burr	38	32.4	26-45	4.16	12.84
Anterior tine branching distance (on lateral side, from top of burr to a point at intersection of central lines along axes of shaft and anterior tine).	33	76.9	31-116	8.17	10.62
Length of anterior tine (includes estimates)	14	262	160-400	49.53	18.90
Diameter of anterior tine (4 cm distad from point defined for anterior tine branching distance)	32	27.7	19-55	6.60	23.84
Diameter of beam (4 cm distad from point defined for anterior tine branching distance)	32	36.2	27-47	5.20	14.35
Burr angle (angle between shaft axis and plane of burr)	40	770	670-900	5.23	6.82

Table 6. Postcranial measurements

Metacarpal measurements (in mm)				
Specimen	Length	Proximal width	Distal width	Midshaft width
UWBM 95625	213	31.4	33.1	20.1
LACM 154790	192	30.9	31.8	19.1
Tibia measurements (in mm)				
LACM 10928	----	----	31.1	----
LACM 154787	----	----	37.9	----
LACM 154788	----	----	37.4	----
LACM 154789	----	----	28.6	----
SDSM 22240	----	44.7	----	----
SDSM 22309	----	----	34.2	----
UWBM 35226	287	51.6	33.6	22.1
UWBM 92878	289	50.8	35.4	23.6
UWBM 95621	----	----	34.8	----
UWBM 95622	----	----	34.9	----
WHC-0003	299	54.2	34.0	25.4
Metatarsal measurements (in mm)				
LACM 10959	----	----	31.8	18.6
LACM 120151	229	25.3	31.9	17.6
LACM 143477	----	25.3	32.1	17.7
SDSM 22246	235	28.0	33.2	18.9
SDSM 22250	----	----	28.2	----
UWBM 40463	----	25.8	----	15.5
UWBM 95615	----	----	32.6	----
UWBM 95618	----	----	30.7	18.1
UWBM 95619	----	----	28.5	21.3
UWBM 95623	259	31.9	38.4	21.7
WHC-0004	264	30.5	38.9	23.0

PLATES

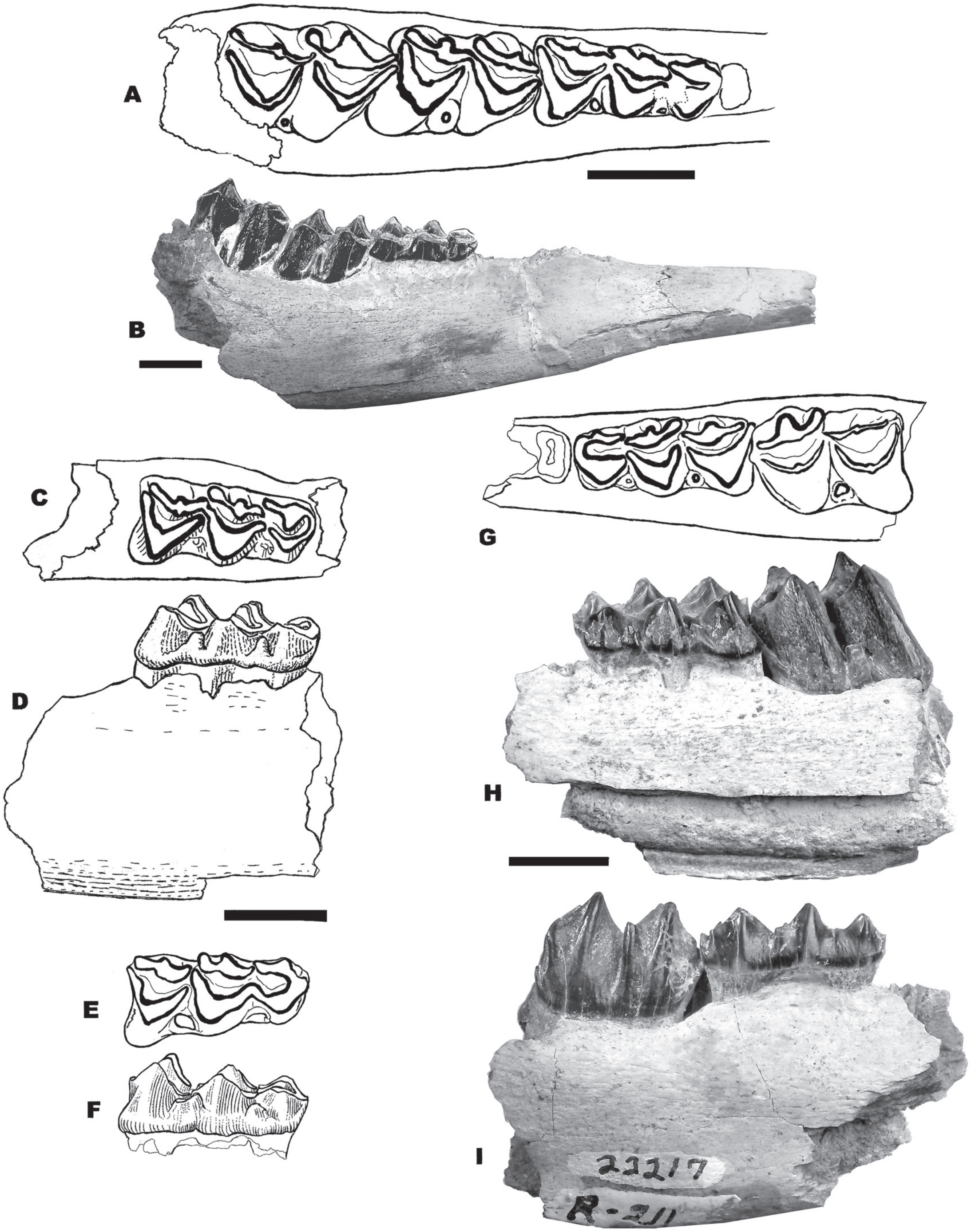

Plate 1. *Bretzia pseudalces*, juvenile lower dentitions. A-B, SDSM 22216, R jaw fragment with dp4-m2; C-D, CRCM 58-132, RdP4; E-F, UWBM 95595, Rdp$_4$; G, H, I, SDSM 22217, L jaw fragment with dP4-m1. Scale bars are 1 cm.

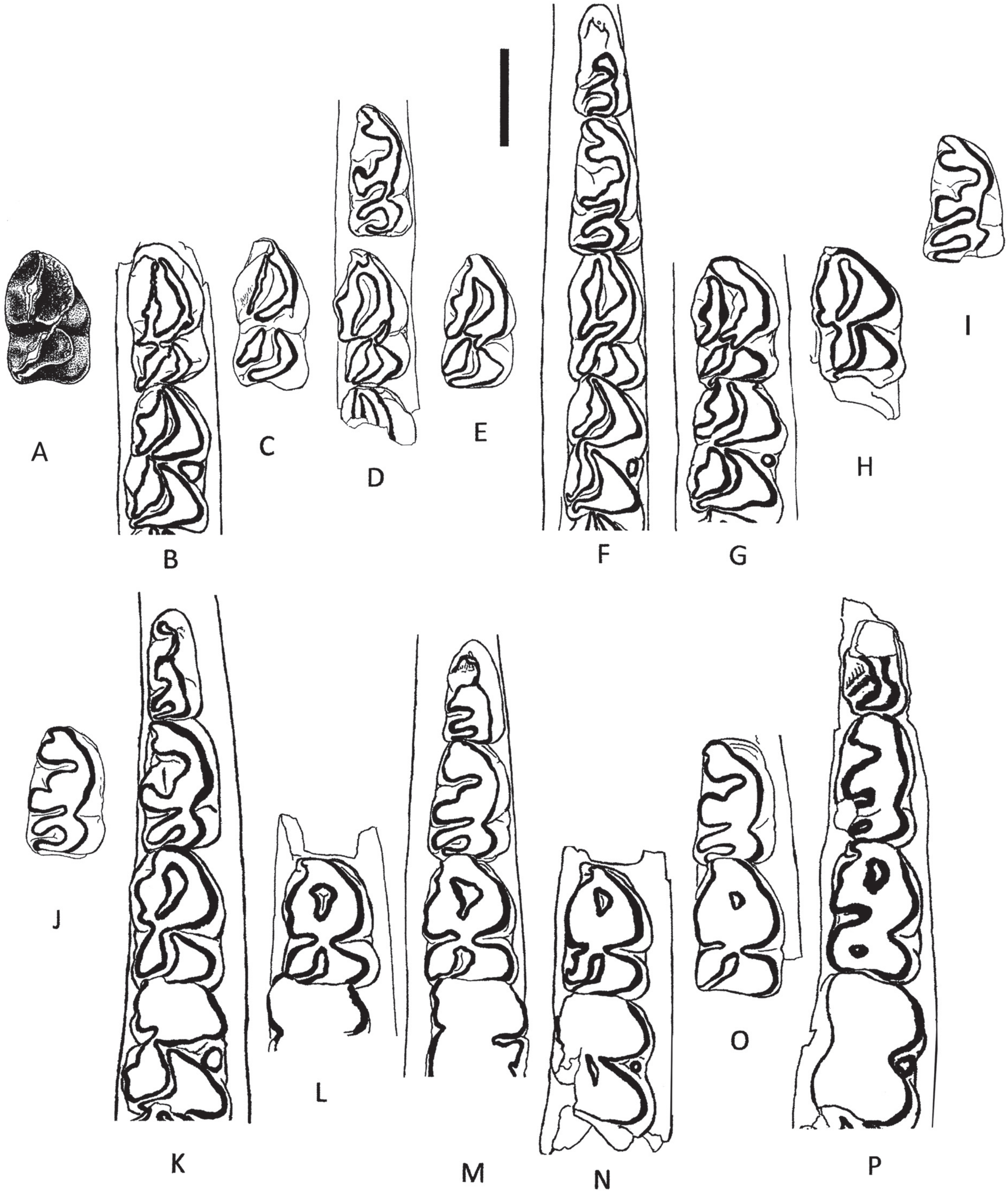

Plate 2. *Bretzia pseudalces* dental patterns. Comparative lower premolars (and M_1 where present) in order of increasing wear. A, UWBM 50402; B, UWBM 92882; C, SDSM 22222; D, UWBM 92884; E, SDSM 22221; F, UWBM 92895 (WHC-0005); G, UWBM 95604; H, LACM 154778; I, UWBM 95599; J, SDSM 22220; K, UWBM 92880; L, LACM 11816; M, UWBM 41520; N, LACM 120094; O, CRCM 58-149; P, LACM 154776. Left side specimens reversed for easier comparison. Scale bar is 1 cm.

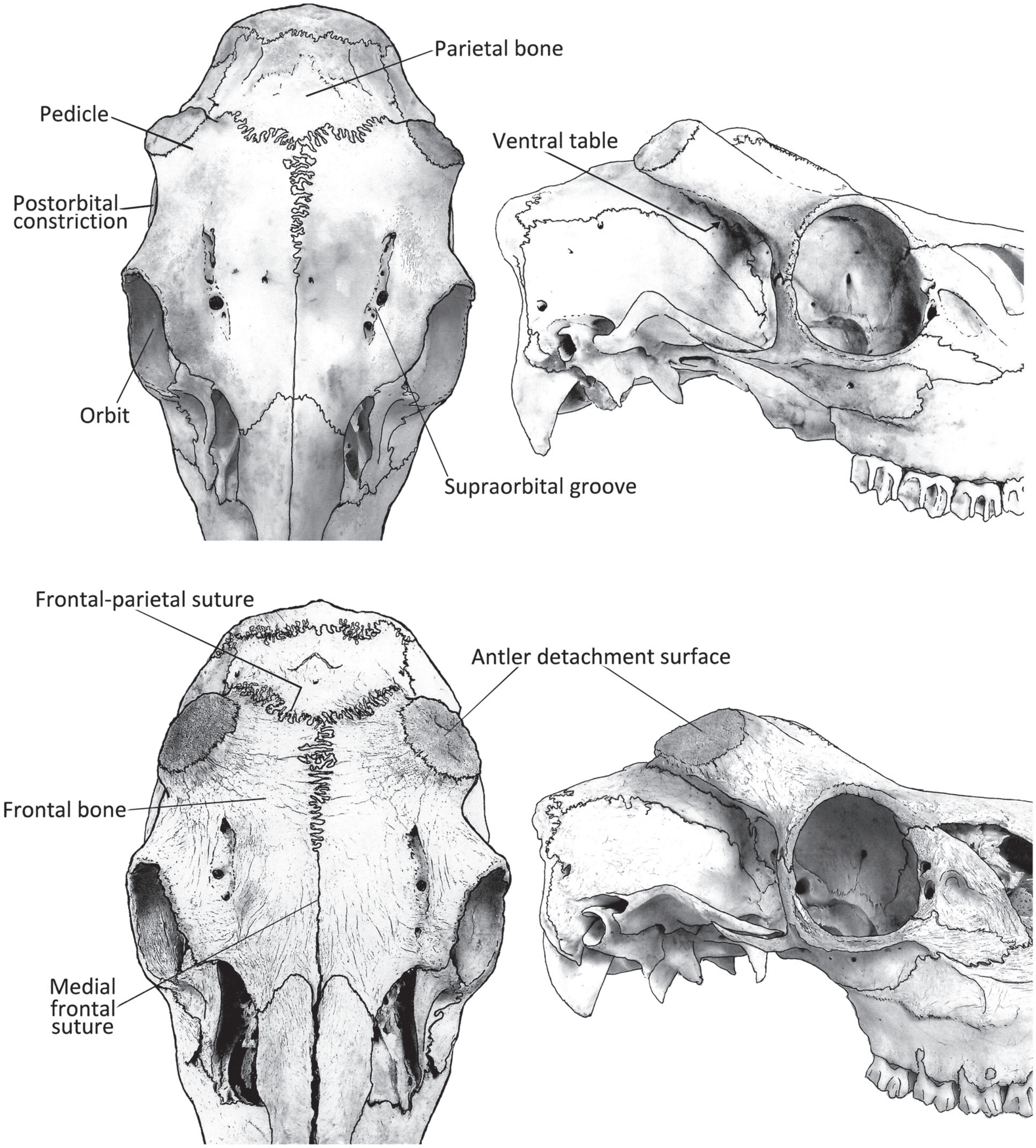

PLATE 3. Skulls of *Odocoileus hemionus* from Oregon (two individuals), both having naturally dropped antlers, showing position and condition of pedicles. Top, frontal and right lateral view of young adult; bottom, frontal and right lateral view of old adult.

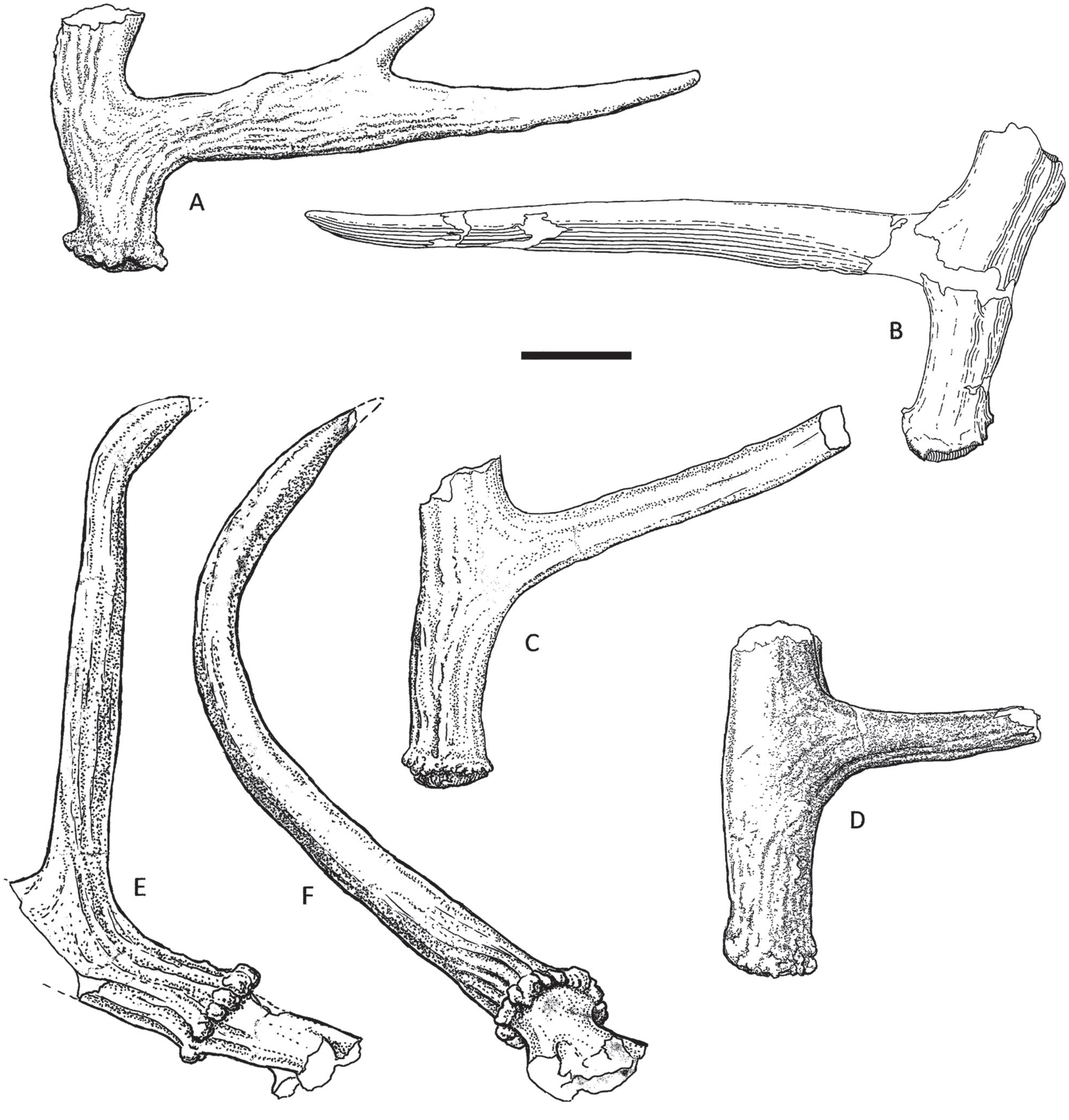

PLATE 4. Antler anterior tines, A-D, medial view; E, lateral view; F, anterior view. A, UWBM 92877, left antler; B. UWBM 42972 (paratype), right antler; C. WHC-0015, left antler; D. SDSM 22205, left antler, E-F, LACM 120168, right antler and partial frontal bone. Scale bar equals 5 cm.

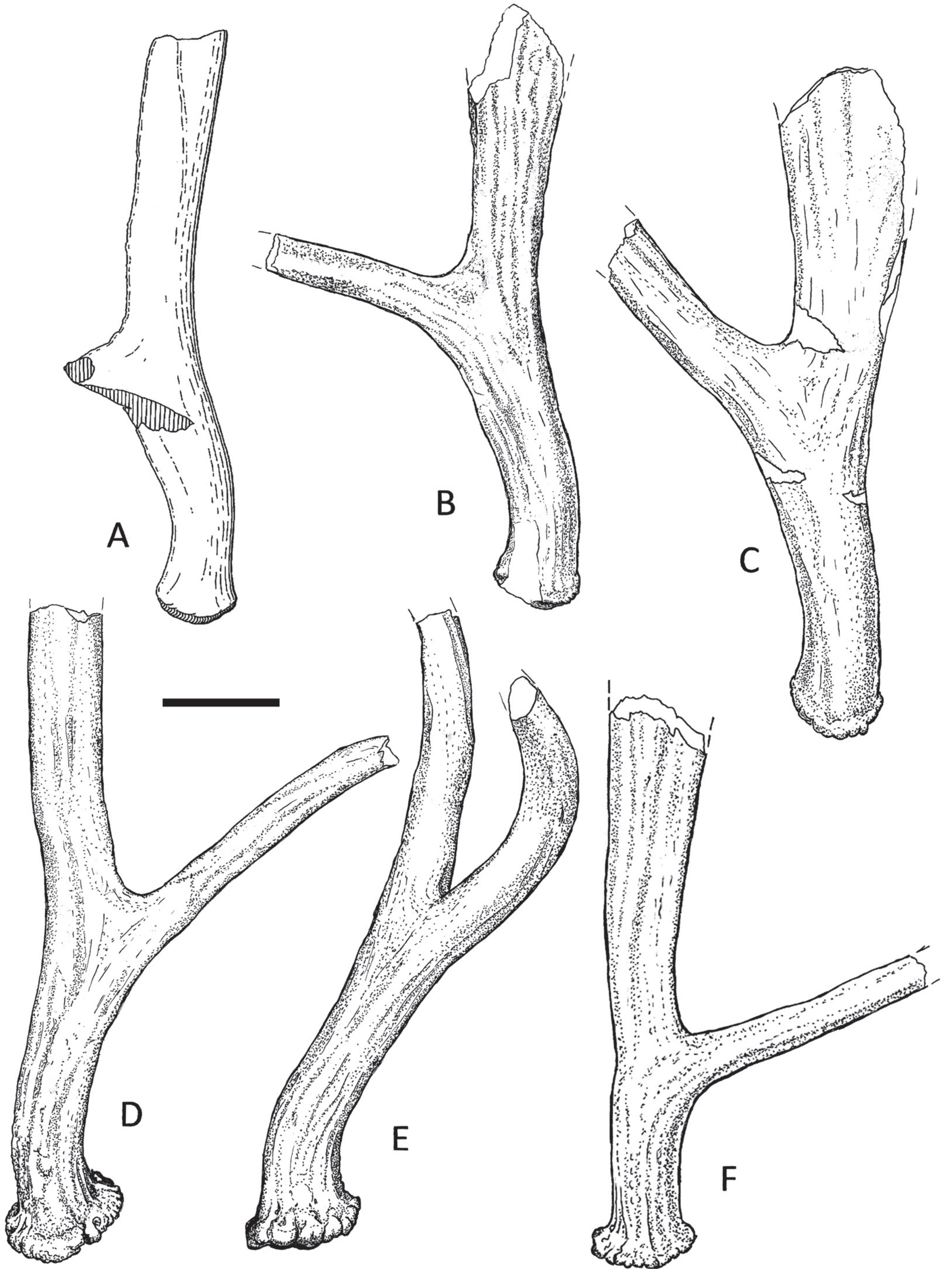

PLATE 5. Adolescent antlers. A. UWBM 41930; B. LACM 11377; right antler; C. LACM 11545, right antler; D., E., LACM WEF 11 (William E. Fry collector number), left antler (D, medial view, E, anterior view); F. WHC-0013, left antler. Scale bar equals 5 cm.

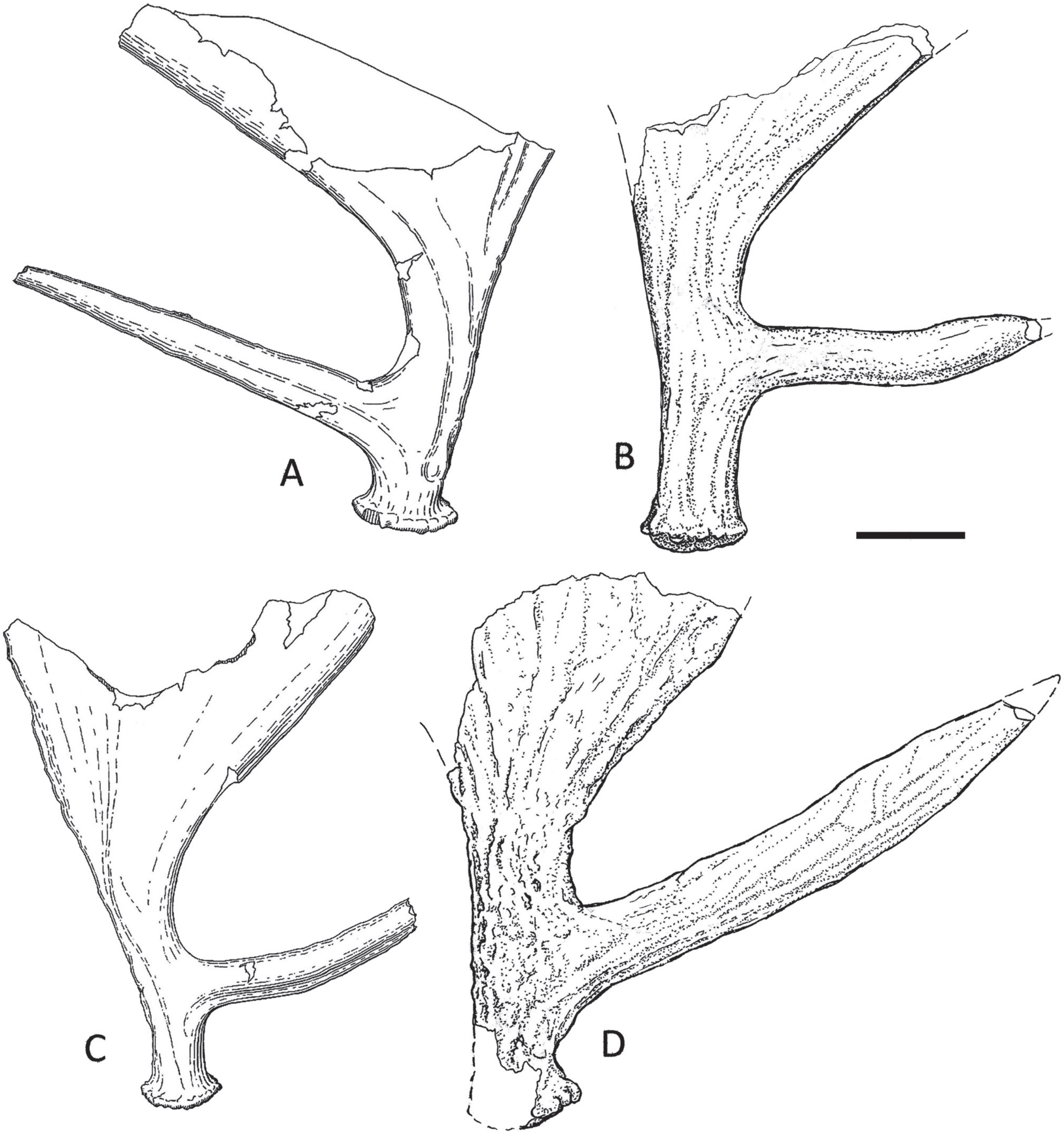

PLATE 6. Mature antlers, all medial view. A. UWBM 42973, right antler; B. WHC-0012, left antler; C. UWBM 42974, left antler. D. WHC-0010, left antler. Scale line is 5 cm.

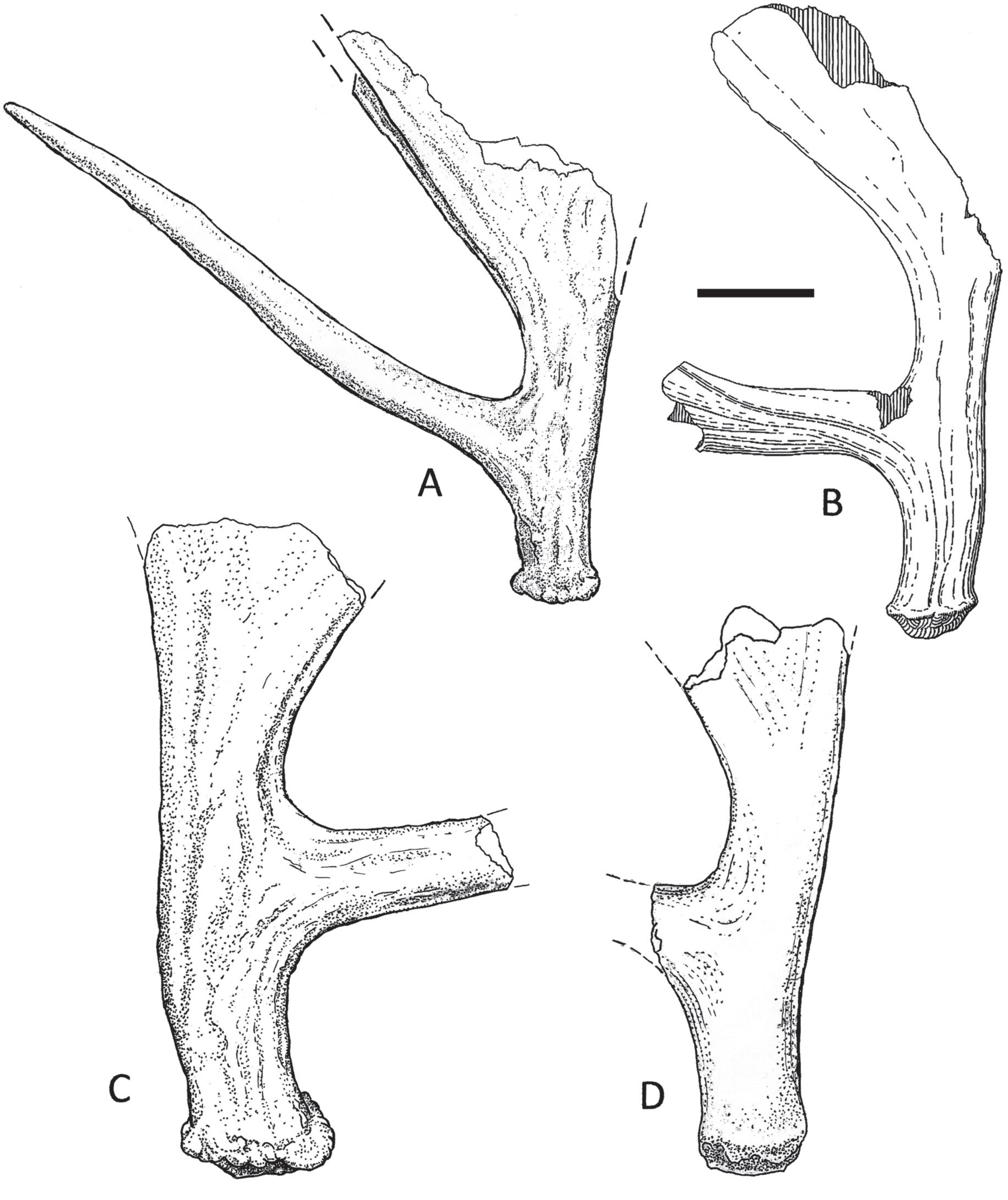

PLATE 7. More mature antlers, all medial view. A. WHC-0009, right antler; B. UWBM 42975, right antler; C. LACM 120162, left antler; D. UWBM 95605, right antler. Scale line is 5 cm.

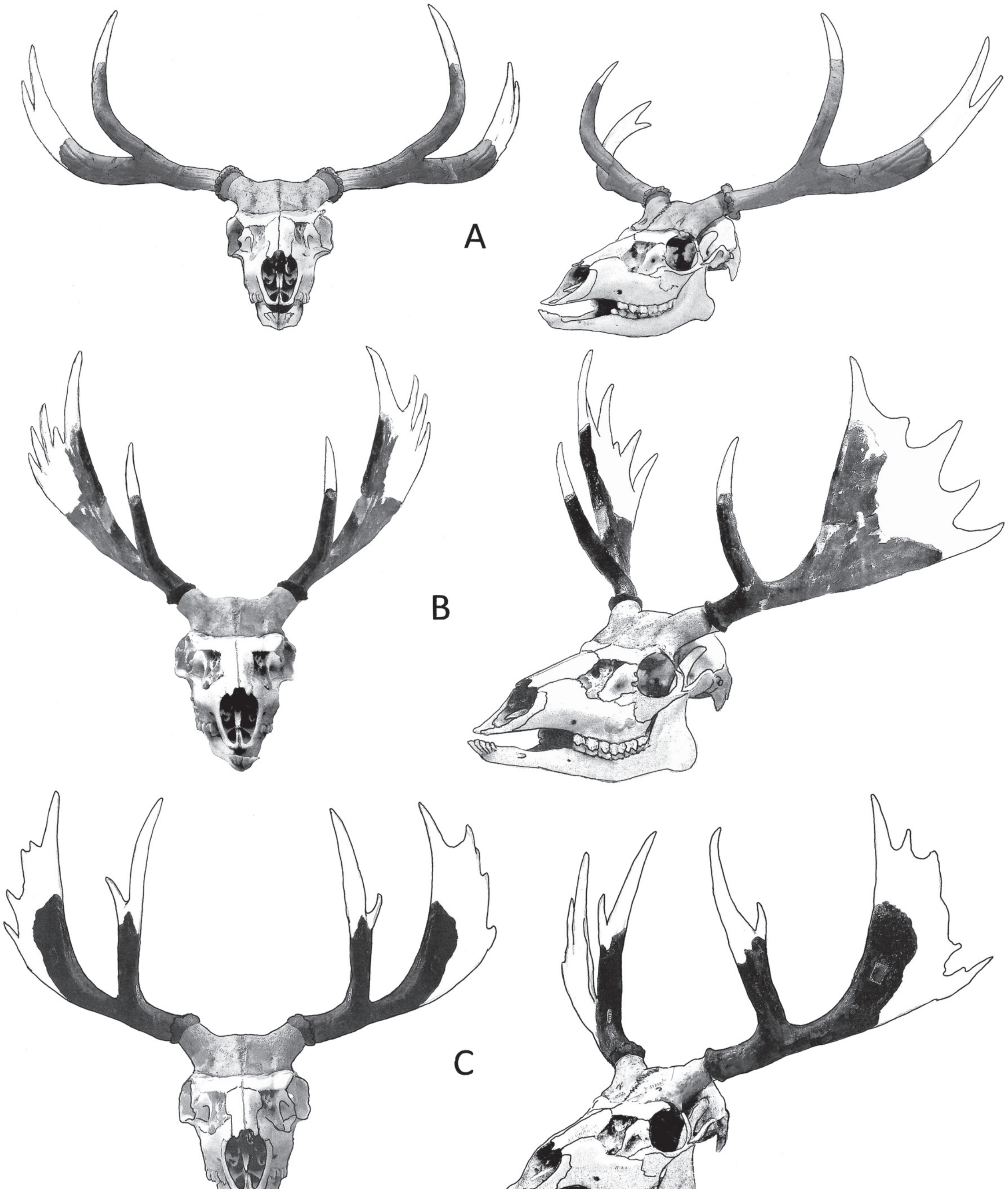

PLATE 8. Reconstruction of life position of three different antlers of *Bretzia pseudalces* using paratype skull fragment (UWBM 37733), mounted on skull of male *Odocoileus hemionus.* A. LACM WEF11 (William E. Fry collector number); B. paratype antler UWBM 42974, and C. paratype UWBM 42975.

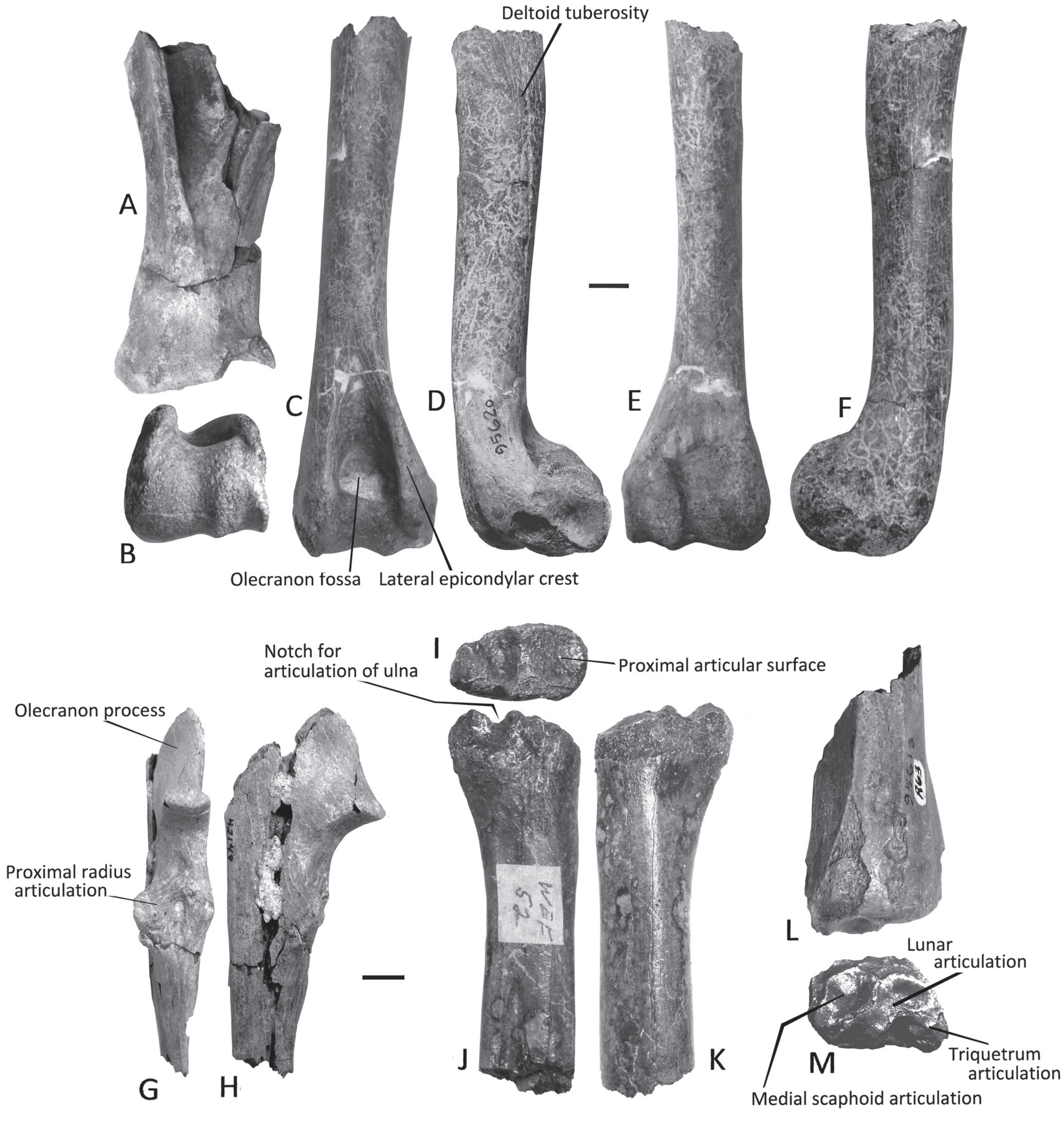

PLATE 9. *Bretzia pseudalces,* front limb bones. A, L scapula, UWBM 51761, lateral view. B-F, R humerus UWBM 95620. B, distal view; C, posterior view; D, lateral view; E, anterior view; F, medial view. G-H, proximal L ulna, UWBM42143, G, anterior and H, lateral views. I-K, Proximal L radius LACM 154784, I, proximal view; J, posterior view, K, anterior view. L-M, distal L radius UWBM 95613, L, anterior view, M, distal view. Scale bar equals 1 cm.

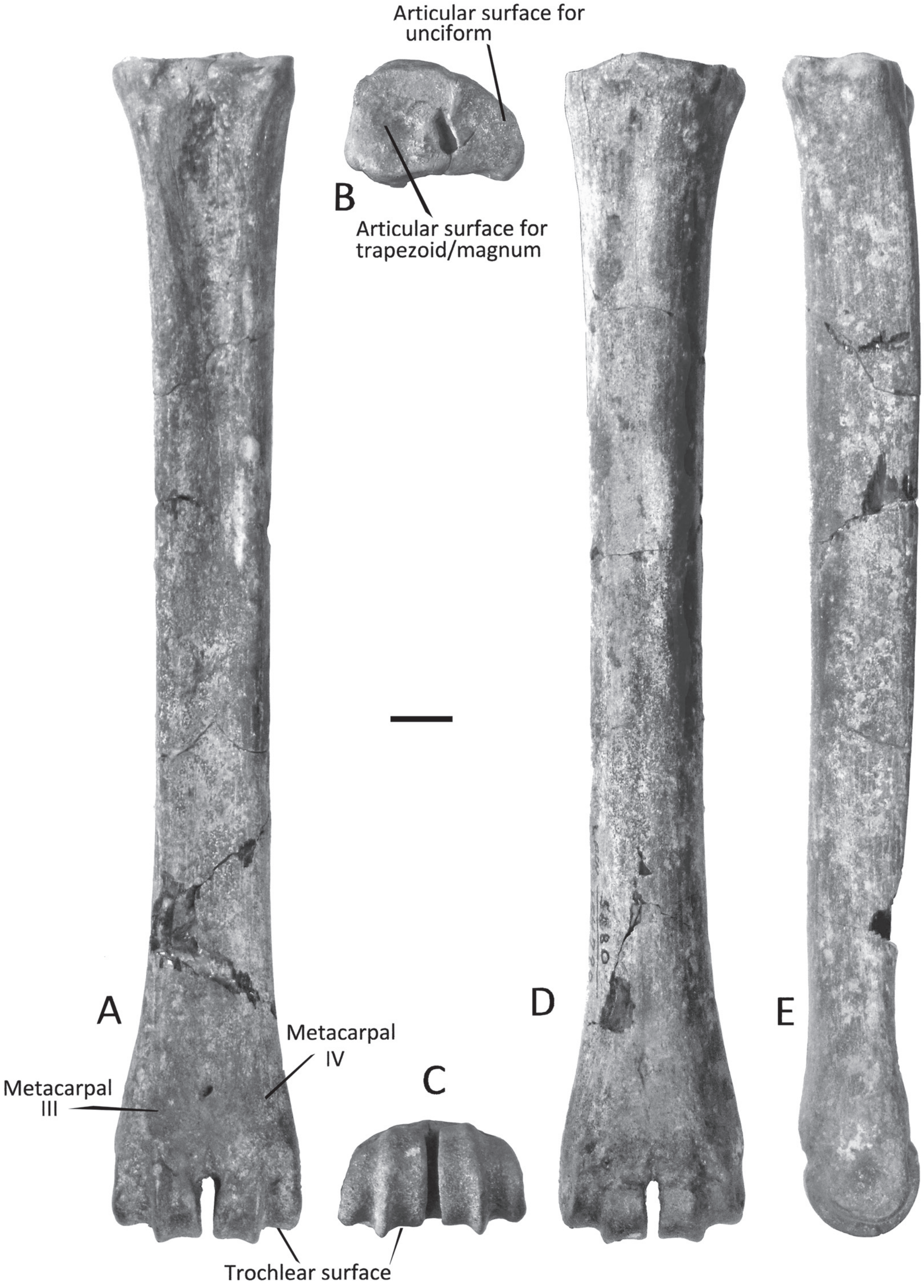

PLATE 10. *Bretzia pseudalces*, right metacarpals III-IV, LACM 154790. A, posterior view; B, proximal view; C, distal view; D, anterior view; E, left lateral view. Scale bar equals 1 cm.

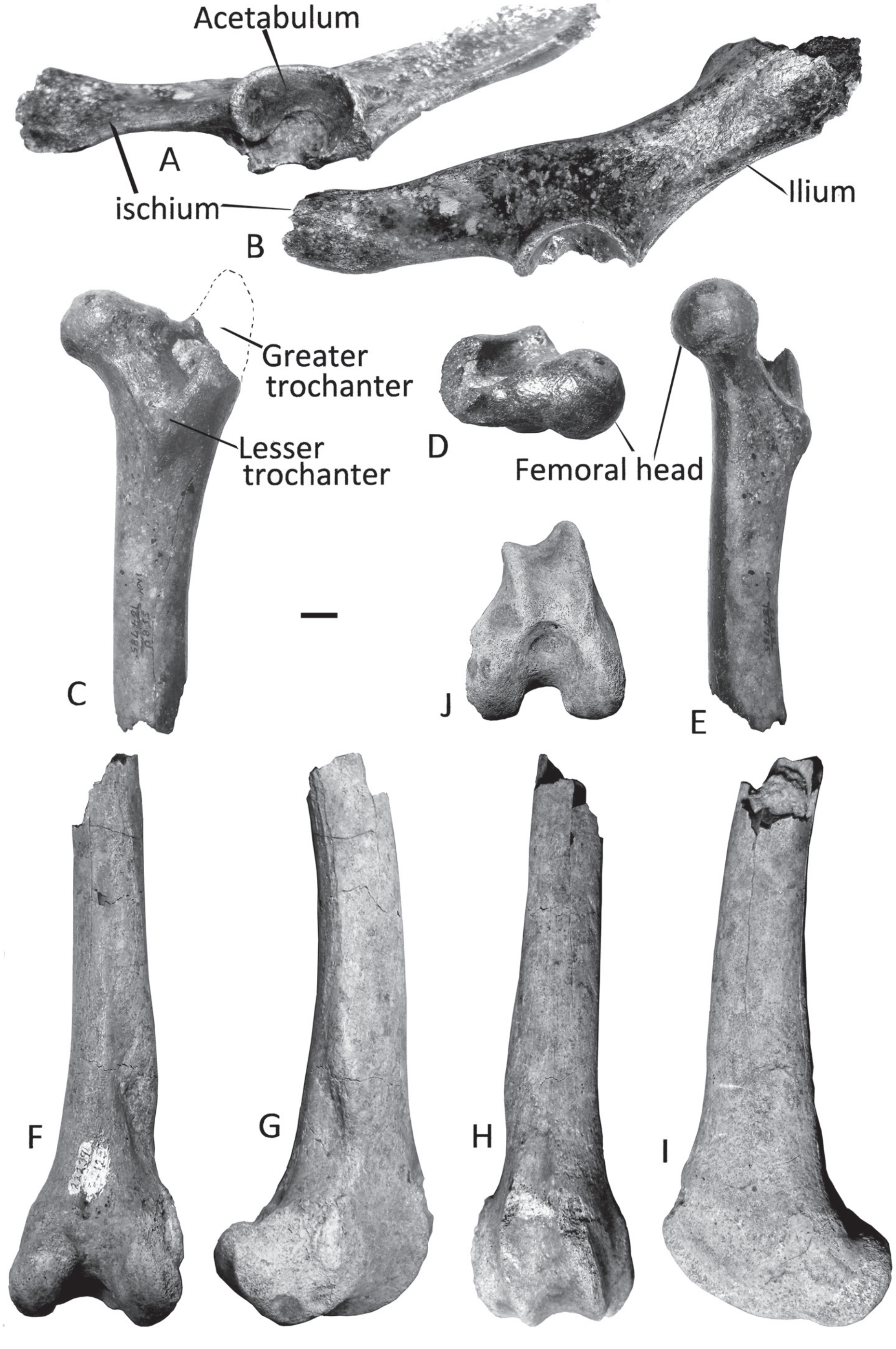

PLATE 11. *Bretzia pseudalces,* hind limb bones. A-B, partial pelvis, right side, UWBM 49519, anterior at right. A, ventral view; B, lateral view. C-E, proximal right femur, LACM 154785, C, posterior view; D, proximal view; E, medial view. F-J, distal right femur SDSM 22239, F, posterior view; G, lateral view, H, anterior view; I, medial view, J, distal view. Scale bar equals 1 cm.

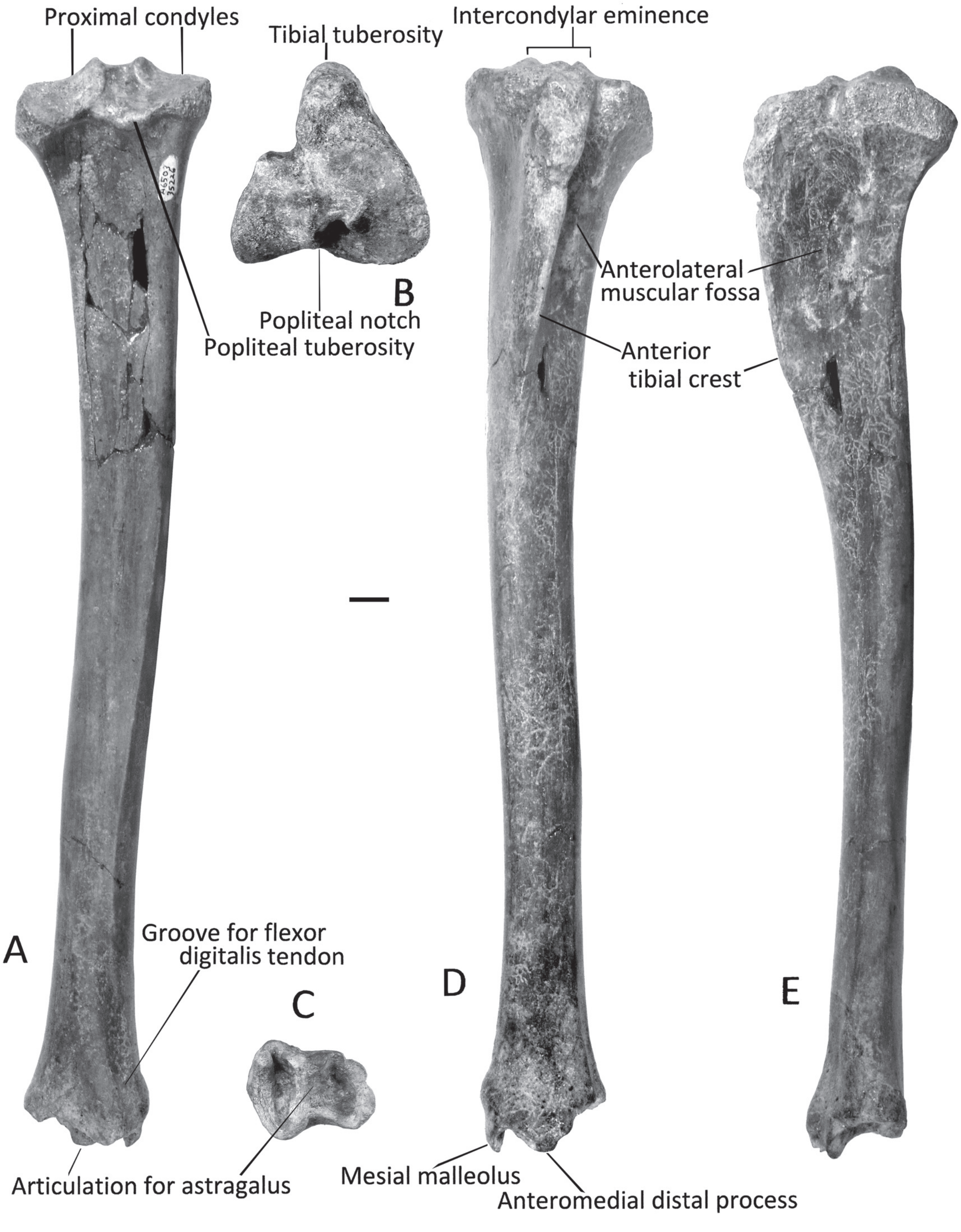

PLATE 12. *Bretzia pseudalces*, left tibia, UWBM 35226. A, posterior view; B, proximal view; C, distal view; D, anterior view; E, left lateral view. Scale bar equals 1 cm.

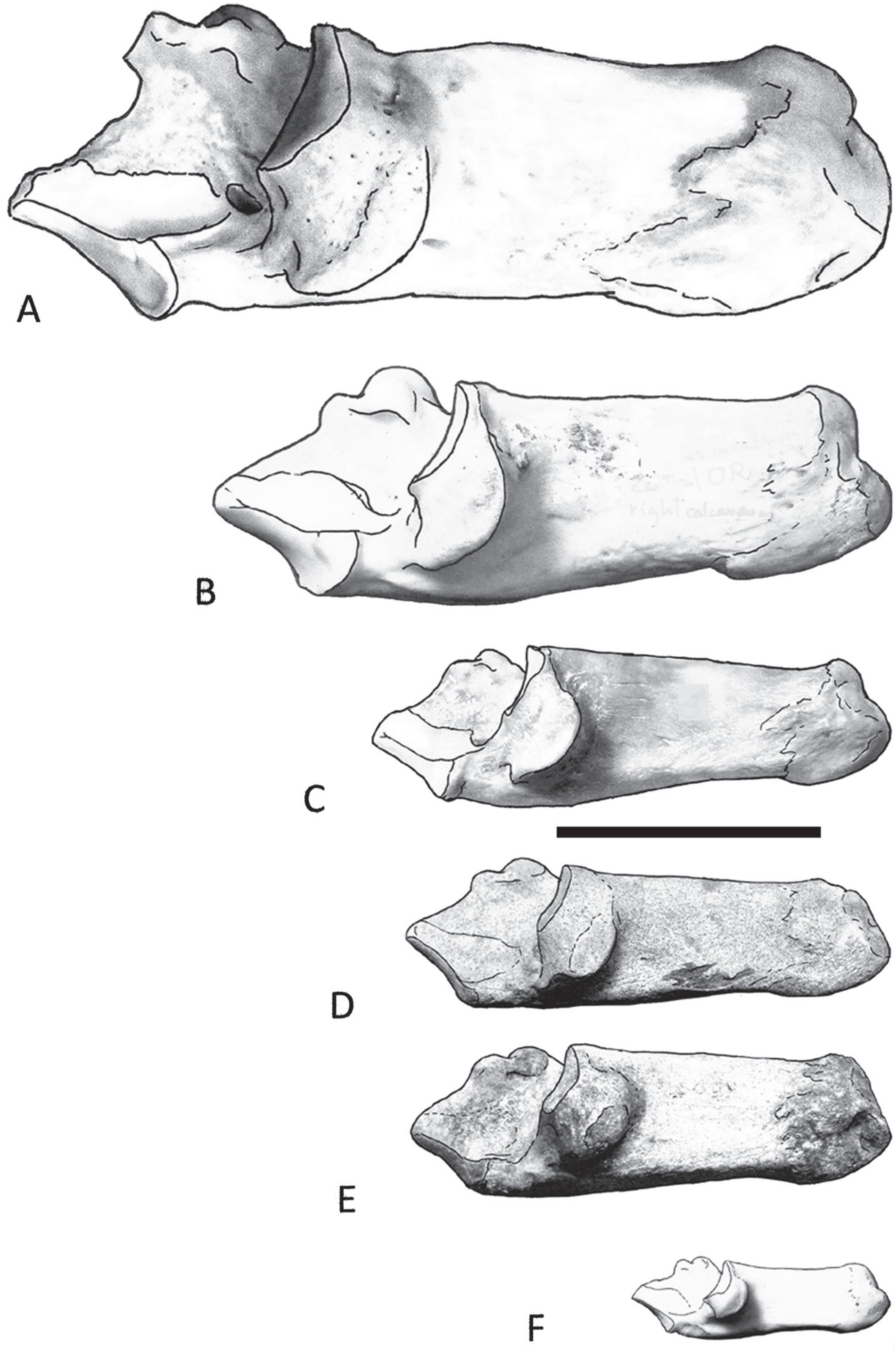

PLATE 13. Cervid calcanea; comparison of size and shape of *Bretzia pseudalces* to extant North American species, medial view of right calcanea. A. *Alces americana* (length 170mm), B. *Cervus canadensis* (133mm), C. *Odocoileus hemionus* (100mm), D, E. *Bretzia pseudalces* (both 93mm, E reversed), F. *Mazama americana* (50mm). Scale bar equals 5 cm.

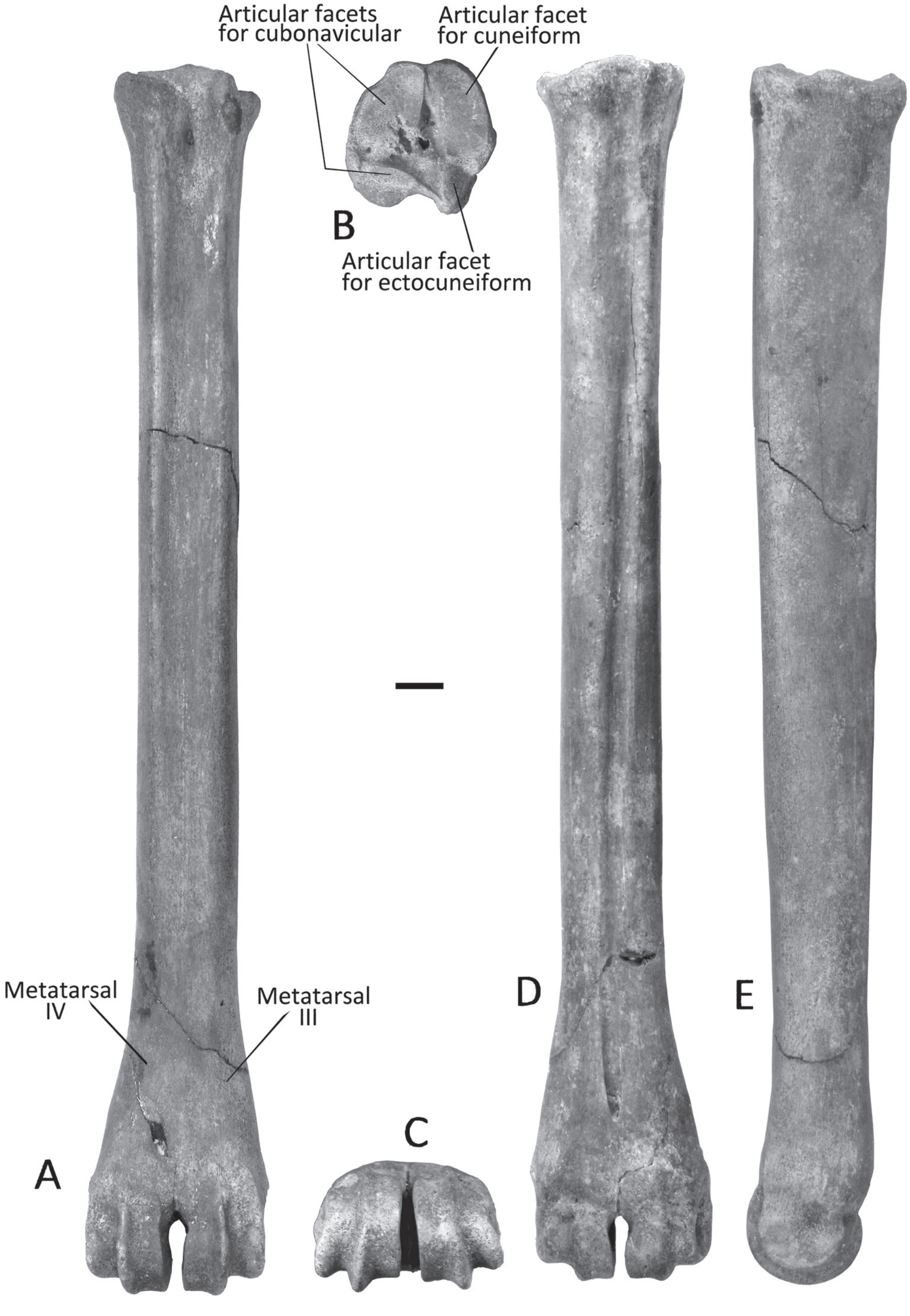

PLATE 14. *Bretzia pseudalces,* fused L metatarsals III and IV, UWBM 95623. A, posterior view; B, proximal view; C, distal view; D, anterior view; E, lateral view. Scale bar equals 1 cm.