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Early Pliocene Deer from the Gray Fossil Site, Appalachian Highlands, Tennessee, USA

Joshua X. Samuels, Olivia R. Williams, Shay Maden, and Blaine W. Schubert

ABSTRACT

The Early Pliocene age Gray Fossil Site (GFS) of northeastern Tennessee is well-known for its diverse and abundant fauna and flora. Perissodactyls, including tapirs and rhinos, are by far the most common large mammals at the site. The only artiodactyls noted from GFS so far are rare remains of several peccary species and a few camelid specimens. This paper describes the first remains of deer from the site, which include a partial juvenile maxilla, an isolated molar, and postcranial elements including humerus, tibiae, astragalus, calcaneum, and phalanges. Comparisons were made to a wide range of modern and fossil cervids, utilizing both qualitative comparisons and quantitative analyses based on measurements from the upper dentition and postcranial elements. The GFS cervid specimens are remarkably similar in both morphology and size to contemporaneous records of the monotypic genus *Eocoileus (E. gentryorum)* from the Early Pliocene of Florida, which supports taxonomic assignment to that species here. *Eocoileus* from the Early Pliocene of Tennessee and Florida are generally smaller than extant and fossil cervids in North and Central America studied here, with the exception of Key deer *(Odocoileus virginianus clavium),* Yucatan brown brocket deer *(O. pandora),* and Central American red brocket deer *(Mazama temama).* Dated to 4.9-4.5 Ma, the GFS deer are among the earliest records of the family in North America and combined with similar age occurrences from Florida and Washington these indicate deer dispersed rapidly across the continent in the latest Miocene or Early Pliocene. Overall similarity of the *Eocoileus* specimens to modern deer *(Odocoileus* spp.) suggest the former occupied comparable niches, being versatile browsers well-suited to occupy a broad range of habitats. The GFS deer records suggest deer have filled a similar role in the forests of the Appalachian region for nearly 5 million years, persisting through dramatic changes in climate and biota over time.

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INTRODUCTION

Deer (Cervidae) are the most abundant and species rich group of ruminants in the New World, and represent key components of nearly every terrestrial ecosystem in the Americas and Eurasia (Hanley, 1996; Geist, 1998; Webb, 2000; Rooney, 2001; Côté et al., 2004). The family dispersed to North America from Asia in the late Miocene or earliest Pliocene, with the earliest records likely being *Bretzia pseudalces* from Washington (Gustafson, 2015; Emery-Wetherell and Schilter, 2020) and *Eocoileus gentryorum* from Florida (Webb, 2000; Webb et al., 2008). In addition to *Bretzia* and *Eocoileus*, Pliocene age occurrences of cervids are known from across the continent (Figure 1; Supplemental Table 1), including many records of *Odocoileus* (Hibbard, 1941; Robertson, 1976; Webb, 1998; Wheatley and Ruez, 2006; Palma-Ramirez et al., 2023) and one record of *Capreolus* (Jiménez-Hidalgo and Bravo-Cuevas, 2015). Age and distribution of these records suggest cervids dispersed and diverged rapidly after their arrival in the Americas (Webb, 2000; Croitor, 2022).

Today, there are seven cervid species that occur in North America, including two that historically occur in the southern Appalachian Highlands region *(Odocoileus virginianus* and *Cervus canadensis)*. Deer, particularly *O. virginianus*, are the most abundant large herbivores in modern communities of the southeastern United States, and represent a large proportion of herbivore biomass within ecosystems (VerCauteren et al., 2011; Greenspoon et al., 2023). While currently abundant

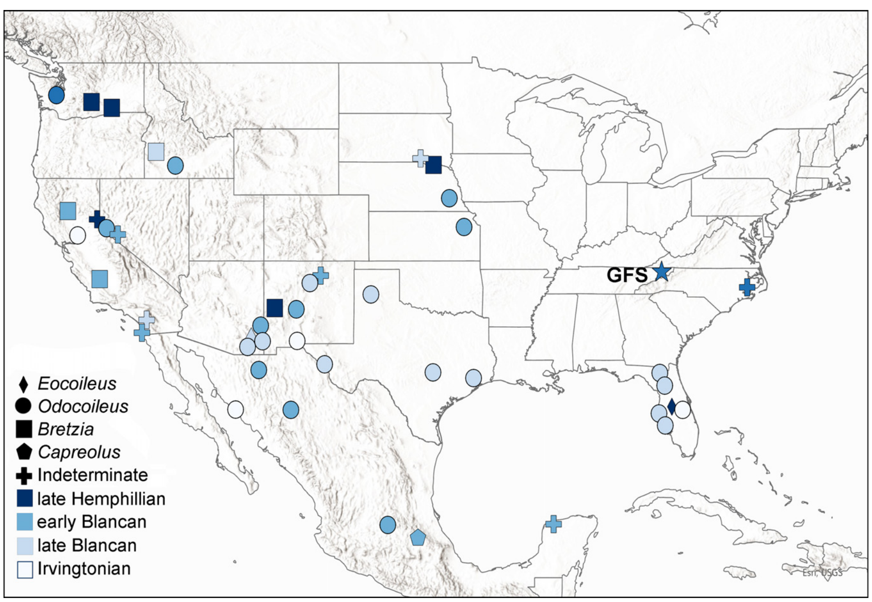

FIGURE 1. Late Miocene to early Pleistocene fossil occurrences of Cervidae in North America. Colors indicate age (NALMA) for each occurrence and symbols indicate taxa as follows: Square - *Bretzia*, Diamond - *Eocoileus*, Circle - *Odocoileus*, Pentagon - *Capreolus*, Plus -indeterminate/contentious. New cervid occurrence from Gray Fossil Site of Tennessee is indicated by a Star. Data derived from the MIOMAP/FAUNMAP databases (Carrasco et al., 2007; Graham and Lundelius, 2010), NOW Database (The NOW Community, 2024), and recent publications (Gustafson, 2015; Jiménez-Hidalgo and Bravo-Cuevas, 2015; Emery-Wetherell and Schilter, 2020; Palma-Ramirez et al., 2023). Full occurrence data listed in Supplemental Table 1.

and similarly well-represented in Pleistocene age sites from eastern North America, there are few records of the family in the region prior to the Pleistocene. The only occurrences described thus far are Early Pliocene (late Hemphillian or early Blancan) records of *Eocoileus gentryorum* from the Palmetto Fauna of Florida (Webb, 2000; Webb et al., 2008) and early records of *Odocoileus* from a number of late Blancan and early Irvingtonian sites in Florida (Robertson, 1976).

Here, we describe the first cervid fossils from the Early Pliocene age Gray Fossil Site of Tennessee, which represent the first ruminants known from the site. The specimens described here are among the oldest records of the family in North America and are the only pre-Pleistocene records of deer from the Appalachian Highlands. These early deer help reveal the origin of a ubiquitous component of Appalachian forests and improve understanding of Neogene faunal evolution in the southern Appalachians.

MATERIALS AND METHODS

Fossil cervid specimens are typically identified and diagnosed based on morphology of the antlers (Gustafson, 2015), which poses a challenge to providing taxonomic identifications of other skeletal material. There are characteristics of the dentition that vary across cervid taxa (Webb, 1998; Webb, 2000; Gustafson, 2015; Emery-Wetherell and Schilter, 2020), but identification of a specimen to species level may be impossible when the type specimen is an antler (Gustafson, 2015). Dental nomenclature used here follows Bärmann and Rössner (2011) and Gustafson (2015); we use dP3 and dP4 to refer to the upper deciduous third and fourth premolars, and M1 and M2 for the upper first and second molars. We have gathered eight measurements from the upper dentition and 18 from postcranial elements of cervids (measurement definitions and references are provided in Supplemental Table 2). Measurements of the teeth and postcranial elements, to the nearest 0.01 mm, were made using Mitutoyo Absolute digital calipers. Measurements of upper teeth include maximum anteroposterior length and transverse breadth taken at occlusal level. Specimens were photographed using a Nikon DSLR D7000 with a Micro Nikkor 60 mm lens.

Comparative specimens of both extant and fossil cervid species were examined at the following institutions: American Museum of Natural History (AMNH); Florida Museum of Natural History, University of Florida (UF); Gray Fossil Site & Museum, Zoology collection (ETMNH Z); National Museum of Natural History, Smithsonian Institution (USNM); University of Michigan Museum of Paleontology (UMMP). Since publication of Webb (2000), additional cervid material has been discovered in the Palmetto Fauna localities in the Central Florida Phosphate Mining District in Polk County, Florida, including elements not represented in the original type and hypodigm series of *Eocoileus gentryorum* (appendix 4.1 in Webb, 2000). These unpublished UF specimens include a range of dental and postcranial specimens directly comparable to material in the original Palmetto Fauna sample described by Webb (2000).

Some comparative specimens of Pliocene *Odocoileus* from the Rexroad Fauna of Kansas and Hagerman Local Fauna of Idaho are referred to here as *O. brachyodontus*, following their original designation; Wheatley and Ruez (2006) consider that taxon to be a *nomen dubium*, but they only studied the dentition of several specimens and indicated further study was warranted. GFS cervid material was also compared to specimens and measurements from a wide range of publications (including Vislobokova et al., 1995; Gustafson, 2015; Jiménez-Hidalgo and Bravo-Cuevas, 2015; Emery-Whetherell and Schilter, 2020; Palma-Ramirez et al., 2023). A complete listing of studied specimens and measurement data are included in Supplemental Table 3. All specimens described here are housed at the Gray Fossil Site & Museum (cataloged under the acronym ETMNH), Gray, Tennessee.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

Studies of the geology of the Early Pliocene age Gray Fossil Site suggest it formed as an ancient sinkhole with a relatively small and deep lake that filled with sediments over the course of ~4,500 to 11,000 years (Shunk et al., 2006, 2009). Cores from the site reveal rhythmite sediments in the upper lacustrine strata, with alternating layers of fine-grained silty clay and coarse-grained, organic rich sediments (Shunk et al., 2006, 2009). Both fauna and flora from the site are diverse and well-preserved (e.g., Parmalee et al., 2002; Wallace and Wang, 2004; Zobaa et al., 2011; Mead et al., 2012; Ochoa et al., 2012, 2016; Worobiec et al., 2013; Oberg and Samuels, 2022). Both macro- and microfossils of plants reveal a forest dominated by oak *(Quercus),* hickory *(Carya),* and pine *(Pinus),* accompanied by a variety of herbaceous taxa (Ochoa et al., 2016; and references therein).

Ochoa et al. (2016) interpreted the environment at the site as a woodland or woodland savanna with frequent disturbance. Isotopic analyses of ungulate and proboscidean teeth from GFS support the presence of relatively dense forest, but suggest more open grass-dominated habitats occurred within the dispersal range of large herbivores (DeSantis and Wallace, 2008). Both isotopic (DeSantis and Wallace, 2008) and ecometric analyses (Schap et al., 2021) suggest the climate had little seasonal variation in temperature and precipitation. Among the fauna are multiple organisms that are indicative of aquatic environments, specifically fish, neotenic salamanders, aquatic turtles, *Alligator*, a desman mole, and beavers (Parmalee et al., 2002; Boardman and Schubert, 2011; Mead et al., 2012; Bourque and Schubert, 2015; Jasinski, 2018; Oberg and Samuels, 2022; Maden, 2023). Presence of reptiles intolerant of extended freezing conditions (e.g., *Alligator* and *Heloderma*) (Parmalee et al., 2002; Mead et al., 2012) and mammals characteristic of forested habitats (e.g., tree squirrels, flying squirrels, tapirs, and the ailurid *Pristinailurus)* (Wallace and Wang, 2004; DeSantis and MacFadden, 2007; Hulbert et al., 2009; Crowe, 2017; Samuels et al., 2018; Grau-Camats et al., 2025) further support interpretation of the site as a relatively warm and closed forest. A range of large and small mammals from GFS represent immigrant taxa from Eurasia, including ailurids, meline badgers, several moles, and a giant flying squirrel (Wallace and Wang, 2004; Oberg and Samuels, 2022; Grau-Camats et al., 2025). In total, the site's flora and fauna represents a unique combination among biotas of North America.

There has been some controversy over age estimates for the Gray Fossil Site, based primarily on occurrence of *Teleoceras* (Short et al., 2019). The extinction of rhinoceroses in North America has been traditionally considered to have occurred at the end of the Hemphilllian NALMA (Wood et al., 1941; Lundelius et al., 1987), and the absence of rhinoceroses has been interpreted as characterizing Blancan faunas. However, *Teleoceras* is now known from multiple sites that include Blancan taxa (Bell et al., 2004; Farlow et al., 2001, 2010; Samuels et al., 2018; Martin, 2021), and Gustafson (2012) asserted that the presence of *Teleoceras* at a site is insufficient justification for assigning a Hemphillian NALMA age. Improved sampling and understanding of microfauna at both Pipe Creek Sinkhole in Indiana and GFS have led to revised interpretations of their ages. Martin (2021) and Martin and Kelly (2023) place Pipe Creek Sinkhole as a basal Blancan age site based on occurrences of *Ogmodontomys* and *Pliophanacomys* at the site, as occurrences of arvicolines south of 55°N latitude are used to define the Blancan NALMA (Bell et al., 2004). As a result of those arvicoline occurrences, Martin (2021) and Martin and Kelly (2023) interpret *Teleoceras* as a holdover taxon at Pipe Creek Sinkhole. Arvicolines have not been recovered from the Gray Fossil Site, but several other taxa characteristic of early Blancan faunas do occur, including the leporids *Alilepus vagus* and *Notolagus lepusculus*, cricetids *Neotoma, Peromyscus,* and *Symmetrodontomys*, and the mephitid *Buisnictis breviramus* (Samuels et al., 2018; Samuels and Schap, 2021; Xu, 2023).

Based on biochronology of mammal taxa with good fossil records and limited chronologic ranges, the age of GFS is currently estimated to be Early Pliocene, between 4.9 and 4.5 Ma, near the Hemphillian - Blancan transition (Samuels et al., 2018; Samuels and Schap, 2021; Xu, 2023). We elect for a conservative interpretation of the age of GFS (Early Pliocene, either in the latest Hemphillian or early Blancan NALMA), but note that none of the mammal taxa from the site are restricted to the Miocene or the Hemphillian NALMA, while multiple taxa are restricted to the Pliocene and characteristic of Blancan faunas. It is possible that GFS dates to the end of the Hemphillian, and the site's records of *Symmetrodontomys* (also known from Pipe Creek), *Peromyscus*, and *Notolagus lepusculus* represent first appearances of those taxa. Alternatively, the records of *Teleoceras* at the site may represent the last known rhinoceroses in North America (Short et al., 2019), having survived into the early Blancan where they co-occurred with a number of novel rodent and lagomorph taxa. Both GFS and Pipe Creek Sinkhole are geographically distant from most other records of *Teleoceras*, and the forested habitats of eastern North America may have represented a refugium where those rhinoceroses survived later than most other parts of the continent.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Family CERVIDAE Goldfuss, 1820
Subfamily CAPREOLINAE Brookes, 1828
Genus *EOCOILEUS* Webb, 2000
Eocoileus gentryorum Webb, 2000
(Figures 2-6, Tables 1-2)

Referred Specimens. ETMNH 6166 partial right maxilla with dP3 and dP4; ETMNH 40000 left M2;

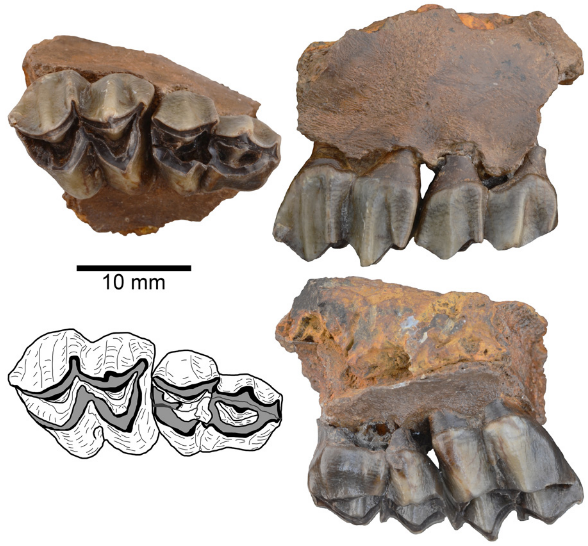

FIGURE 2. Maxilla specimen with dP3 and dP4 of *Eocoileus gentryorum* from the Gray Fossil Site, TN (ETMNH 6166) shown in occlusal, labial, and lingual views, along with a line drawing highlighting morphological features. Scale bar equals 10 mm.

ETMNH 10559 distal right humerus; ETMNH 8030, ETMNH 14923 right tibia; ETMNH 17218 left astragalus; ETMNH 12448 partial right calcaneum; ETMNH 19528 metapodial distal condyle; ETMNH 10546, ETMNH 13918 proximal phalanx

Locality. Gray Fossil Site, Washington County, Tennessee.

Age. Early Pliocene (late Hemphillian or earliest Blancan).

Diagnosis. In the GFS cervid the upper molar protocone is fused to the metaconule, there is a small entostyle between the lingual crescents, and the posterior crest extending from the upper molar protocone is bifurcated, which are traits common among capreoline cervids. In contrast to the GFS cervid, *Eocoileus gentryorum*, and extant *Odocoileus*, the upper molar protocone and metaconule are unfused in *Cervus, Bretzia,* and dromomerycids. The GFS cervid upper molar displays rugose anterior and posterior cingula bearing small cuspules, similar to some specimens of *E. gentryorum* from Florida. These cingula are distinct, but not rugose in *Bretzia* and are weak or absent in studied specimens of *Odocoileus, Capreolus,* and *Mazama*. The GFS cervid astragalus has a straight proximal edge of the sustentacular facet, as is typical of capreolines. In the GFS cervid and *E. gentryorum* the sustentacular facet of the astragalus is more rectangular in shape (anteroposteriorly elongate) than in *Bretzia* and *Odocoileus*. Morphological features of both the teeth and postcranial elements, along with size of the specimens, are within the range of variation of known specimens of *E. gentryorum* and support assignment to that species.

Description—upper dentition. ETMNH 6166 represents a fragmentary portion of the right maxilla with the dP3 and dP4 preserved (Figures 2 and 3), and ETMNH 40000 is an isolated left M2 (Figure 3). The upper dentition is selenodont and brachydont, with crescentic protocone and metaconule lingually and rhomboidal paracone and metacone labially. Crests extend from the anterior and posterior margins of each of those cusps. Enamel on the cusps is not distinctly crenulate, and there are no cingula surrounding the lingual cusps. The dP3 of ETMNH 6166 is relatively asymmetric and narrower anteriorly than posteriorly. The paracone and protocone of the dP3 are distinctly smaller than the metacone and metaconule. The parastyle, mesostyle, and metastyle of the dP3 are all distinct, and the paracone rib is more prominent than the indistinct metacone rib. A small spur extends labially from the posterior crest of the metaconule. In contrast to the relatively asymmetric dP3, the dP4 of ETMNH 6166 displays a trapezoidal shape with protocone and metaconule of similar size and paracone and metacone of similar size. The dP4 parastyle and mesostyle are prominent, and both are larger than the metastyle. The paracone rib and metacone rib of the dP4 are also distinct, though the former is more pronounced. The dP4 has a distinct entostyle present between the paracone and metaconule. The posterior crest of the protocone of the dP4 shows no evidence of bifurcation or presence of a protoconal fold, and there is no metaconule spur extending from the posterior crest of the metaconule. Though the dP4 is only slightly worn, the posterior crest of the protocone is fused to the anterior crest of the metaconule. The dP4 lacks both anterior and posterior cingula.

The GFS M2 (ETMNH 40000) is heavily worn, and it displays a trapezoidal shape with protocone and metaconule of similar size and paracone and metacone of similar size. A distinct entostyle is present between the paracone and metaconule of the M2. The M2 posterior crest of the protocone is bifurcated in ETMNH 40000, forming a small enamel island (protoconal fold) where it fuses to the anterior crest of the metaconule. There is a small metaconule spur in ETMNH 40000 that extends labially from the posterior crest of the metaconule. The M2 (ETMNH 40000) has a clear

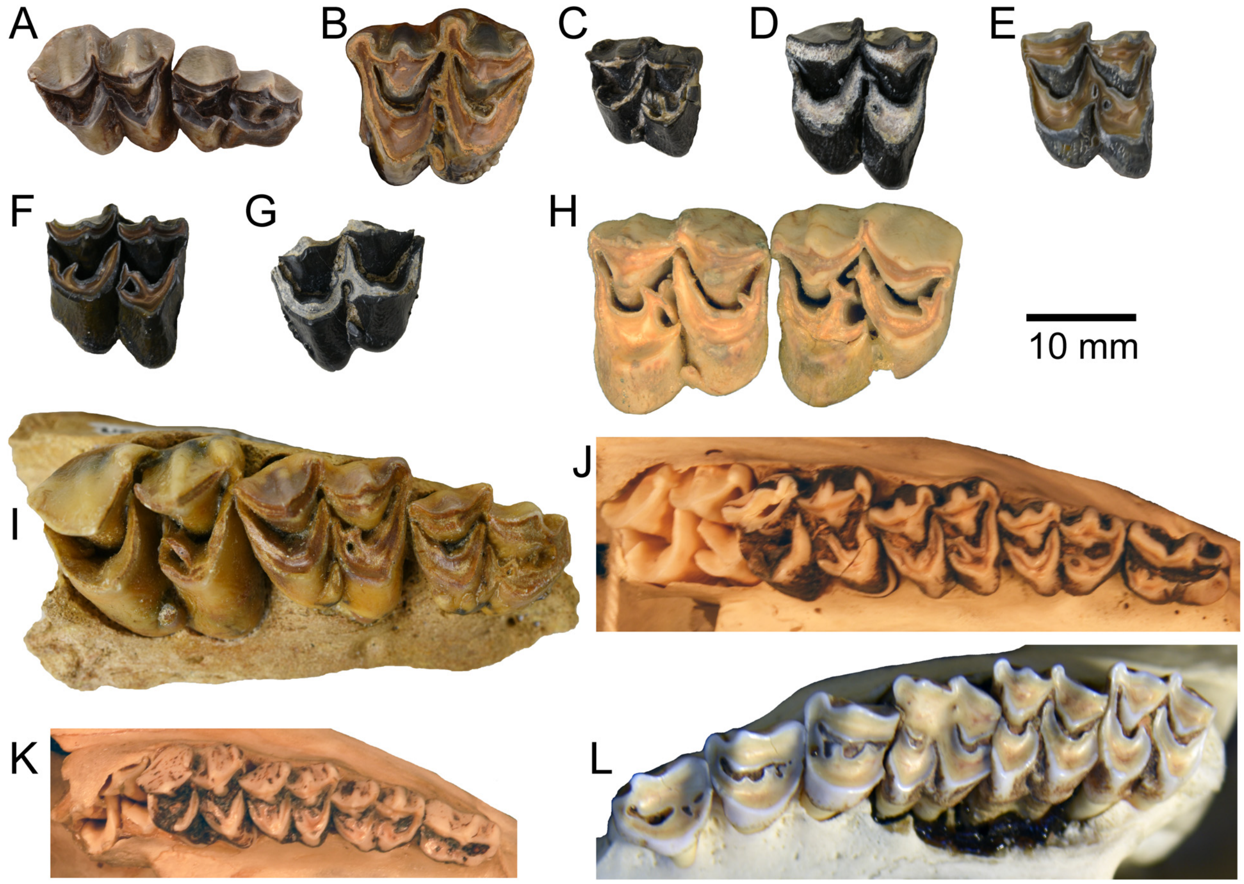

FIGURE 3. Dentition of *Eocoileus gentryorum* from the Gray Fossil Site compared to a sample of fossil and extant cervids: A) ETMNH 6166 *Eocoileus gentryorum* right dP4 and dP3; B) ETMNH 40000 *Eocoileus gentryorum* left M2; C) UF 27479 *Eocoileus gentryorum* (Early Pliocene) right dP4; D) UF 6716 *Eocoileus gentryorum* right M1; E) UF 6712 *Eocoileus gentryorum* right M1; F) UF 162947 *Eocoileus gentryorum* right M2; G) UF 27518 *Eocoileus gentryorum* right M2; H) UMMP 28140 *Odocoileus brachyodontus* left M2 and M3; I) UF 276885 *Odocoileus virginianus* right dP3 - M1; J) USNM 108274 *Odocoileus virginianus yucatanensis* right dP2 - M2; K) USNM 61217 *Mazama temama* right dP2 - M2; L) AMNH 35488 *Capreolus capreolus* left P2 - M3. A – G are Early Pliocene in age, H is Pliocene, I is early Pleistocene, J and K are modern. Scale bar equals 10 mm.

anterior cingulum with a transversely elongate cingular cuspule along the anterior margin of the protocone, as well as a rugose posterior cingulum on the lingual and posterior margins of the metaconule bearing small cuspules.

Postcranial Material. A partial right humerus recovered from the site (ETMNH 10559, Figure 4) preserves the distal end and most of the diaphysis. The proximal end of the bone is missing, there is some weathering and damage to the medial portion of the trochlea, and the thin bone of the olecranon and coronoid fossa has eroded away to form an oval-shaped hole just proximal to the distal articulation. The distal articulation of ETMNH 10559 shows morphology typical of ruminants, with a capitulum characterized by a raised spline (carina of Gustafson, 2015) and distinct grooves in the capitulum and trochlea, which restrict mediolateral movements of the elbow joint. The lateral epicondyle and supracondylar ridge are fairly prominent, as are the medial projection associated with the origin of the flexor muscle complex and medial caudal protuberence.

Two nearly complete right tibiae have been recovered (ETMNH 8030 and ETMNH 14923, Figure 5). The proximal epiphysis and portions of the proximal portion of the diaphysis are missing in ETMNH 8030, while some portions of the proximal diaphysis and distal diaphysis are missing in ETMNH 14923. Each tibia is particularly gracile, and the tibial spine extends from the proximal epiphysis to nearly halfway down the diaphysis. The proximal end of ETMNH 14923 has a fairly broad and low intercondylar eminence, and the lat-

FIGURE 4. Humerus of *Eocoileus gentryorum* (ETMNH 10559) from the Gray Fossil Site, TN in anterior view, along with a comparative sample of fossil cervids: A) ETMNH 10559 *Eocoileus gentryorum* distal right humerus; B) UF 134788 *Eocoileus gentryorum* distal right humerus; C) USNM 299483 *Odocoileus brachyodontus* distal right humerus; D) UF 239717 *Odocoileus virginianus* right humerus. A and B are Early Pliocene in age, C is Pliocene, D is early Pleistocene. Scale bars equal 20 mm.

FIGURE 5. Tibiae of *Eocoileus gentryorum* from the Gray Fossil Site, TN in anterior view, along with a comparative sample of fossil and extant cervids: A) ETMNH 8030 *Eocoileus gentryorum* right tibia; B) ETMNH 14923 *Eocoileus gentryorum* right tibia; C) UF 212246 *Eocoileus gentryorum* proximal left tibia; D) UF 68022 *Eocoileus gentryorum* distal left tibia; E) UF 276268 *Odocoileus virginianus* left tibia; F) AMNH 35301 *Capreolus capreolus* left tibia. A – D are Early Pliocene in age, E is early Pleistocene, F is modern. Scale bars equal 20 mm.

eral surface has a prominent facet for articulation with the head of the fibula. The distal end has a prominent medial malleolus and deep fossae for articulation with the condyles of the astragalus.

The left astragalus (ETMNH 17218, Figure 6A-D) has some erosion evident across its surface, but the morphology of the bone is preserved with the exception of the medial tibial shelf, which is partially lost. The lateral and medial proximal condyles are prominent, and the proximal trochlear groove is relatively broad. There is a deep and mediolaterally broad interarticular fossa, as well as a prominent tibial stop (Gustafson, 2015). The lateral cubonavicular condyle has a distinct distal

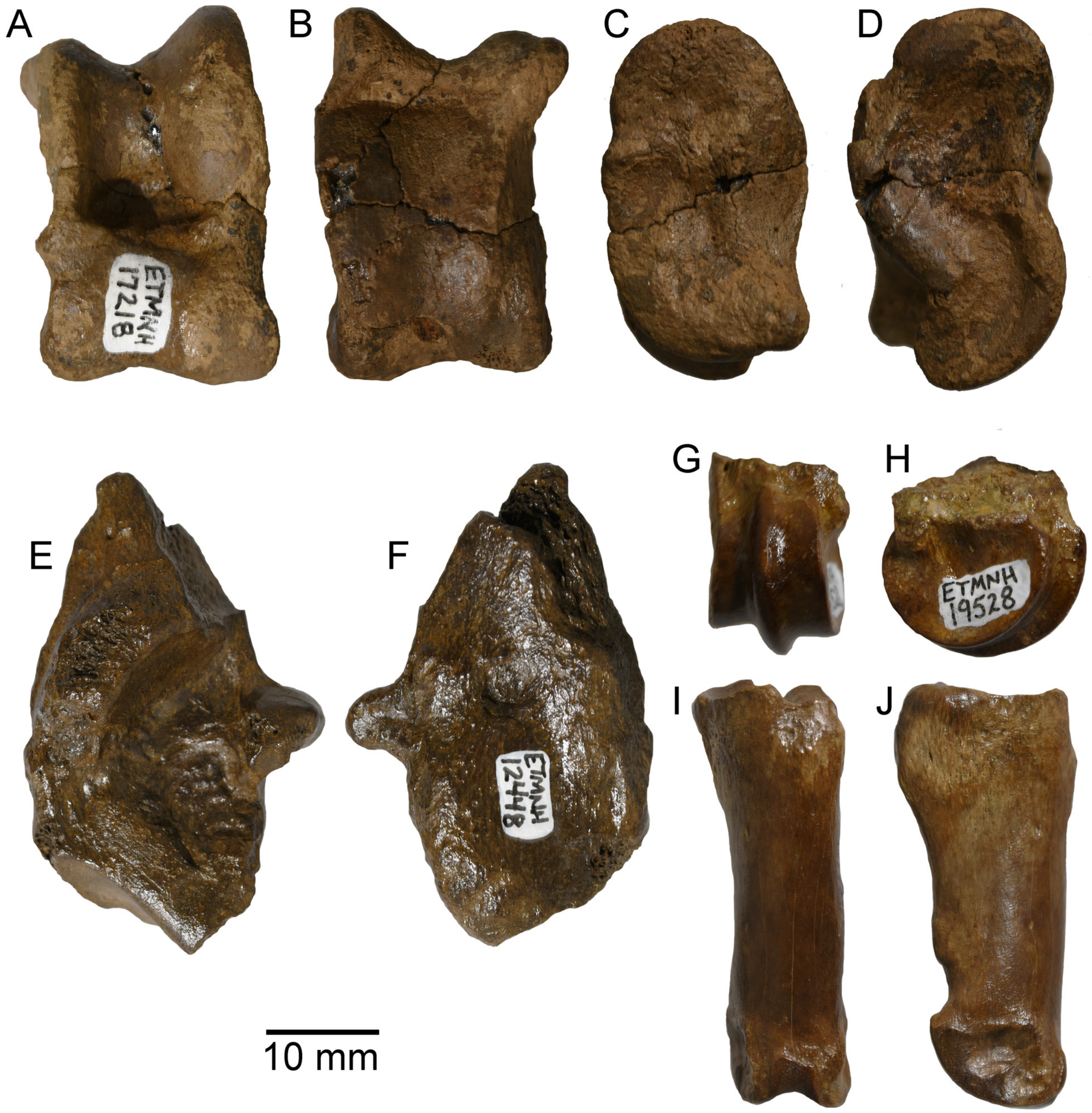

FIGURE 6. Pes elements of *Eocoileus gentryorum* from the Gray Fossil Site, TN: left astragalus ETMNH 17218 in A) anterior, B) posterior, C) lateral, and D) medial views; right calcaneum ETMNH 12418 in E) medial and F) lateral views; metapodial distal condyle ETMNH 19528 in G) anterior and H) lateral views; proximal phalanx ETMNH 10546 in I) anterior and J) lateral views. Scale bars equal 10 mm.

keel, which is relatively medially placed. The distal trochlea, between the lateral and medial cubonavicular condyles, is shallow. The sustentacular facet is roughly rectangular in shape (anteroposteriorly elongate) and has a relatively small lateral process on its proximal corner, though this feature is somewhat worn. The proximal edge of the sustentacular facet is relatively straight and at a right angle to the long axis of the bone.

The partial right calcaneum (ETMNH 12448) has the articular end preserved well, but most of the body and tuber calcanei are missing (Figure 6E-F). The preserved portion of the calcaneal body suggests the bone would have tapered toward the

TABLE 1. Dental measurements (in mm) of *Eocoileus gentryorum* from the Gray Fossil Site, and a comparative sample of upper dentition of Neogene cervid species. Measurements for *Bretzia pseudalces* derived from Gustafson (2015) and *Capreolus constantini* derived from Vislobokova et al. (1995). Complete listing of all measurements is included in Supplemental Table 3.

Taxon	Locality / Age	Specimen	dP3L	dP3W	dP4L	dP4W	M1L	M1W	M2L	M2W
Eocoileus gentryorum	Gray Fossil Site, TN Early Pliocene	ETMNH 6166 ETMNH 40000	13.13	9.5	13.31	12.28			17.43	15.48
Eocoileus	Palmetto Fauna,	Mean						13.88		
gentryorum	FL	Min			13.59	13.08	12.50	14.88	14.78	16.92
	Early Pliocene	Max					13.73		15.48	
Odocoileus brachyodontus	Fox Canyon, KS Pliocene	UMMP 28140							16.35	18.56
Odocoileus	Various (USA	Mean	12.47	11.15	15.11	13.77	15.50	14.24	16.57	15.32
virginianus (multiple	and Mexico)	Min	10.15	9.57	11.97	10.73	12.13	12.10	13.47	10.31
subspecies)	Extant	Max	14.66	13.44	17.65	15.31	17.78	16.26	20.28	17.95
Odocoileus virginianus	Inglis 1A Early Pleistocene	UF 276885	13.47	12.52	16.16	16.29	17.83	16.31		
Odocoileus	Various Extant	Mean					16.34	16.27	17.58	17.31
hemionus		Min	11.24	12.75	16.45	15.84	14.33	15.39	15.60	15.97
		Max					17.49	17.38	18.94	19.09
Odocoileus pandora	Extant Yucatan, Mexico	USNM 108287					10.42	9.45	10.82	10.73
Bretzia pseudalces	Ringold Fauna,	Mean					14.8	16.15	16.72	17.25
	WA	Min					13	15	15.7	15.9
	Early Pliocene	Max					16.2	17	17.4	17.9
Capreolus	Various	Mean					11.30	12.20	11.86	12.51
capreolus	Extant and	Min					10.94	11.25	11.54	11.70
	Holocene	Max					11.67	12.74	12.24	14.47
Capreolus	Udunga, Russia	Min					12.5	14.5	12.8	15.5
constantini	Late Pliocene	Max					13	16	14.7	17.2
Mazama temama	Yucatan, Mexico	Mean					10.84	10.79		
	Extant	Min	8.24	6.31	9.15	7.46	9.85	9.41	10.59	11.46
		Max					11.77	12.01		
Cervus canadensis	Various	Mean					25.21	26.23	28.15	25.21
	Extant	Min					22.54	25.25	24.12	22.43
		Max					27.79	27.38	31.01	26.54

tuber calcanei. The sustentaculum is broken but appears relatively small and obliquely oriented to the long axis of the bone. The sulcus for the deep flexor tendon is well-developed. The fibular condyle is particularly prominent and S-shaped, and there is a small shelf between the fibular facet and the interosseus fossa. The astragalar facet is broad and slightly convex. The cubonavicular facet faces relatively distally and extends onto a prominent triangular distal projection of the calcaneum.

The only metapodial element is ETMNH 19528, which represents a metapodial distal condyle (Figure 6G-H). The inner and outer trochlear surfaces are similarly broad and separated by a prominent and steeply inclined ridge. There are small, but distinct pits at the posterior (palmar) end of the trochlear surfaces. Though fragmentary, the shape of ETMNH 19528 indicates the presence of a pronounced intertrochlear notch.

There are two proximal phalanx specimens (ETMNH 10546, ETMNH 13918), and both taper gently distally (Figure 6I-J). The proximal articular surfaces are concave with a deep midsagittal groove, and the lateral glenoid is cavity shallower than the medial one. Small articular facets are present at the proximal posterior (palmar) surface. The distal articular surface has distinct medial and lateral condyles separated by a broad groove. Just anterior to the distal articulation on the posterior (palmar surface) is a distinct projection for insertion of digital flexors.

TABLE 2. Postcranial measurements (in mm) of *Eocoileus gentryorum* from the Gray Fossil Site, and a comparative sample of Neogene cervid species. Measurements for *Bretzia pseudalces* derived from Gustafson (2015), *Capreolus constantini* derived from Vislobokova et al. (1995) for Russia and Jiménez-Hidalgo and Bravo-Cuevas (2015) for Mexico. Elements are as follows: Hu = humerus, Ti = Tibia, Ast = Astragalus, Ph = Proximal Phalanx. Complete listing of all measurements is included in Supplemental Table 3.

Taxon	Locality / Age	Specimen	Hu APD	Hu MLD	HuDi ArtML	HuDi ArtAP	HuDi ML	HuDi AP	Ti L	Ti APD	Ti MLD	Ti PrML	Ti DiML	Ast L	Ast W	Ph L	Ph PrML	Ph DiML
Eocoileus gentryorum	Gray Fossil Site, TN Early Pliocene	ETMNH 10559 8030 14923 17218 10546 13918	20.68	15.47	24.95	16.58	30.44	26.78	237.64 252.56	15.98 18.84	17.16 16.9	41.35 44.22	28.2 26.45	34.26	20.45	35.73 36.58	13.08 12.83	10.87 10.59
Eocoileus gentryorum	Palmetto Fauna, FL Early Pliocene	Mean Min Max	22.62 18.88 29.73	16.27 15.56 17.88	28.16 24.99 30.39	17.68 16.10 19.63	31.18 27.47 33.99	29.88 27.08 32.21		19.97	18.64	42.12	28.03 26.57 30.66	33.51 30.13 35.41	20.25 19.36 21.19	35.18	9.42	7.52
Odocoileus virginianus (multiple subspecies)	Various (USA and Mexico) Extant	Min Max	21.36 26.50	16.31 22.16	32.32 38.81	19.47 20.58	35.18 36.11	35.49 38.93		17.81 17.83	20.15 20.93	50.48 53.28	30.77 30.86	28.6 37.75	17.73 23.54	34.40 50.25	14.65 15.57	12.47 13.21
Odocoileus virginianus	Various, FL Early Pleistocene	Min Max	22.87 26.50	19.95 22.16	33.59 38.81	20.01 25.29	38.09 43.88	35.22 41.76	271.93	22.21	22.01	44.50	33.00	36.87 39.77	22.95 25.88	48.17 48.49	13.74 14.94	11.67 12.35
Odocoileus hemionus	Various Extant	Min Max	23.29 27.91	19.21 23.71	36.93 42.16	20.87 24.37	35.03 43.47	35.02 40.89		18.56 21.97	22.2 27.98	51.65 61.76	34.36 38.70	35.63 42.45	20.63 28.24	44.24 48.66	14.54 16.81	12.61 14.05
Odocoileus brachyodontus	Hagerman, ID Late Pliocene	USNM 299483 418959		19.51	37.38	24.79	43.52	43.37						54.34	37.77	48.82	14.46	11.75
Bretzia pseudalces	Ringold Fauna, WA Early Pliocene	Mean Min Max		16.5				35.5	291.67 287 299		23.7 22.1 25.4	50.33 44.7 54.2	34.19 28.6 37.9	44.8	29			
Capreolus capreolus	Extant	Min Max							236.97 241.77	13.09 13.16	14.24 15.27	39.12 39.86	25.11 25.49	27.82 29.46	18.78 19.56			
Capreolus constantini	Udunga, Russia Late Pliocene	Min Max					31 33.2	31.4					27.5					
Capreolus constantini	Hidalgo, Mexico Late Pliocene	Min Max					40.52	38.23 39	275		24.7	59.5				43.12	16.38	13.27

Comparisons. Characteristics of the GFS cervid specimens are consistent with those of other early cervids in North America, and details of the dentition and postcrania facilitate comparisons to both fossil and extant cervid taxa. Upper dentition of *Eocoileus* has not been previously figured nor have any of the deciduous teeth, specimens from Tennessee and Florida as well as a range of comparative taxa are figured here (Figures 2 and 3). The dP3 of ETMNH 6166 is narrower anteriorly (smaller protocone and paracone) than in other cervids studied (Table 1, Figure 3, but note that dP3 was only present in specimens of *Odocoileus virginianus*, *O. hemionus*, and *Mazama temama*). The relatively small dP3 protocone of ETMNH 6166 is similar to the dP3 protocone of other pecorans like the Dromomerycidae, possibly reflecting retention of a plesiomorphic state in the deciduous dentition of this early cervid. In both GFS cervid specimens, the posterior crest of the upper molar protocone is fused with anterior crest of the metaconule early in wear. Fusion of the protocone to metaconule is typical of worn upper molars in cervids, but does show variability in studied specimens of *Eocoileus, Odocoileus, Capreolus,* and *Mazama* (illustrated in Figure 3). According to Gustafson (2015), the protocone and metaconule are always unfused in *Bretzia*, and those cusps are similarly unfused in the upper molars of dromomerycids. In both upper molar specimens from GFS, there is a small entostyle present between lingual crescents, as is typical of cervids. The upper molar entostyle is always present in *Bretzia* (Gustafson 2015), but occurrence is variable in some other taxa: *Eocoileus gentryorum* (present in 3 of 5), *Mazama temama* (present in 2 of 4), and the small subspecies of white-tailed deer from the Yucatan of Mexico *(O. virginianus yucatanensis)* (present in 1 of 4). The posterior crest extending from the M2 protocone is bifurcated in ETMNH 40000, which is typical of cervids. Note that this bifurcation does variably occur in studied specimens of *Eocoileus gentryorum* (bifurcated in 4 of 5) and *Capreolus capreolus* (bifurcated in 3 of 4). The occurrence of anterior and posterior cingula varies in specimens of *Eocoileus gentryorum* from Florida (Figure 3). In ETMNH 40000 (Figure 3B) there is a rugose posterior cingulum on the lingual and posterior margins of the metaconule bearing small cuspules, and similar features are present in UF 27518 from Florida (Figure 3G). While anterior and posterior cingula are present in *Bretzia* (Gustafson, 2015), similarly rugose cingula were not seen among studied samples of any other cervid taxa from North America. More pronounced cingula are present in some earlier fossil cervids from Eurasia (Vislobokova, 2012; Croitor, 2014, 2018). It is important to note that the unusual features of ETMNH 6166 (small dP3 protocone, lack of bifurcation of posterior crest of dP4 protocone) led the lead author to initially identify that specimen as a dromomerycid (noted in the biostratigraphic list of Samuels et al., 2018), but broader examination of those features has documented their occurrence in other cervid samples.

The sizes of upper teeth from GFS are interesting, as ETMNH 6166 is similar in size to a dP4 specimen (UF 27479) in the sample of *Eocoileus gentryorum* from Florida (Table 1, Figure 7A) and smaller than Pliocene *Bretzia pseudalces* and *Capreolus constantini*, and modern *Odocoileus* other than *O. pandora, O. virginianus clavum,* and *O. virginianus yucatanensis.* In contrast, ETMNH 40000 is longer but narrower than M2 specimens of E. *gentryorum* from Florida (Figure 7B), comparable in size to modern and Pleistocene records of *Odocoileus virginianus*. The disparate sizes of these specimens may reflect sexual dimorphism or other forms of intraspecific variation in the sample of deer from GFS. Among the sample of *O. virginianus* studied here there is large variation in tooth size (Figure 7, Supplemental Table 3), greater than 25% among individuals (even when excluding *O. virginianus clavium* and *O. virginianus yucatanensis*). While ETMNH 40000 is relatively large, nearly as large as Pliocene *Odocoileus brachyodontus* (UMMP 28140) and early Pleistocene *O. virginianus* (UF 276885), the morphological features of the specimen are within the range of variation of known specimens of *E. gentryorum* and support assignment to that species rather than some other cervid taxon.

The right humerus from GFS, ETMNH 10559, is very similar in size to specimens of *Eocoileus gentryorum* from Florida (Table 2, Figure 8), but far smaller than Pliocene records of *Odocoileus brachyodontus, Capreolus constantini,* and *Bretzia pseudalces* and modern *O. virginianus* and *O. hemionus*. The structure of the distal articulation of ETMNH 10559 is typical of cervids (Figure 4), with the medial trochlea substantially mediolaterally broader than the lateral capitulum. The lateral epicondyle and supracondylar ridge of ETMNH 10559 are relatively prominent in comparison to extant *Odocoileus*, which is also true of late Pliocene *O. brachyodontus* (USNM 299483) from the Hagerman local fauna of Idaho (Figure 4). Similarly, the medial projection associated with the origin of the flexor muscle complex is prominent in ETMNH 10559, *O. brachyodontus* USNM 299483, and some extant *O. virginianus*, much more so than in studied specimens of *Eocoileus gentryorum* from Florida or *B. pseudalces* (Gustafson, 2015). The medial caudal protuberance is large in ETMNH 10559, similar to that of *O. virginianus* (Jacobson, 2003) and larger than in *O. hemionus*.

The cervid tibiae recovered from GFS (ETMNH 8030, 14923) are both from the right side, indicating they come from two different individuals. These tibiae are relatively gracile (Figure 5, Table 2), like studied specimens of *Eocoileus gentryorum* from Florida and extant *Capreolus capreolus*, and slenderer than those of *Odocoileus virginianus*, *C. constantini*, and *Bretzia pseudalces*. As in *E. gentryorum* from Florida and *O. virginianus*, the tibial spine (=anterior tibial crest of Gustafson, 2015) extends from the proximal epiphysis to nearly halfway down the diaphysis, which contrasts with the relatively shorter tibial crest of *B. pseudalces*, *C. capreolus*, and *C. constantini* (Gustafson, 2015; Jiménez-Hidalgo and Bravo-Cuevas, 2015). The relatively broad and low intercondylar eminence in the proximal end of ETMNH 14923 (Figure 5B) is similar to specimens of *E. gentryorum* from Florida, *B. pseudalces*, and extant *Odocoileus*, as is the structure of the distal end, which has a prominent medial malleolus and deep fossae for articulation with the astragalus.

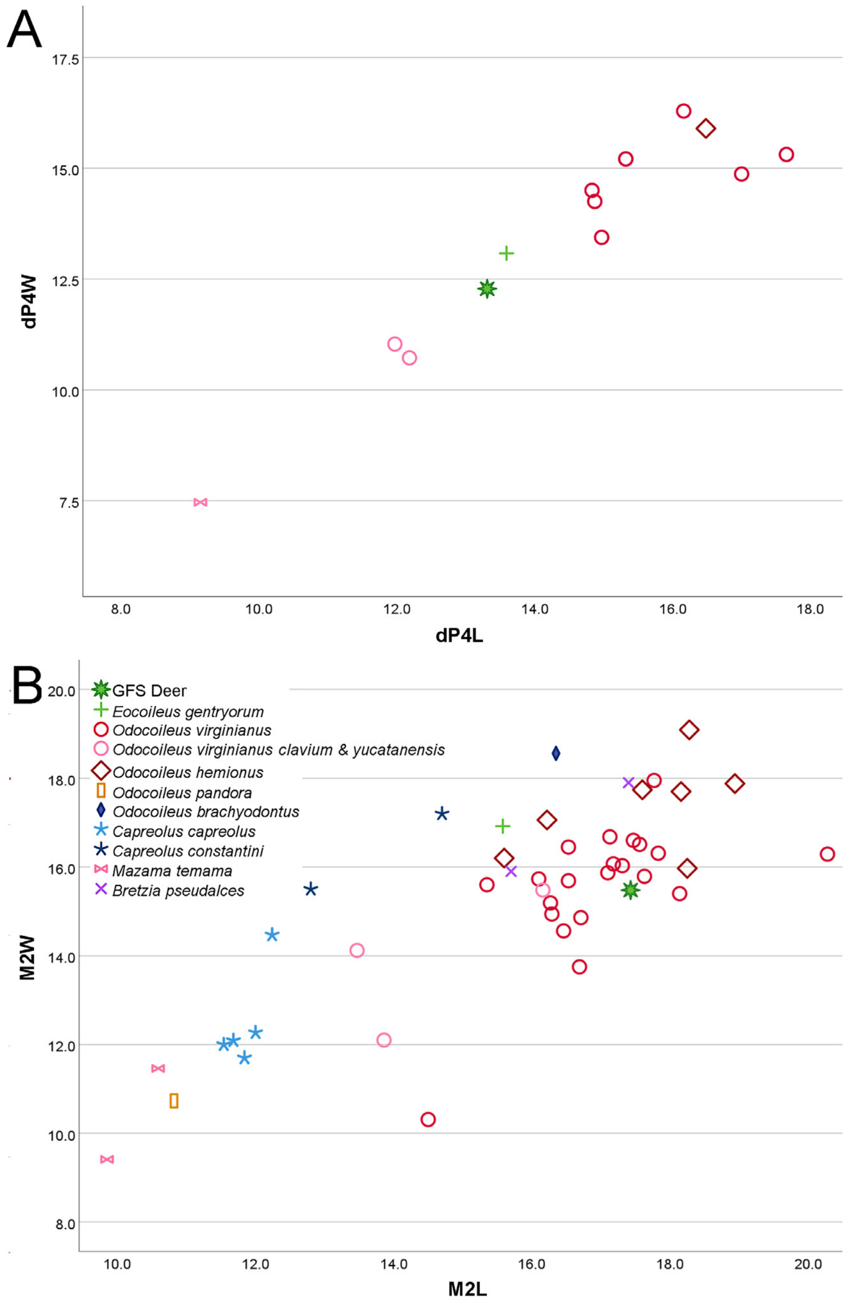

FIGURE 7. Bivariate plots of upper tooth lengths and widths in millimeters of extant and fossil Cervidae. A) dP4; B) M2. Complete listing of all measurements is included in Supplemental Table 3.

Morphology and size of the GFS astragalus (ETMNH 17218, Figure 6A-D) falls within the range of variation of specimens of *Eocoileus gentryorum* from Florida and is smaller than the studied specimens of *Odocoileus hemionus* and *O. virginianus* from multiple subspecies, with the exception of the Key Deer *O. virginianus clavium* (Table 2, Figure 8B). The astragali of *E. gentryorum* and *O. virginianus* are relatively anteroposteriorly elongate compared to *O. brachyodontus*, *Bretzia*, and *Capreolus*. As is the case for specimens of *Eocoileus gentryorum* from Florida, the sustentacular facet of ETMNH 17218 is more rectangular in shape (anteroposteriorly elongate) than in *Bretzia* and *Odocoileus (O. brachyodontus* and *O. virginianus).* The straight proximal edge of the sustentacular facet in ETMNH 17218 is also seen in *Odocoileus, Mazama, Capreolus,* and *Bretzia* (Morejohn and Dailey, 2004; Gustafson, 2015; Palma-Ramírez et al., 2023). Jacobson (2003)

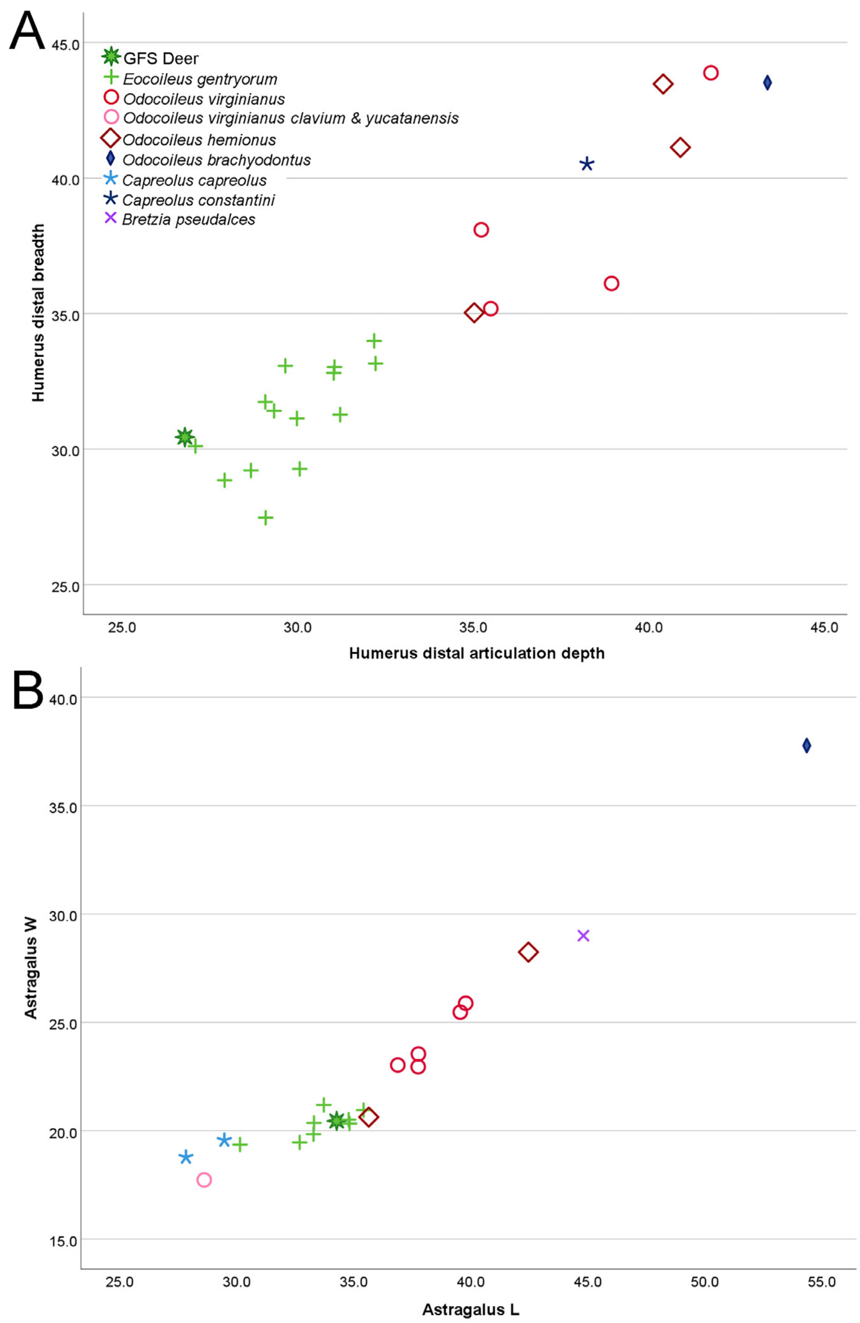

FIGURE 8. Bivariate plots of selected postcranial measurements in millimeters in extant and fossil Cervidae. A) humerus distal breadth and distal articulation depth; B) astragalus length and width. Complete listing of all measurements is included in Supplemental Table 3.

noted a well-defined ridge running at an angle medially to laterally along the distal edge of the lateral proximal condyle in *O. virginianus*, but not *O. hemionus*. ETMNH 17218 has erosion to its surface in that area, precluding confident assessment of that feature, but that ridge is present in *E. gentryorum* (UF 27516) and early Pleistocene *O. virginianus* (UF 276402) from Florida. The incomplete preservation of the right calcaneum from GFS (ETMNH 12448, Figure 6E-F) precludes detailed comparisons to other cervid taxa. Morphological features and size of ETMNH 12448 fall within the range of variation observed among studied specimens of *Eocoileus gentryorum* from Florida (UF 27530, 125058, 135604); the GFS calcaneum is also similar in morphology to an incomplete calcaneum of *Odocoileus brachyodontus* (USNM 418959) from the Pliocene of Idaho, but the GFS specimen is substantially smaller.

ETMNH 19528 (Figure 6G-H), a metapodial distal condyle, is similar in morphology to several metatarsal specimens of *Eocoileus gentryorum* from Florida (UF 134798, 134199). Those specimens all have distal condyles with similarly broad inner and outer trochlear surfaces separated by a steeply inclined ridge, as well as small pits at the posterior ends of the trochlear surfaces. Both metatarsals of *Eocoileus* also display a deep intertrochlear notch, as is suggested by the morphology of ETMNH 19528. The GFS and Florida *Eocoileus* specimens have distal condyles similar in size, and these are all substantially smaller than in studied specimens of *Odocoileus (O. virginianus, O. hemionus,* and *O. brachyodontus)* and dimensions reported for *Bretzia* (Gustafson, 2015) and *Capreolus* (Vislobokova et al., 1995; Jiménez-Hidalgo and Bravo-Cuevas, 2015). The two proximal phalanges from GFS (ETMNH 10546, ETMNH 13918) are similar in length and general shape to a phalanx identified as cf. *Eocoileus* sp. from Fort Green Mine in Florida (UF 216983). The morphology of both the GFS and Florida specimens referred to *Eocoileus* is similar to studied specimens of extant and fossil *Odocoileus (O. virginianus, O. hemionus,* and *O. brachyodontus).* The GFS phalanges are more mediolaterally robust than UF 216983 (Table 2), showing similar robustness to that of *Capreolus constantini* from Mexico (Jiménez-Hidalgo and Bravo-Cuevas, 2015). With the exception of Key deer *(O. virginianus clavium),* the GFS and Florida specimens are also smaller than all studied specimens of *Odocoileus* (Table 2), those noted by Palma-Ramírez et al. (2023), and proximal phalanges reported for *Capreolus* (Jiménez-Hidalgo and Bravo-Cuevas, 2015). The insertion for the distal flexor on the posterior surface of the phalanx is more prominent in the GFS specimens than in the Florida phalanx, similarly to that of *O. brachyodontus* from Idaho (USNM 418959). It is also worth noting that the morphology of the proximal articular surfaces of ETMNH 10546 are compatible for articulation with the distal metapodial condyle of ETMNH 19528 (Figure 6I-J).

DISCUSSION

The rare records of a cervid from the Gray Fossil Site, referred here to *Eocoileus gentryorum*, are the first ruminants recovered from this well-known site. Much has been written about the GFS tapirs (Hulbert et al., 2009; McConnell and Zavada, 2013; Maclaren et al., 2018; DeSantis et al., 2020; Schap and Samuels, 2020) and rhinos (Short et al., 2019), and those large perissodactyls are clearly the predominant members of the large herbivore guild. Tapirs at GFS have an MNI of >160 and rhinos 11 (Inabinett, personal commun.). Equids, which are particularly abundant at most fossil sites from the Early Pliocene, are only currently represented by 15 total specimens from GFS, which have been referred to *Cormohipparion emsliei* by Wallace et al., 2011 (in Schubert and Mead, eds. 2011). Far less is known about the artiodactyls from GFS, the best known of which are tayassuids (Doughty et al., 2018), represented by at least four individuals. Rare remains of camel have also been noted from GFS (Wallace and Wang, 2004), currently being described as representing two taxa (Maden and Samuels, In Preparation).

Morphology and size of the GFS deer specimens are consistent with the range of variation of contemporaneous *Eocoileus gentryorum* from Florida. Unfortunately, the type specimen and figured specimens in the original description of *E. gentryorum* (Webb, 2000) do not overlap with the GFS materials, but elements referred to *E. gentryorum* in the original publication (appendix 4.1 of Webb, 2000) and additional Palmetto fauna specimens referred to *Eocoileus* in the UF collection match GFS dental and postcranial specimens well. While an antler or cranium from GFS might someday indicate that this represents a distinct species, at this time the most parsimonious conclusion is that the Tennessee and Florida samples are one species, thus we refer to the GFS cervid as *Eocoileus gentryorum*. These Early Pliocene deer from Tennessee and Florida are smaller than extant and fossil cervids in North and Central America, with the exception of Key deer *(O. virginianus clavium),* Yucatan brown brocket deer *(Odocoileus pandora),* and Central American red brocket deer *(Mazama temama).*

The *Eocoileus* specimens described here from Tennessee are among the oldest records of Cervidae in North America and the only pre-Pleistocene records of deer from the Appalachian region. The earliest records of the family Cervidae in North America date to the late Miocene or earliest Pliocene, including occurrences of *Bretzia pseudalces* in Washington (Gustafson, 2015; Emery-Wetherell and Schilter, 2020) and *Eocoileus gentryorum* in Florida (Webb, 2000; Webb et al., 2008). Along with the early occurrence of *Eocoileus* at GFS are early records of *Bretzia* from California, New Mexico, and Nebraska. In addition to

Bretzia and *Eocoileus*, other Pliocene age occurrences of cervids include *Odocoileus* (Hibbard, 1941; Robertson, 1976; Webb, 1998; Wheatley and Ruez, 2006; Palma-Ramirez et al., 2023) and *Capreolus* (Jiménez-Hidalgo and Bravo-Cuevas, 2015). In sum, the North American fossil record of cervids indicates rapid dispersal across the continent in the late Miocene or Early Pliocene (Figure 1, Supplemental Table 1) and early divergence of modern taxa (Webb, 2000; Croitor, 2022).

Deer (Cervidae) are the most abundant and species-rich group of ruminants in the New World, and represent key components of nearly every terrestrial ecosystem in the Americas and Eurasia (Hanley, 1996; Geist, 1998; Webb, 2000; Rooney, 2001; Côté et al., 2004). Similarity of the GFS deer to *Eocoileus* and extant deer (*Odocoileus* spp.) suggest they occupied similar niches, providing an important point of continuity between Early Pliocene and modern mammal communities in the Appalachian Highlands. These deer are versatile browsers capable of occupying a wide range of habitats, and these new fossils may indicate they have survived in the Appalachian forests through dramatic climate changes of the Pliocene and Pleistocene. Though fragmentary, these early deer fossils help reveal the origin of a ubiquitous component of Appalachian forests and improve understanding of Neogene faunal evolution in the southern Appalachians.

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SUPPLEMENTAL MATERIAL

SUPPLEMENTAL TABLE 1. Late Miocene to early Pleistocene occurrences of Cervidae in the fossil record of North America. Geographic and chronologic data were derived from a wide range of literature sources, as well as occurrences listed in the MIOMAP/FAUNMAP Databases (Carrasco et al., 2007; Graham and Lundelius, 2010; http://www.ucmp.berkeley.edu/neomap/) and NOW Database (The NOW Community, 2024; http://nowdatabase.org/). Note that some occurrences lack generic assignments while others are contentious, these are labeled as “indet.” below.

Locality Number (NOW Database)	Locality Name	Age	NALMA	Taxon	Lat., Long. Coordinates
Pacific Northwest PN2B	Craig's Hill	7.41-4.9 Ma	late Hemphillian	cf. *Bretzia* sp.	46.633, -120.549
Pacific Northwest PN3C	White Bluffs local fauna	4.98-4.81 Ma	latest Hemphillian or earliest Blancan	*Bretzia pseudalces*	46.279, -119.192
Pacific Northwest PN4	Ringold fauna	4.91-2.63 Ma	early Blancan	*Odocoileus* sp.	47.0425, -122.893056
Pacific Northwest PN23A	Hagerman Local Fauna	3.79-3.40 Ma	early Blancan	*Odocoileus brachyodontus*	42.776846, -114.949329
Pacific Northwest PN23C	Birch Creek	2.63-1.8 Ma	late Blancan	*Bretzia* sp.	43.613739, -116.237651
California Coast CC39	Upper Etchegoin Formation	4.2-3.6 Ma	early Blancan	*Bretzia* sp.	35.9, -120
California Coast CC43A	Tehama Local Fauna	4.91-2.63 Ma	early Blancan	*Bretzia* sp.	40.024, -122.123
California Coast CC46	Aguanga	2.63-1.8 Ma	late Blancan	indet	33.442, -116.865
Northern Great Basin NB13C	Anza-Borrego/ Vallecito Creek	2.63-0.9 Ma	late Blancan or early Irvingtonian	*Odocoileus* sp.	38.555605, -121.468926
Northern Great Basin NB35IIIA	Washoe Local Fauna	5.91-4.91 Ma	late Hemphillian	indet	39.160833, -119.753889
Northern Great Basin NB35IIIB	Buckeye Creek Local Fauna	4.91-2.63 Ma	early Blancan	*Odocoileus* sp.	38.976667, -119.539722
Northern Great Basin NB36	Wichman Faunule	4.91-1.8 Ma	early or late Blancan	indet	38.66666667, -118.9166667
West Coast Marine WM26	San Diego Formation	4.91-2.63 Ma	early Blancan	indet	32.715, -117.1625
Southern Great Basin SB14F	Curtis Ranch	2.63-1.8 Ma	late Blancan	*Odocoileus* sp.	32.11361, -109.92111
Southern Great Basin SB15A	Duncan Arizona	4.91-2.63 Ma	early Blancan	*Odocoileus* sp.	33.101667, -109.268611
Southern Great Basin SB18II	111 Ranch	2.63-1.8 Ma	late Blancan	*Cervus* sp.	32.801731, -109.632858
Southern Great Basin SB31D	San Simon Local Fauna	2.63-1.8 Ma	late Blancan	*Odocoileus* sp.	32.267800, -109.228000
Southern Great Basin SB34IIA	Walnut Canyon local fauna	5.91-4.91 Ma	late Hemphillian	indet	34.156, -108.319
Southern Great Basin SB34IV	Pearson Mesa Local Fauna	2.63-1.8 Ma	late Blancan	*Odocoileus* sp.	35.667222, -105.964444
Southern Great Basin SB35C	Arroyo de la Parida	4.91-2.63 Ma	early Blancan	*Odocoileus* sp.	34.081, -106.884
Southern Great Basin SB37D	Mesilla Basin Fauna B	2.63-0.9 Ma	late Blancan or early Irvingtonian	*Odocoileus* sp.	32.16667, -106.8333
Southern Great Basin SB38IIC	Arroyo Ojito Formation	4.91-2.63 Ma	early Blancan	indet	35.667222, -105.964444

Locality Number (NOW Database)	Locality Name	Age	NALMA	Taxon	Lat., Long. Coordinates
Southern Great Basin SB50	Red Light Local Fauna	2.63-1.8 Ma	late Blancan	*Odocoileus* sp.	30.75, -105
Southern Great Basin SB63	Minaca Mesa & Hearst Ranch, Chihuahua	4.91-2.63 Ma	early Blancan	*Odocoileus* sp.	28, -107.25
Southern Great Basin SB65	Rancho Viejo, Guanajuato	4.91-1.8 Ma	early or late Blancan	*Odocoileus* sp.	21.01666667, -100.7833333
Central America CA6B	Noc Ac, Merida, Mexico	4,91-2.63 Ma	early Blancan	indet	21.066668, -89.71668
Southern Great Plains SP1H	Cita Canyon Local Fauna	2.63-1.8 Ma	late Blancan	*Odocoileus* sp.	34.97, -101.9
Southern Great Plains SP5	Blanco Local Fauna	2.63-1.8 Ma	late Blancan	*Odocoileus brachyodontus*	29.910577, -95.060882
Southern Great Basin SB49	Huspeth Local Fauna	2.63-1.8 Ma	late Blancan	*Odocoileus* sp.	30.267222, -97.763889
Central Great Plains CP97	Pickstown and Wood Sand Pit	2.63-1.8 Ma	late Blancan	indet	43.21, -98.59
Central Great Plains CP116F	Santee fauna	5.91-4.91 Ma	late Hemphillian	*Bretzia pseudalces*	42.815833, -97.725278
Central Great Plains CP117A	Lisco Local Fauna	4.91-2.63 Ma	early Blancan	*Odocoileus* sp.	40.809868, -96.675345
Central Great Plains CP128C	Rexroad Local Fauna	4.91-2.63 Ma	early Blancan	*Odocoileus brachyodontus*	39.055833, -95.689444
East Coast Marine EM8B	Lee Creek Mine	5.333-3.6 Ma	late Hemphillian or early Blancan	indet	35.4, -76.8
Gulf Coast GC13B	Palmetto Fauna	5.0-4.7 Ma	late Hemphillian or early Blancan	*Eocoileus gentryorum*	28.18222, -81.82417
Gulf Coast GC14A	Santa Fe River	2.63-1.8 Ma	late Blancan	*Odocoileus* sp.	30.23, -82.63
Gulf Coast GC15A	Haile 15A	2.63-1.8 Ma	late Blancan	*Odocoileus virginianus*	29.61667, -82.36667
Gulf Coast GC16	St. Petersburg Times Site	2.63-1.8 Ma	late Blancan	*Odocoileus* sp.	27.78333333, -82.68333333
Gulf Coast GC17A	Macasphalt Shell Pit Local Fauna	2.63-1.8 Ma	late Blancan	*Odocoileus virginianus*	27.366667, -82.45
Gulf Coast GC18IV	Nashua Formation	1.8-0.9 Ma	Irvingtonian	*Odocoileus virginianus*	28.133333, -81.631667
Central East America CE1	Gray Fossil Site	4.9-4.5 Ma	latest Hemphillian or early Blancan	*Eocoileus gentryorum*	36.386559, -82.498451
	Stanton County, NB		latest Pleistocene or early Holocene	*Bretzia nebrascensis*	41.950, -97.223
	Lincoln County, SD		latest Pleistocene or early Holocene	*Bretzia nebrascensis*	43.280, -96.720
	Atotonilco El Grande Formation	4.2-2.63 Ma	early Blancan	*Capreolus constantini*	20.307, -98.765
	los Hornitos	3.9-2.6 Ma	Blancan	*Odocoileus virginianus*	30.413, -109.386
	El Golfo de Santa Clara	1.8-0.9 Ma	Irvingtonian	*Odocoileus virginianus*	28.009, -110.924

SUPPLEMENTAL TABLE 2. Definitions of dental and postcranial measurements in this study. Measurements generally follow von den Driesch (1976); note that proximal phalanx measurements directly match those of Palma-Ramirez et al. (2023).

dP3L = deciduous P3 length

dP3W = deciduous P3 width

dP4L = deciduous P4 length

dP4W = deciduous P4 width

M1L = M1 length

M1W = M1 width

M2L = M2 length

M2W = M2 width

HuAPD = Humerus midshaft anteroposterior diameter

HuMLD = Humerus midshaft mediolateral diameter

HuDiArtML = Humerus distal articular (capitulum and trochlea) mediolateral breadth (=BT of von den Driesch, 1976)

HuDiArtAP = Humerus distal articular (capitulum and trochlea) anteroposterior breadth

HuDiML = Humerus distal mediolateral epicondylar breadth (=Bd of von den Driesch, 1976)

HuDiAP = Humerus distal anteroposterior epicondylar breadth

TiL = Tibia length (=GL of von den Driesch, 1976)

TiAPD = Tibia midshaft anteroposterior diameter

TiMLD = Tibia midshaft mediolateral diameter

TiPrML = Tibia proximal end mediolateral breadth (=Bp of von den Driesch, 1976)

TiDiML = Tibia distal end mediolateral breadth (=Bd of von den Driesch, 1976)

AstL = Astragalus maximum anteroposterior length (=GLl of von den Driesch, 1976)

AstW = Astragalus maximum mediolateral width (=Bd of von den Driesch, 1976)

PhL = Proximal phalanx length (=GL of von den Driesch, 1976)

PhPrML = Proximal phalanx proximal end mediolateral breadth (=Bp of von den Driesch, 1976)

PhDiML = Proximal phalanx distal end mediolateral breadth (=Bd of von den Driesch, 1976)

SUPPLEMENTAL TABLE 3. Dental and postcranial measurements (in mm) of all specimens of *Eocoileus gentryorum* from the Gray Fossil Site, and a comparative sample of Neogene and modern cervid species. For UF specimens of *E. gentryorum* we indicate whether specimens were among the referred list in Webb (2000) or identified as such later. (This table is supplied as a spreadsheet for download at https://palaeo-electronica.org/content/2025/5616-early-pliocene-deer-from-tennessee)