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Winston P. Smith[1], Institute of Arctic Biology, University of Alaska – Fairbanks, 10915 Glacier Highway Juneau, Alaska 99801,

Leslie N. Carraway, Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Nash Hall, 2820 SW Campus Way, Corvallis, OR 97331

Thomas A. Gavin, Department of Natural Resources & the Environment, Cornell University, 226 Mann Drive, Ithaca, NY 14853

and

Jonathan A. Jenks, Department of Natural Resource Management, South Dakota State University, Box 2140B University Station, Brookings, SD 57007

Reconsidering Subspecific Taxonomy of *Odocoileus virginianus* in Oregon and Washington

Running footer: New Subspecies of *Odocoileus virginianus*

1 Table, 5 Figures, 3 Supplemental Tables (available online only)

[1]Author to whom correspondence should be addressed. Email: winstonpaulsmith@gmail.com

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Abstract

Two subspecies of white-tailed deer *Odocoileus virginianus* are recognized in the northwestern United States: *O. v. leucurus* (Douglas, 1829), and *O. v. ochrourus* Bailey, 1932. Historically, *O. v. leucurus* was common along the lower Columbia River and the name was applied to all populations in western Oregon as far south as Grants Pass. Today, *O. v. leucurus* is limited to populations along the Lower Columbia River with another in Douglas County, Oregon. Examination of 35 electrophoretic loci in 1988 did not support current subspecific taxonomy of *O. virginianus* in Oregon. Analysis of 18 cranial dimensions among three disjunct populations of *O. virginianus* in 2003 revealed variation that sorted into three corresponding distinct morphological groups in Oregon. Analyses of mtDNA and microsatellites at 15 autosomal loci from three subspecies of *O. virginianus* and 2 subspecies of *O. hemionus* (Rafinesque, 1817) revealed that each *O. v. leucurus* population possessed unique haplotypes, whereas *O. v. ochrourus* shared haplotypes with populations to the east. The most genetically differentiated whitetails were the 2 populations of *O. v. leucurus* (F_{ST} = 0.31), which were similarly differentiated from *O. v. ochrourus* (F_{ST} = 0.17–0.19); F_{ST} between *O. h. hemionus* and *O. h. columbianus* (Richarson, 1829) was 0.10. Thus, *O. v. leucurus* populations appear morphologically and genetically more different from each other than either is from *O. v. ochrourus*. Moreover, genetic differentiation among the three *O. virginianus* populations exceeds differentiation for existing subspecies of *O. hemionus*. We conclude the evidence warrants describing a new subspecies of *O. virginianus* in southwestern Oregon.

Keywords: cranial variation, genetic differentiation, isolated populations, subspecies

Introduction

White-tailed deer (*Odocoileus virginianus* Zimmermann, 1780) occur throughout much of the western hemisphere north of the equator; most authors recognize 30 subspecies in North and Central America (Hall 1981) and 8 additional subspecies in South America (Mendez-Arocha 1955, Smith 1991) with historical, but "unsatisfactory", taxonomic support (Gutiérrez et al. 2017, Burgin et al. 2020:3230). The Columbian white-tailed deer, *O. v. leucurus* (Douglas, 1829), originally described as *Cervus leucurus*, is one of two currently recognized subspecies of *O. virginianus* indigenous to the northwestern United States (Smith 1991).

According to his journal (Douglas 1914:58-59), David Douglas killed several white-tailed deer in the vicinity of the Multnomah (Willamette) River Falls. This is the location of the circled dot on Bailey's (1936:90) map, thus restricting the type locality of *O. v. leucurus* to the Willamette River Falls in the vicinity of Oregon City, Clackamas County, Oregon. Prior to Bailey's (1932) description of *O. v. ochrourus* (type locality: Coolin, south end of Priest Lake, Bonner County, Idaho), all white-tailed deer in Washington and Oregon, eastward into Montana, Idaho, and Wyoming were regarded as *O. v. leucurus*.

Douglas (1914) reported *Cervus leucurus* throughout the central river bottomlands of western Oregon, perhaps as far south as the Umpqua River Valley in what is now Douglas County. Crews (1939) extended the distribution south to Grants Pass, Josephine County, Oregon. To our knowledge, the relationship between deer from Douglas County and deer from the region of the type locality never was examined rigorously. When Bailey (1932) described *O. v. ochrourus***,** he compared his type specimen to white-tailed deer collected by Jewett (1914) from Douglas County, rather than to deer collected at or near the type locality of *O. v. leucurus*. Data

supporting the original descriptions of these two subspecies were limited and ambiguous, which was typical of that period (Smith et al. 2003).

Before European settlement, white-tailed deer occurred throughout most of western Oregon and the lowlands of southwestern Washington, and were common in broad river valleys and adjacent oak (*Quercus*) savannas because of their association with riparian vegetation and oak woodlands (Douglas 1829, Smith 1985a). Accompanying settlement was extensive development of western Oregon that supplanted much of the native vegetation and culminated in extirpation of *O. v. leucurus* from almost all of its historic distribution, most notably the Willamette Valley (Smith 1985a). According to Jewett (1914) and Bailey (1936), *O. v. leucurus* persisted in the Willamette Valley until late in the 19th century. Today, it occurs along the Lower Columbia River (LCR) as several island subpopulations upriver from a Washington mainland subpopulation. A second population, also known as the Roseburg herd, is located in interior valleys of the Umpqua River, Douglas County (DC), Oregon (Smith 1981, 1985a). *Odocoileus v. leucurus* remains allopatric to other western subspecies; according to Smith (1991), the nearest *O. v. ochrourus* is found about 300 km east of the current distribution of *O. v. leucurus*.

In 1967, the limited distribution of *O. v. leucurus* and imminent threat to remaining habitat prompted the US Fish and Wildlife Service to federally list the LCR population as endangered (Federal Register 1967). The DC population was added to the list in 1978 (Smith 1985a). Several reports documented the status of *O. v. leucurus* or provided information on its population ecology (Gavin et al. 1984; Smith 1985a, 1987; Smith et al. 2003), but only two examined its taxonomy or population genetics (Gavin and May 1988, Hopken et al. 2015).

Smith et al. (2003) analyzed variation in 18 cranial dimensions among three disjunct populations (northern Idaho, lower Columbia River, and Douglas County) of *O. virginianus* in the Pacific

Northwest to examine the hypothesis that they represented a single taxon. They found substantial variation in cranial dimensions among the three populations, which sorted graphically into three distinct morphological groups that corresponded with each population and exhibited east-west and north-south geographical gradients. Although their findings clearly challenged current taxonomy and rejected the hypothesis that the three groups represented a single taxon, Smith et al. (2003) cited a lack of sufficient evidence to make an unambiguous determination that the distinguishing morphological attributes had an evolutionary basis (Wehausen and Ramey 2000). Gavin and May (1988) compared allozymes from 35 loci among several *O. virginianus* populations representing three putative subspecies, including *O. v. ochrourus*, to evaluate the taxonomic status of *O. v. leucurus*. The genetic distance between the two *O. v. leucurus* populations and between each of the *O. v. leucurus* populations and the populations of *O. v. ochrourus* in eastern Washington and Oregon was less than the difference between two recognized subspecies of widely separated geographical regions. However, their study documented variation only at a single locus and recommended that an examination of additional evidence should be done before assigning subspecific status to any populations of *O. v. leucurus*. Hopken et al. (2015) also examined the genetics of deer of the Pacific Northwest and included *Odocoileus hemionus* (originally *Cervus hemionus*; Rafinesque 1817) in their assessment. Hopken et al. (2015:643) concluded that LCR and DC populations "may not be a monophyletic subspecies distinct from" *O. v. ochrourus* and stated that broader sampling was required to resolve subspecies relationships.

The focus of our paper is to further evaluate subspecific taxonomy of three disjunct populations of *Odocoileus virginianus* in the Pacific Northwest. We define subspecies as isolated, evolving populations of a species that are allopatric and phenotypically distinct, in which quantifiable

attribute differences are correlated with evolutionary independence as evidenced by population genetic structure (Braby et al. 2012). To accomplish this, we: 1) review cranial morphology of white-tailed deer from Douglas County, Oregon and the Lower Columbia River region, along with the historic distribution of *O. v. ochrourus* (Smith et al. 2003); 2) review recently published molecular data of five recognized subspecific taxa in the genus *Odocoileus* (including *O. hemionus*) in the Pacific Northwest (Hopken et al. 2015); 3) compare recent measures of genetic distance and genetic diversity among three disjunct populations of *O. virginianus*; and 4) compare genetic differentiation among three populations of *O. virginianus* to similar estimates among recognized subspecies of *O. hemionus* (Hopken et al. 2015).

Methods

Cranial Morphology

Mensural data on *O. virginianus* (Figure 1) from northern Idaho (group 1: 6 females, 12 males), the LCR region in Washington and Oregon (group 2: 65 females, 52 males), and DC in Oregon (group 3: 80 females, 49 males) are those reported by Smith et al. (2003). We added measurements of the cranium and mandible of an adult female collected 16 June 2020, and of an adult male collected 12 November 2020 from the DC population to compare their dimensions with those reported by Smith et al. (2003:Table 1).

Data were analyzed in SPSS 10.0.7 (SPSS, Inc., Chicago, IL) using the general linear model within a multivariate multiple analysis of variance (GLM MANOVA). Principal component analysis (PCA; Hair et al. 1987, Diersing 2019) was conducted with Systat 13.1 (Systat Information: Systat, Inc. 13, Palo Alto, CA). Sample locality (n = 3) and sex were treated as factors; age of individual deer was a covariate. Significance was evaluated at the α = 0.05 level.

Initially, a GLM MANOVA was performed only with specimens having complete datasets (group 1: 4 females and 2 males from Idaho; group 2: 14 females and 15 males from the lower Columbia River; and group 3: 29 females and 10 males from Douglas County). A second GLM MANOVA was performed after data for each specimen were standardized by dividing each measurement by the area of its foramen magnum ($A = 0.25\pi \times \text{width} \times \text{height}$) to reduce the effects of size (Radinsky 1967) and to examine potential differences among collection localities in skull configuration, which can be reflected in multivariate combinations of standardized cranial dimensions. We conducted a covariance-based PCA on standardized data for the 11 dimensions listed in Table 1 deemed significant in the second GLM MANOVA (Supplemental Table S1, available online only) to distinguish specimens among localities: 6 females and 3 males from Idaho (group 1); 19 females and 21 males from the lower Columbia River (group 2); and 37 females and 11 males from Douglas County (group 3). To further examine variation among locations, we conducted a MANOVA of PCA factor loadings, including an "all-pairs comparison" hypothesis test, and present a graphical plot of specimens among the three localities. Specimens examined are listed in Supplemental List S2, available online only.

Molecular Data

We searched the literature for molecular data that characterized and compared the population genetics of the three groups of *O. virginianus*. Specifically, we sought data on shared and unique haplotypes from mtDNA analyses, shared and unique markers from microsatellite DNA analyses, and estimates of genetic diversity and differentiation among the three groups. We also sought similar genetic data from studies that included putative subspecies of *Odocoileus hemionus* to use in comparisons when assessing the three groups of *O. virginianus*. These data

were available from a single study (Piaggio and Hopken 2009), which was further examined and elaborated on by Hopken et al. (2015).

Hopken et al. (2015) examined *Odocoileus* spp. samples from Oregon, Washington, Idaho, Nebraska, and Wyoming. Their final sampling included 80 deer from the LCR region of Oregon and Washington, 44 from Oregon (DC), and 77 from northeastern Oregon and southeastern Washington (NWWTD). Samples of *O. virginianus* in Idaho (IDWTD; $n = 10$), Nebraska (NEWTD; $n = 2$), and Wyoming (WYWTD; $n = 3$) served as outgroups. Hopken et al. (2015) also sampled *O. h. columbianus* (BTD; $n = 25$) from Douglas County and southern Washington and *O. h. hemionus* (MD; $n = 22$) from northeastern Oregon to include as outgroups and assess levels of hybridization. Mitochondrial DNA sequencing was accomplished by amplifying the hypervariable region I (HVI) of the mitochondrial DNA control region; for genomic sequencing, 17 microsatellite loci were amplified (Anderson et al. 2002, Piaggio and Hopken 2009:Table 1) in four multiplex panels (Hopken et al. 2015).

In 2021, we obtained fresh tissue samples from an adult male and adult female collected in Douglas County. We sent these samples to the same laboratory where samples in Hopken et al. (2015) were sequenced and analyzed. We compared sequences of the adult male (GenBank accession number OM524484) and adult female (GenBank accession number OM524483) to those reported in Hopken et al. (2015; GenBank accession numbers KP308220–KP308271).

Results

Cranial Morphology

There was substantial variation among populations in cranial dimensions (Table 1). The initial GLM MANOVA of the original data (Smith et al. 2003:Table 1) indicated that significant differences ($F = 3.991$–121.948, $df = 2$, $P < 0.022$) among specimens from the three sample

localities occurred for all variables. However, when the interaction of collection locality and sex was considered, only basilar length, least interorbital breadth, zygomatic breadth, and mastoid breadth were significantly different among localities (F = 3.256–9.487, df = 2, $P < 0.05$). A plot of basilar length and zygomatic breadth illustrated a decrease in size of male and female *O. virginianus* with northern Idaho > LCR > DC (Figure 2A). The second GLM MANOVA revealed significant differences (F = 3.14–12.56, df = 2, $P < 0.05$) in standardized skull dimensions for specimens among the three localities that included the following variables: basilar length, nasal length, breadth of the braincase, greatest width of nasals, least width of nasals, mastoid breadth, length of upper molariform series, maxillary length, palatilar length, depth of rostrum, and width of external nares (Supplemental Table S1, Figure 2B).

Values for these 11 standardized variables for specimens from the three localities were analyzed in a PCA (Figure 3). PC1 accounted for 93.2% of the variation in cranial morphology, and PC2 accounted for an additional 2.4% of the variation (Supplemental Table S3, available online only). In the plot of PC1 and PC2 (Figure 3), a MANOVA revealed the 3 localities were different from each other (location 1 vs. 2: Wilks's lambda = 0.557, F-ratio = 37.98, df = 2.93, $P < 0.0001$; location 1 vs. 3: Wilks's lambda = 0.456, F-ratio = 55.44, df = 2.93, $P < 0.0001$; and location 2 vs. 3: Wilks's Lambda = 0.333, F-ratio = 93.17, df = 2.93, $P < 0.0001$). Even after controlling for differences related to sex or age, ANOVA (F-ratio = 99.88, $P < 0.0001$) revealed specimens from group 3 (DC) were distinguishable on PC1 from those of groups 1 and 2 (Idaho and LCR, respectively; Bonferroni test, $P < 0.0001$) by a combination of shorter basilar and nasal lengths, narrower braincase, and narrower nasals (Table 1). On PC2, ANOVA (F-ratio = 33.36, $P <$ 0.0001) revealed specimens from northern Idaho (group 1) were distinguishable from those of group 2 (LCR) and group 3 (DC) (Bonferroni test, $P < 0.0001$) by having longer basilar lengths

and broader braincases. Idaho deer (group 1) also had narrower faces (i.e., smallest width of nasals) than LCR specimens (group 2). Thus, it is apparent that with size related to age or sex accounted for, DC specimens were on average smaller, with shorter faces and narrower skulls, than specimens from northern Idaho or the Lower Columbia River (Table 1).

Mitochondrial Diversity and Distribution

We examined the results of mitochondrial DNA sequences generated by Hopken et al. (2015) for 291 individuals (LCR = 80, DC = 44, IDWTD = 10, NEWTD = 2, NWWTD = 77, WYWTD = 3, BTD = 52, and MD = 23); 614 base pairs were sequenced successfully. Within the entire sample, 52 haplotypes were identified; 27 occurred in individuals identified as *O. virginianus* and 25 in deer identified as *O. hemionus*. The DC population contained a single unique haplotype (Hopken et al. 2015:Figure 3) with a private allele at the K locus (Hopken et al. 2015:Table 1). The LCR population contained three unique haplotypes and a private allele at locus BM4208 (Hopken et al. 2015:Table 1), with island and mainland subpopulations showing varying combinations and frequencies of each haplotype. None of the haplotypes in the LCR population were isolated within an island subpopulation or on either side of the Columbia River. However, differences in haplotype frequency demonstrated that, although mtDNA gene flow occurred among the subpopulations (regional panmixia), there was no range-wide admixture (Hopken et al. 2015). Some white-tailed deer in the LCR population contained *O. h. columbianus* haplotypes.

Microsatellite Diversity

Odocoileus taxa were genotyped at 15 autosomal loci by Hopken et al. (2015). Genetic diversity varied among putative taxa and populations. Mean number of alleles was 3.4–6.6, allelic richness was 3.4–6.0, and mean observed (HO) and expected (HE) heterozygosity were 0.4–0.7

per sampling locality (Hopken et al. 2015:Table 1). Both LCR and DC populations had lower genetic diversity compared with *O. v. ochrourus* (NWWTD), and also was lower than estimates of other *O. virginianus* from western North America (Cullingham et al. 2011). Within *O. virginianus*, NWWTD had the highest number of private alleles (APR = 22). LCR and DC samples each had one private allele. *Odocoileus hemionus hemionus* and *O. h. columbianus* had one and eight private alleles, respectively (Hopken et al. 2015).

Population Structure and Differentiation

The clustering algorithm in STRUCTURE v2.2 (Pritchard et al. 2000) used the highest posterior probability to determine number of genetic clusters, which was asymptotic at $k = 4$ (Piaggio and Hopken 2009:Figure 6, Hopken et al. 2015). Figure 4 illustrates a Structure Q-Plot of individual genotypes in which the three *O. virginianus* populations were assigned to one of three clusters that corresponded geographically with LCR (cluster 1), DC (cluster 2), or Idaho *O. v. ochrourus* (cluster 3). Two of cluster 3 individuals had 21% and 47% of their genotypes assigned to cluster 1 or cluster 2, respectively, and one individual in cluster 1 was assigned to *O. hemionus*. Two of cluster 1 individuals had 10% and 23% of their genotypes assigned to cluster 3. Two different individuals from cluster 1 were assigned 10% and 29% to cluster 2. One individual from cluster 2 had 31% of its genotype assigned to cluster 3. A previously unspecified cluster (cluster 4) contained all *O. hemionus* individuals (Figure 4). The clusters identified with STRUCTURE were used to estimate genetic divergence. As expected, the greatest genetic divergence (F_{ST} = 0.40–0.49) was between *O. virginianus* and *O. hemionus* (Hopken et al. 2015:Table 2). The greatest genetic divergence among *O. virginianus* populations was between DC and LCR (F_{ST} = 0.31), whereas *O. v. ochrourus* had similar values with LCR and DC (F_{ST} = 0.19 and 0.17

respectively). D_{EST} was 0.14–0.19 among the *O. virginianus* populations; the greatest divergence was between DC and LCR (Hopken et al. 2015:Table 2).

Based on corroborating morphological and molecular data, we conclude there are three distinct, disjunct populations and that current taxonomy of *O. virginianus* in Oregon warrants revision. The morphological and molecular data presented and cited throughout this publication further explain why the DC population of *O. virginianus* should be recognized as a separate subspecies, which we propose as

Family Cervidae Goldfüss, 1820

Subfamily Capreolinae Brookes, 1878

Tribe Odocoileini Pocock, 1923

Genus *Odocoileus* Rafinesque, 1832

Species *Odocoileus virginianus* (Zimmermann, 1780)

Odocoileus virginianus douglasi, new subspecies

Holotype—Skull and mandible of a road-killed adult male (Figure 5) collected 12 November 2020 and deposited in the Mammal collection of the Burke Museum of Natural History and Culture (UWBM 83081), University of Washington, 4300 15th Ave NE, Seattle, WA 98105.

Type locality—Oregon Highway 138 near Glide High School, Douglas County, Oregon, 43°17′56.56″N, 123°05′47.34″W (10T 492168 4794011).

Paratype—Skull and mandible of an 11-year-old female collected on 16 June 2020, 150 m east of Scotts Valley Road, 4.3 km NNE of Elkhead, Douglas County, Oregon, 43°34′18.50″N, 123°09′19.61″W and deposited in the Mammal collection at the Burke Museum of Natural History and Culture (UWBM 83080), University of Washington. This female had been captured

on 6 January 2009, ear-tagged, and fitted with a radio-transmitter as a yearling on Foster Lane, 43°16′05.22″N, 123°11′15.08″W (10T 484778 4790596), 8 km west of the type locality. State biologists relocated her to near Scotts Valley Road in northern Douglas County, Oregon. We selected this female as a paratype to function as an allotype to show morphological differences attributable to sex.

Diagnosis—Skull small with a short rostrum and narrow braincase. Basilar length, least interorbital breadth, and mastoid breadth all average smaller than those dimensions in samples of *O. v. leucurus* and *O. v. ochrourus*. Unique haplotype not shared with other populations of Northwestern white-tailed deer. Restricted to Umpqua River valley in Douglas County, Oregon.

Description—Odocoileus v. douglasi is at the smaller end of a geographical trend of decreasing size in both sexes from east to west and north to south (see Table 1). Mensural differences in basilar length, least interorbital breadth, zygomatic breadth, and mastoid breadth are significantly different between the three white-tailed deer subspecies. *Odocoileus v. ochrourus* is the largest and *O. v. leucurus* is intermediate in size. The F_{ST} measure of genetic distance (0.31) is greater between *O. v. douglasi* and *O. v. leucurus* than between adjacent subspecies of *Odocoileus hemionus* (F_{ST} = 0.10 between *O. h. hemionus* and *O. h. columbianus*).

Distribution—The geographic distribution is limited to Douglas County in southwestern Oregon, extending from Deer Creek, 10 km NE Mildred Kanipe State Memorial Park, south to Cow Creek, 5 km SW Riddle (Smith 1985a, USFWS 2013). The southeastern-most sightings were along Morgan Creek, 2 km north of its intersection with the South Umpqua River (Smith 1985a); the northwestern boundary extends at least to Dodge Canyon Creek near Highway 138, 12 km NW Sutherlin (USFWS 2013). The eastern and western boundaries are along the Umpqua River, 9 km E Glide, and 6 km W Umpqua, respectively. The total distribution encompasses about

1,425 km^2 (USFWS 2013). The distribution of *O. v. douglasi* is not continuous throughout because of the interspersion of small mountains and associated coniferous forests (Smith 1985a). The highest population densities of this taxon occurred along the south bank of the North Umpqua River between Glide and Winchester, north of Buckhorn Road (Smith 1985a, 1987). The natural vegetation of the region is classified as *Quercus* Woodland Community and is typical of the Interior Valley Zone of western Oregon (Franklin and Dyrness 1973). Smith (1985b) described plant associations within the interior valleys of the North Umpqua River.

Etymology—The new subspecies is named after David Douglas, a Scottish botanist who explored much of the Columbia River region during the early 19th century describing the fauna and flora. He described the subspecies *O. v. leucurus* in 1829 while in London, England, after his first trip (1824–1827) to the Oregon Territory (Douglas 1914).

Discussion

We expected under the current taxonomy that populations of *O. virginianus* from the Lower Columbia River region and Douglas County (*O. v. leucurus*) would be similar morphologically and genetically, yet distinguishable from populations in eastern Oregon, eastern Washington, and Idaho (*O. v. ochrourus*). Our results demonstrated significant differences among all three populations for several cranial dimensions (Table 1). Sample locality was the primary determining factor in a general linear model that examined standardized cranial dimensions of males and females among multiple age classes (Supplemental Table S1). There also was an obvious decrease in size of female and male *O. virginianus* from east to west and north to south, with individuals along the Lower Columbia River intermediate in size compared to individuals from northern Idaho and Douglas County (Figure 2). Principal component analysis clearly delineated three distinct morphological populations (Figure 3).

Similar geographical variation in cranial dimensions was reported for *Ovis canadensis* Shaw, 1804 (Wehausen and Ramey 1993, 2000), *Sus scrofa* Linnaeus, 1758 (Genov 1999), *Ursus americanus* Pallas, 1780 (Kennedy et al. 2002), and *O. virginianus* Zimmerman, 1780 (Molina and Molinari 1999). The primary consideration when interpreting cranial variation in the context of subspecific taxonomy is whether morphological variation is indicative of parallel genetic divergences, or is largely ecophenotypic variation that resulted from regional differences in habitat or other environmental differences (Wehausen and Ramey 2000, Kennedy et al. 2002, Patton and Conroy 2017, Diersing 2019). Some taxa show continuous variation in skull morphology corresponding to climatic or other environmental gradients (Kennedy et al. 2002), whereas other taxa show abrupt dissimilarity associated with geographical isolation (Diersing 2019) and display substantial genetic dissimilarity among regional populations (Miller 1995, Patton and Conroy 2017).

In our assessment, mtDNA and microsatellite data parallel morphological evidence that discriminated three distinct populations and provides evidence indicating substantial genetic dissimilarity and little or no recent or ongoing gene flow among these isolated regional populations (Piaggio and Hopken 2009, Hopken et al. 2015). The population of *O. v. douglasi* contained a single, unique haplotype with a private allele at the K locus; the *O. v. leucurus* population (LCR) had three unique haplotypes and a private allele at locus BM4208. The *O. v. ochrourus* population shared haplotypes with populations to the east and had 22 private alleles. Further evidence of genetic isolation among the three *O. virginianus* populations was revealed by analyses of autosomal microsatellite loci. Genetic diversity (mean allele richness and heterozygosity) across 16 loci was lower for *O. v. leucurus* and *O. v. douglasi* populations than for *O. v. ochrourus* or *O. hemionus* populations; *O. v. douglasi* had the lowest genetic diversity

(Hopken et al. 2015:Table 1). The most compelling evidence of genetic isolation among the three populations of *O. virginianus* was provided by the analysis of genetic differentiation or divergence (Hopken et al. 2015:Table 2). According to Wright (1978), an F_{ST} value of 0.10 indicates moderate genetic divergence, whereas values between 0.15 and 0.25 represent greater genetic differentiation; $F_{ST} > 0.25$ represents significant genetic differentiation. The F_{ST} values among the three *O. virginianus* populations all were greater than the F_{ST} value between *O. h. hemionus* and *O. h. columbianus* ($F_{ST} = 0.10$), which are two recognized regional subspecies of *O. hemionus*. Of particular significance regarding the question of subspecific status was the finding that *O. v. leucurus* and *O. v. douglasi* populations showed the greatest genetic divergence ($F_{ST} = 0.31$), which was markedly greater than the genetic differentiation between either of these populations and *O. v. ochrourus* (0.15 and 0.19). A plot of factorial correspondence analysis of deer genotypes revealed three distinct white-tailed deer groups separated on the first two axes with no shared individuals (Piaggio and Hopken 2009:Figure 7).

Hopken et al. (2015) concluded that the subspecific status of *O. v. leucurus* was not supported by their genetic data, but acknowledged that the *O. virginianus* populations west of the Cascades (LCR and DC) were isolated and morphologically distinct. Their conclusion was based on finding minimal mtDNA phylogenetic divergence among the Oregon populations and a standardized genetic definition of subspecies as "groups that are phylogenetically distinguishable from other groups at multiple genetic traits" (Hopken et al. 2015:645). They proposed further that because "anthropogenic effects most likely caused the contemporary differentiation, ecological and genetic connectivity should be restored to historical condition" (Hopken et al. 2015:645). Translocation was recommended to restore connectivity and to mitigate low genetic diversity and an increased risk of negative inbreeding consequences.

This perspective ignores significant morphological differentiation between the LCR and DC populations, arguing that intraspecific genetic variation is organized hierarchically rather than genealogically, which is inappropriate at this categorical level (Patton and Conroy 2017). Furthermore, this view largely disregards the marked differences in climate, vegetation, and community ecology between the lower Columbia River region and southwestern Oregon (Gavin et al. 1984; Smith 1985a,b), all of which have imposed selective pressures unique to local habitat and environmental conditions. Conservation goals should focus on maintaining local ecological and evolutionary processes rather than maintaining specific phenotypes (Moritz 1999), with less attention on the evolutionary continuum from populations to species (Coates et al. 2018). Taxonomic units shape the view of how nature is organized (Avise 1994) and have become the foundation of conservation goals and efforts (Cook and MacDonald 2001).

We readily acknowledge the fundamental nature of genetics and lineage in taxonomy, which is a perspective advanced initially by Hennig in 1966 (cited in Patton and Conroy 2017). Indeed, much of the infraspecific literature has focused on delineating geographically isolated molecular clades (Patton and Conroy 2017). However, imposing clade structure as a prerequisite for infraspecific taxonomy not only ignores the underlying genetic basis of morphological features, it is contrary to Hennig's own philosophy (Patton and Conroy 2017). The purpose for examining the taxonomy of species is to recognize and acknowledge all geographically separated reproductive communities with distinguishing features as subspecies. This conceptual framework establishes a "nonhierarchical, nonreciprocal monophyletic definition for infraspecific taxa" (Patton and Conroy 2017:1019). Braby et al. (2012:699) defined subspecies as "groups that comprise evolving populations representing partially isolated lineages of a species that are allopatric, phenotypically distinct … and that these character differences are correlated with

evolutionary independence according to population genetic structure." Patton and Conroy (2017) also emphasized the importance of acknowledging the underlying genetic basis of phenotypic attributes that diagnose subspecies, noting that if these population segments have separate evolutionary histories so might the attributes that distinguish the subspecies.

Formal recognition of subspecies should not be a strict application of a molecular-only perspective of an organism's history (Patton and Conroy 2017, Diersing 2019). Geographically separated, reproducing populations with distinguishing phenotypic attributes should be acknowledged and recognized as subspecies (Braby et al. 2012, Patton and Conroy 2017). The population of *O. v. douglasi* is isolated geographically and genetically from *O. virginianus* along the lower Columbia River and northeastern Oregon (Piaggio and Hopken 2009, Hopken et al. 2015). *Odocoileus v. douglasi* is morphologically and genetically distinguishable from conspecifics along the lower Columbia River and northeastern Oregon. The emergence of unique haplotypes and genetic differentiation in the context of geographically isolated populations that experience markedly different, environmentally mediated selective pressures indicate the LCR and DC populations of *O. virginianus* are evolving along separate trajectories and undergoing allopatric speciation (Anderson and Weir 2022).

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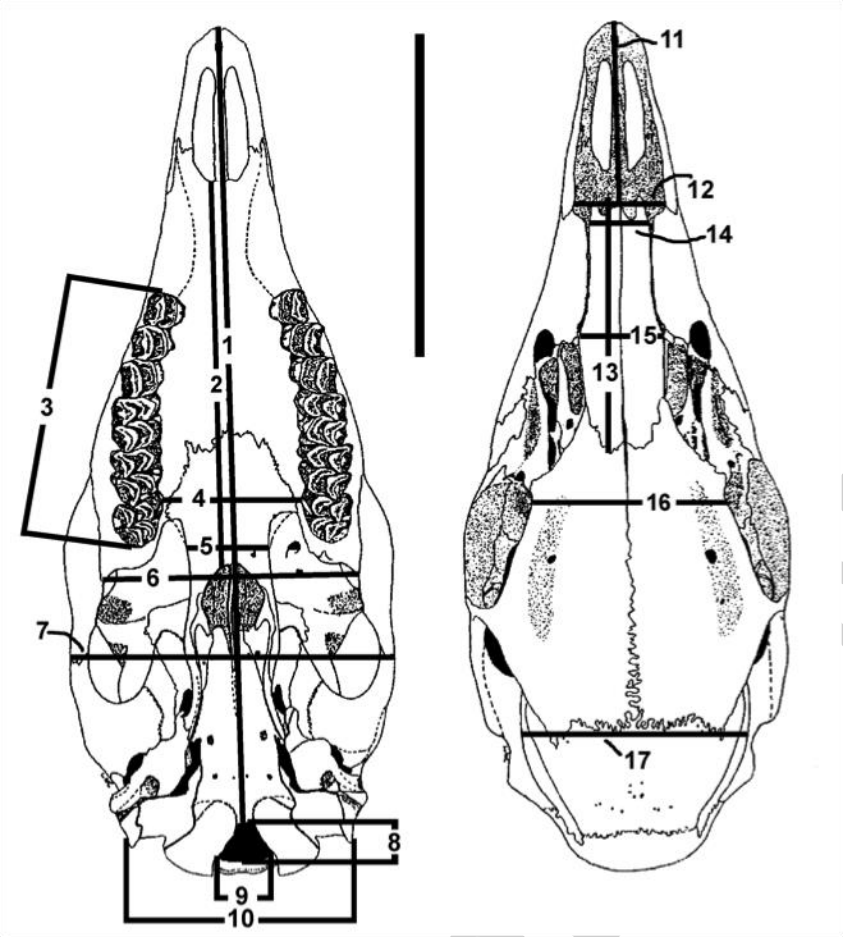

Figure 1. Cranium of female white-tailed deer (*Odocoileus virginianus*) illustrating dimensions recorded (Smith et al. 2003): 1) basilar length; 2) palatilar length; 3) length of upper molariform series at alveolus; 4) breadth between M3s; 5) postpalatal breadth; 6) maxillary breadth; 7) zygomatic breadth; 8) height of foramen magnum; 9) width of foramen magnum; 10) mastoid breadth; 11) length of external nares; 12) breadth of external nares: 13) nasal length; 14) least nasal breadth; 15) greatest nasal breadth; 16) least interorbital breadth; and 17) breadth of braincase. The last dimension recorded (18) was depth of rostrum (not illustrated), which was measured with the cranium resting on a flat surface and is the distance from the dorsal side of the premaxillae to the flat surface. Scale bar equals 10 cm.

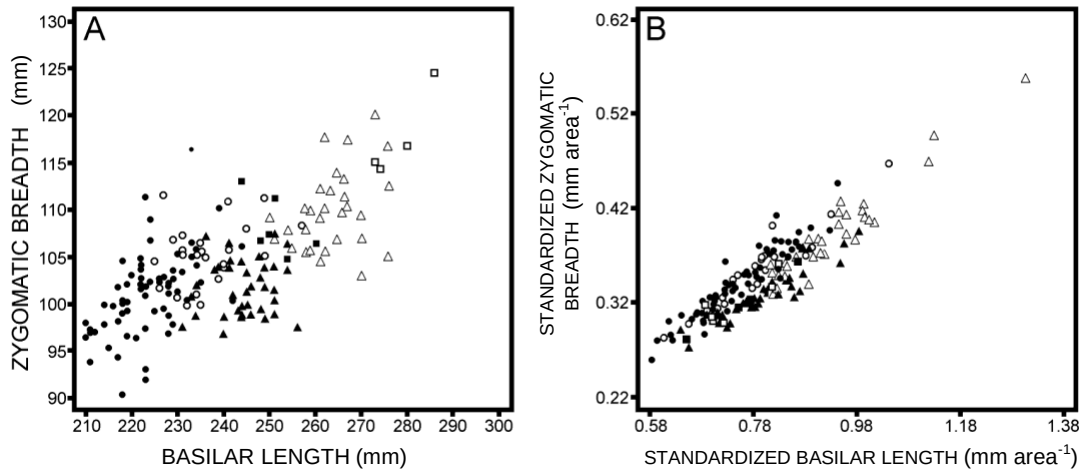

Figure 2. A) Plot of basilar length and zygomatic breadth (Smith et al. 2003) illustrating a decrease in size of female and male *Odocoileus virginianus* from northern Idaho (females ■, males □), to the Lower Columbia River region in Washington and Oregon (females▲, males Δ), and to Douglas County, Oregon (females ●, males ○). B) Plot of standardized basilar length and standardized zygomatic breadth (length in mm divided by area of its foramen magnum) illustrating the same pattern for female and male *Odocoileus virginianus* from the same collection localities.

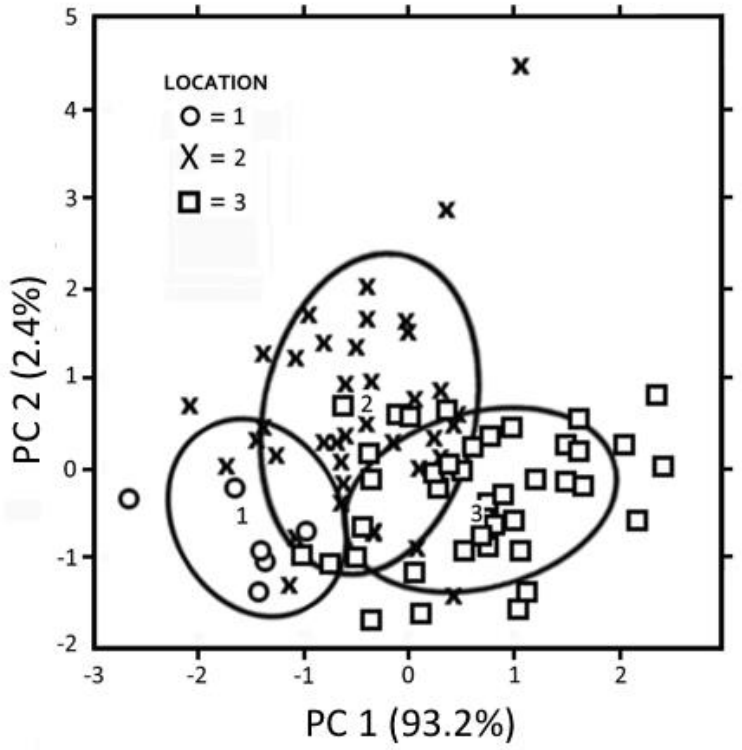

Figure 3. Principal components analysis plot of female and male *Odocoileus virginianus* skulls from group 1 (northern Idaho), group 2 (lower Columbia River in Washington and Oregon) and group 3 (Douglas County, Oregon). PC1 accounted for 93.2%, and PC2 for 2.4% of the variation among individuals. Numbers denote centroids of ellipses that represent 2 standard errors of multifactorial space around each group. Localities sorted into three distinct slightly overlapping morphological groups. Differences in cranium dimensions are characterized as follows: specimens from group 3 have relatively shorter and narrower skulls; and specimens from group 1 have a longer rostrum (longer nasals) and narrower cranium than those in group 2.

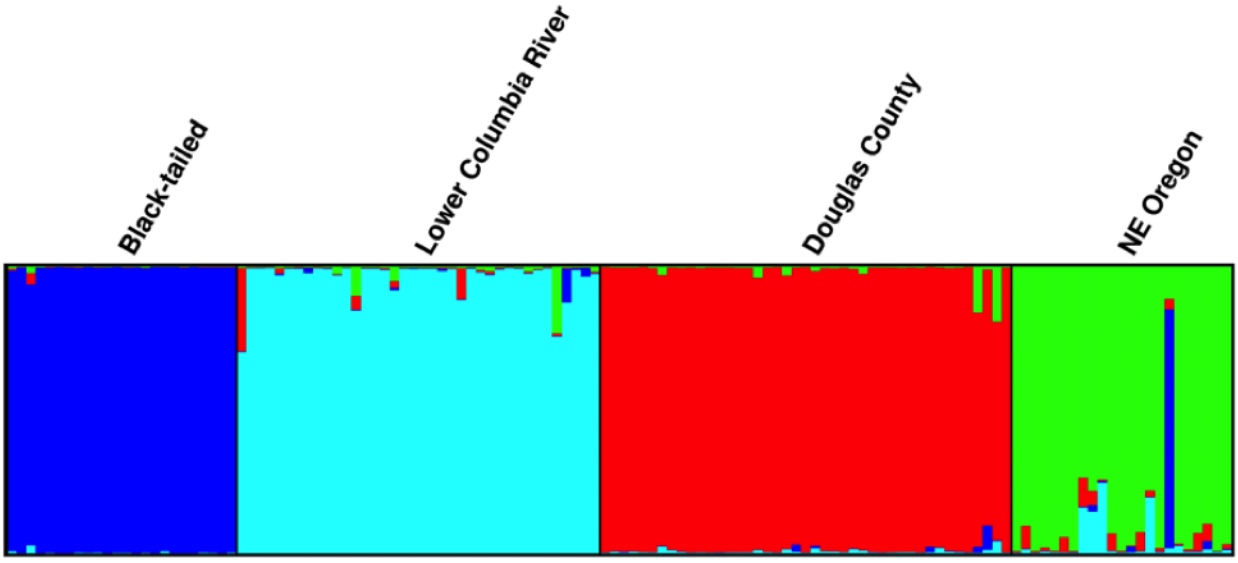

Figure 4. Barplot from cluster analyses of Pacific Northwest deer genotypes implemented in STRUCTURE v2.2 (as published in Piaggio and Hopken 2009:Figure 6). Each vertical bar represents an individual genotype, and each color represents one of $k = 4$ clusters; the dark blue is black-tailed deer (*Odocoileus hemionus columbianus*). The black diagonal lines above the remaining 3 clusters indicate sampling locations. In the northeastern Oregon cluster, note the individual (column with dark blue) that has significant assignment to *O. h. columbianus*.

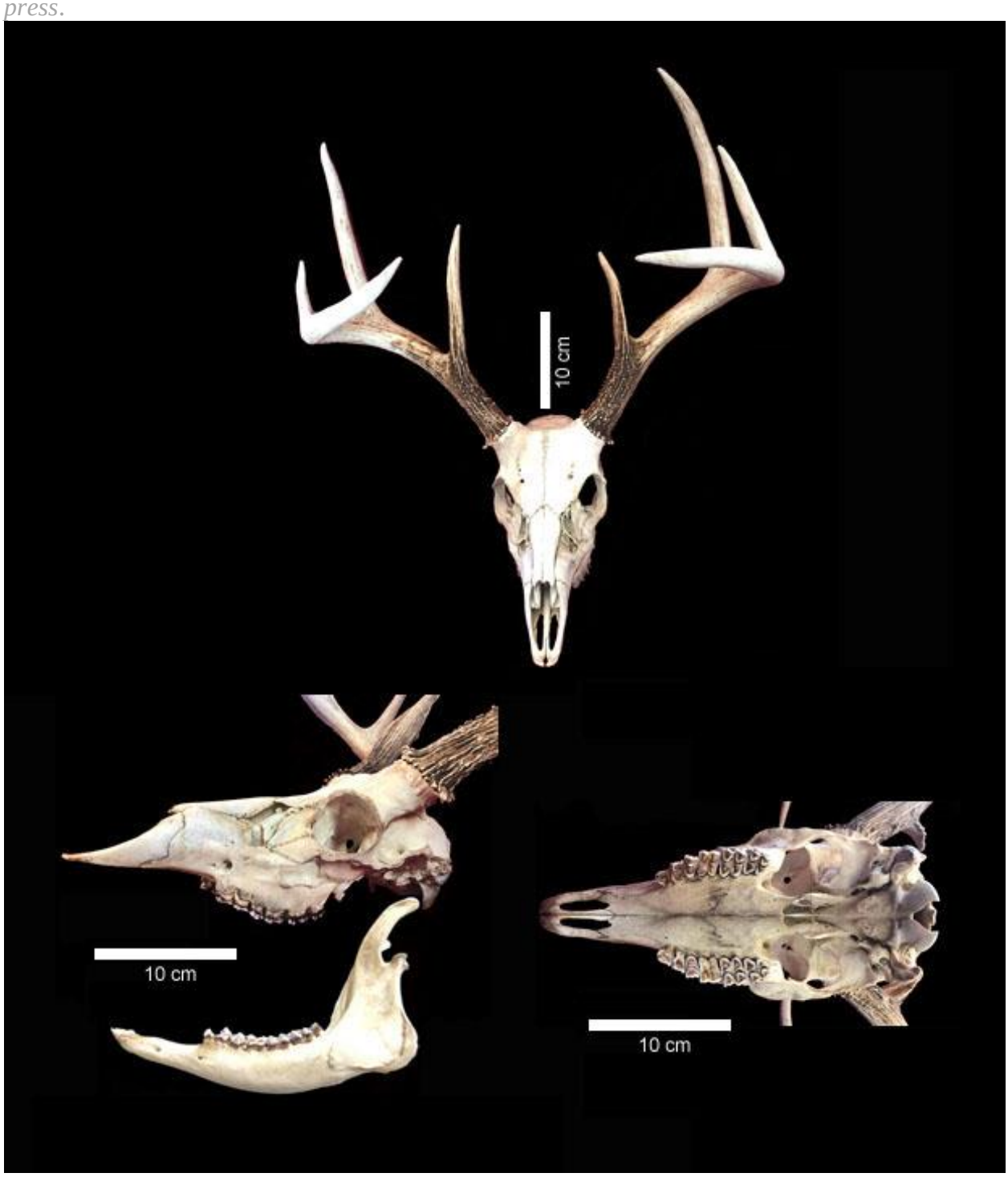

Figure 5. Images of skull with antlers, lateral view of skull and left mandible, and ventral view of skull of Holotype of *Odocoileus virginianus douglasi* (UWBM 83081).

Tables

Table 1. Means ± SE (range) (mm) of measurements of skull dimensions for female and male *Odocoileus virginianus* that are statistically significant ($P < 0.05$; Supplemental Table S1) among locations (northern Idaho, the lower Columbia River in Washington and Oregon, and Douglas County, Oregon; Smith et al. 2003). Skull measurements for the male Holotype and female Paratype type specimen collected in Douglas County, Oregon are also given.

	Northern Idaho		Lower Columbia River		Douglas Country		Type specimens	
Dimensions	Males	Females	Males	Females	Males	Females	Males	Females
Basilar length	278.3 ± 3.0 (273–286)	251.2 ± 2.2 (244–260)	262.2 ± 1.5 (244–276)	244.6 ± 1.0 (231–256)	236.0 ± 1.6 (225–257)	223.7 ± 0.9 (210–244)	253.0	225.0
Palatilar length	135.6 ± 1.5 (130.8–139.6)	125.8 ± 2.0 (120.2–131.6)	125.7 ± 0.8 (114.3–140.0)	118.8 ± 0.6 (109.3–127.5)	113.7 ± 0.6 (104.8–122.4)	109.3 ± 0.6 (97.6–123.1)	119.0	109.0
Length of upper molariform series	76.6 ± 1.2 (73.3–83.6)	74.5 ± 1.2 (70.5–79.1)	76.5 ± 0.4 (71.6–81.8)	73.9 ± 0.5 (67.2–80.8)	72.2 ± 0.5 (66.3–77.3)	70.1 ± 0.5 (57.3–78.6)	74.0	68.0
Breadth between M3s	49.6 ± 0.5 (47.4–53.5)	46.9 ± 0.7 (45.1–49.1)	47.0 ± 0.4 (42.7–54.9)	43.5 ± 0.3 (39.7–49.3)	45.6 ± 0.4 (39.7–52.8)	42.9 ± 0.3 (36.2–47.6)	49.5	37.8
Postpalatal breadth	29.0 ± 0.4 (26.4–30.4)	26.5 ± 0.7 (24.8–28.4)	25.9 ± 0.2 (22.6–30.7)	24.8 ± 0.2 (20.3–30.7)	24.9 ± 0.2 (21.4–29.3)	24.1 ± 0.2 (20.9–27.8)	26.5	26.5
Maxillary breadth	86.5 ± 1.4 (79.7–93.2)	82.4 ± 1.0 (78.5–85.5)	82.9 ± 0.5 (75.8–91.2)	78.5 ± 0.4 (72.7–87.6)	81.9 ± 0.5 (73.9–88.0)	79.1 ± 0.4 (70.3–86.4)	90.0	85.0
Zygomatic breadth	116.7 ± 1.2 (113.0–124.5)	108.3 ± 1.3 (104.9–113.0)	108.7 ± 0.8 (96.5–120.0)	101.4 ± 0.4 (95.9–107.3)	105.7 ± 0.5 (99.9–111.4)	100.9 ± 0.5 (90.4-116.4)	118.0	108.5
Height of foramen magnum	20.7 ± 0.4 (18.0–23.2)	21.8 ± 0.4 (20.7–23.1)	19.0 ± 0.2 (14.4–21.8)	20.0 ± 0.2 (16.9–23.6)	19.6 ± 0.2 (16.7–22.7)	20.2 ± 0.0 (17.4–23.9)	18.0	20.5
Width of foramen magnum	20.4 ± 0.5 (16.2–22.0)	20.8 ± 0.3 (19.9–22.1)	19.3 ± 0.2 (16.5–22.4)	19.5 ± 0.1 (17.1–22.2)	19.7 ± 0.2 (17.0–22.2)	18.9 ± 0.1 (16.3–22.5)	20.5	22.5
Mastoid breadth	86.6 ± 1.2 (82.3–96.5)	73.0 ± 1.4 (68.3–76.9)	75.2 ± 0.7 (64.5–90.6)	65.5 ± 0.3 (59.7–71.5)	69.3 ± 0.5 (62.3–79.7)	62.5 ± 0.4 (54.4–69.0)	74.5	58.5
	78.3 ± 1.4	70.7 ± 1.3	73.4 ± 0.7	69.8 ± 0.6	70.8 ± 0.8	67.0 ± 0.5	67.5	57.5

Length of external nares	(74.3–80.6)	(67.6–76.7)	(62.3–80.3)	(63.8–77.6)	(63.4–80.0)	(53.6–76.5)

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Supplementary Materials

Reconsidering Subspecific Taxonomy of *Odocoileus virginianus* in Oregon and Washington

Winston P. Smith, Leslie N. Carraway, Thomas A. Gavin, and Jonathan A. Jenks

Table S1. Covariate and factors affecting 16 standardized response variables recorded from skulls of *Odocoileus virginianus* from the Lower Columbia River region of Washington and Oregon (LCR), Douglas County, Oregon (DC), and northern Idaho (collection localities). We standardized data for response variables by dividing each measurement by the area of the foramen magnum (Radinsky 1967). The General Linear Model is presented for each statistically significant response variable as SS, MS with *F* and *P* below except for the Error column (which only has SS and MS). The covariate Age class had three levels (2, 3, and > 4 years old) for females and four (2, 3, 4, and ≥ 6 years old) for males. The factors were sex (female, male), collection locality, and their interaction.

Response variables and Multivariate test	Age class df = 1	Sex df = 1	Collection locality df = 2	Collection locality * Sex df = 2	Corrected model df = 6	Error df = 67
Basilar length		0.053, 0.053 7.64, 0.007	0.079, 0.039 5.66, 0.005		0.244, 0.041 5.84, 0.0001	0.467, 0.007
Nasal length		0.005, 0.005 4.68, 0.034	0.025, 0.012 12.56, 0.0001		0.0440, 0.007 7.45, 0.0001	0.066, 0.001
Greatest nasal breadth		0.001, 0.001 7.00, 0.010	0.002, 0.001 4.21, 0.019		0.005, 0.0001 4.54, 0.001	0.013, 0.0001
Least nasal breadth	0.0003, 0.0003 4.34, 0.041	0.001, 0.001 9.70, 0.003	0.001, 0.001 6.26, 0.003		0.003, 0.0001 7.20, 0.0001	0.005, 0.00001
Least interorbital breadth		0.007, 0.007 12.74, 0.001			0.014, 0.002 4.40, 0.001	0.034, 0.0001
Zygomatic breadth		0.009, 0.009 6.68, 0.012			0.026, 0.004 3.09, 0.010	0.095, 0.001
Breadth of braincase		0.003, 0.003 4.17, 0.045	0.005, 0.002 3.67, 0.031		0.015, 0.002 3.80, 0.003	0.043, 0.001

Table S1. Continued.

Response variables and Multivariate test	Age class df = 1	Sex df = 1	Collection locality df = 2	Collection locality * Sex df = 2	Corrected model df = 6	Error df = 67
Mastoid breadth		0.017, 0.017 34.61, 0.0001	0.003, 0.002 3.14, 0.050	0.005, 0.003 5.10, 0.009	0.039, 0.006 13.32, 0.0001	0.032, 0.001
Length of upper molariform series			0.008, 0.004 6.01, 0.004		0.013, 0.002 3.29, 0.007	0.044, 0.001
Maxillary breadth					0.013, 0.002 2.49, 0.031	0.058, 0.001
Breadth between M3s					0.005, 0.001 2.57, 0.027	0.022, 0.001
Palatilar length		0.009, 0.009 4.84, 0.031	0.018, 0.009 4.91, 0.010		0.051, 0.008 4.72, 0.0001	0.121, 0.002
Postpalatal breadth		0.0001, 0.0001 4.04, 0.049			0.001, 0.0002 2.17, 0.057	0.007, 0.0001
Elevation of rostrum			0.006, 0.003 5.69, 0.005		0.010, 0.002 3.31, 0.006	0.035, 0.001
Length of external nares		0.003, 0.003 6.01, 0.017			0.012, 0.002 3.65, 0.003	0.038, 0.001
Breadth of external nares			0.001, 0.001 5.16, 0.008		0.003, 0.001 3.71, 0.003	0.009, 0.001
Wilkes' lambda	Value = 0.550 *F* = 2.65 df = 16 *P* = 0.004	Value = 0.269 *F* = 8.82 df = 16 *P* = 0.0001	Value = 0.088 *F* = 7.74 df = 32 *P* = 0.0001	Value = 0.449 *F* = 1.60 df = 32 *P* = 0.040		

List S2. Specimens examined. Collection localities are listed in alphabetical, then numerical, order. Each locality is followed by the museum collection number. The 97 examined specimens are housed in the following scientific collections, with parenthetical reference to their acronyms: American Museum of Natural History (AMNH); Conner Museum, Washington State University, Pullman (CRCM); Oregon State University, Department of Fisheries, Wildlife, and Conservation Sciences (OSFW); Slater Museum of Natural History, University of Puget Sound, Tacoma, Washington (PSM); and University of Washington Burke Museum, Seattle (USBM).

Idaho, *n* = 9

Bonner Co.: Pend Oreille Lake (PSM5318, 5326); Priest Lake, N Sand Point (PSM4578), Sandpoint area (PSM5321, 5322, 5329); Squaw Valley Drainage on W side of Pucot River (PSM8551, 8552). *Latah Co.:* 2 mi E Deary (CRCM55-467).

Oregon, *n* = 64, collected by Winston P. Smith (WPS) unless otherwise noted after collection number

Clatsop Co.: 1 mi N Clifton, Tenasillahe Island (AMNH244789 [PAV]). *Douglas Co.*: locality unknown (AMNH256655; TAG133*, 146*); 4.3 km NNE Elkhead, 150 m E Scotts Valley Road, 43°34’8.50”N, 123°09’19.61”W (10T 492168 4794011; UWBM83080, PARATYPE, collected by SW Regional Office, Oregon Department of Fish and Wildlife); HWY138 near Glide High School, 43°17’56.56”N, 123°05’47.34”W (10T 492168 4794011; USBM83081, TYPE specimen, collected by SW Regional Office, Oregon Department of Fish and Wildlife); 4 mi S Glide along Whistler's Bend Rd (AMNH256665); 4 mi W Glide along Whistler's Bend Park

Rd (AMNH256673); 4 mi W Glide off Whistler's Lane (AMNH256676); 4 mi SW Glide along Whistler's Lane (AMNH256667—256670); 4 mi W Glide at intersection of Whistler's Lane (AMNH256674); 4 mi SW Glide just off Whistler's Lane (AMNH256671); 5 mi W Glide (AMNH256688); 5 mi W Glide along Bank Rd (AMNH256689, 256690); 5 mi W Glide along Bank Creek Rd (AMNH256681, 256682, 256684); 5 mi W Glide just off Bank Rd (AMNH256695); 5 mi W Glide along Whistler's Bend Park Rd (AMNH256692); 5 mi W Glider in Whistler's Bend Park (AMNH256694); 5 mi SW Glide along Bank Creek Rd (AMNH256687); 5 mi SW Glide, along Whistler's Bend Rd (AMNH256685); 6 mi W Glide off Bank Rd (AMNH256707); 6 mi W Glide, Whistler's Bend Park (AMNH256706); 6 mi SW Glide off Bank Rd (AMNH256699, 256700, 256702); 6 mi SW Glide along Oak Creek (AMNH 256696); 6 mi SW Glide in Whistler's Bend Park (AMNH256698); 7 mi S Glide along Brumbach Rd (AMNH256709); 7 mi W Glide (AMNH131); 1 mi N Roseburg long HWY 99 (AMNH256715); 1 mi E Roseburg along HWY 138E (AMNH256713); 2 mi E Roseburg along HWY 138E (AMNH256717, 256718); 1 mi E Roseburg along HWY 138E (AMNH256722); 3 mi E Roseburg at intersection of Sunshine Rd and HWY 138E (AMNH256723); 5 mi NW Roseburg along Sunshine Rd (AMNH256742); 5 mi NE Roseburg along Dixon Creek (AMNH256734, 256738, 256740); 5 mi ENE Roseburg along Sunshine Rd (AMNH256730—256732, 256744); 6 mi NE Roseburg just off Sunshine Rd (AMNH256754); 6 mi NNE Roseburg along Dixon Creek (AMNH256758); 6 mi NE Roseburg off Sunshine Rd (AMNH256755); 6 mi ENE Roseburg just off Sunshine Rd (AMNH256747—256749, 256752); 7 mi NE Roseburg along North Bank Rd (AMNH256762); 7 mi NE Roseburg on Lindbloom Ranch along N Umpqua River (AMNH256764); 7 mi NNE Roseburg along N Umpqua River (AMNH256766); 6 mi E Wilbur along North Bank Rd (AMNH256768); 1 mi N Winchester along HWY 99

AMNH256770); 1 mi E Winchester along Page Rd (AMNH256769); 3 mi E Winchester along Dixon Creek (AMNH256774); 2 mi NE Winchester along Page Rd (AMNH256771).

Washington, *n* = 24, collected by Thomas A. Gavin (TAG) unless otherwise noted after collection number

No data: (AMNH244797). *Wahkiakum Co*.: 3 mi W, 3 mi N Cathlamet (AMNH244755--244757, 244758--244759 [PAV], 244761 [PAV], 244768, 244772, 244779, 244781, 244782, 244786, 244787, 244801; OSFW4733, 4734; TAG061*, 071*, 075*, 152*, 166*, 203*); 2 mi S Cathlamet, Puget Island (TAG103*).

*These specimens were intended to be accessioned into the Department of Fisheries, Wildlife, and Conservation Sciences Mammal Collection, Oregon State University; however, they were not. The current location of these specimens is unknown.

Table S3. Latent root (eigenvalues), loadings, and percentage of variance of the first 5 principal components from a covariance-based principal components analysis of 11 standardized cranial dimensions from 97 complete *Odocoileus virginianus* crania from three localities. NA = not applicable.

Standardized cranial dimension	Eigenvalue	Loadings				
		PC1	PC2	PC3	PC4	PC5
Basilar length	220.63	11.356	-0.244	-0.028	-0.004	-0.255
Palatilar length	5.78	5.455	-0.122	-0.024	0.021	-0.274
Nasal length	3.14	3.823	-1.531	-0.354	0.314	0.672
Mastoid breadth	2.45	3.210	-0.277	0.757	-0.933	-0.300
Maxillary breadth	1.60	3.138	1.221	0.681	0.221	0.576
Length of upper molariform series	0.93	2.965	0.615	-0.288	0.924	-0.449
Braincase breadth	0.69	2.872	0.787	0.203	0.063	0.27
Rostrum elevation	0.62	2.124	0.874	-1.351	-0.705	0.155
Greatest nasal breadth	0.41	1.540	0.046	0.131	-0.092	0.455
External nares breadth	0.35	1.423	0.127	0.064	-0.055	0.188
Least nasal breadth	0.11	1.097	0.138	0.066	-0.245	0.218
Percentage of total variance	NA	93.205	2.443	1.326	1.033	0.677