

NEW EVIDENCE OF THE EARLIEST DOMESTIC DOGS IN THE AMERICAS

Angela Perri, Chris Widga, Dennis Lawler, Terrance Martin, Thomas Loebel, Kenneth Farnsworth, Luci Kohn, and Brent Buenger

DO NOT CITE IN ANY CONTEXT WITHOUT PERMISSION OF THE AUTHOR(S)

Angela Perri Department of Archaeology, Durham University, South Road, Durham DH1 3LE, United Kingdom (angela.r.perri@durham.ac.uk, corresponding author)

Chris Widga Don Sunquist Center of Excellence in Paleontology, East Tennessee State University, Johnson City, TN 37615, USA

Dennis Lawler Illinois State Museum Research and Collections Center, 1011 East Ash St., Springfield IL 62703, USA; Pacific Marine Mammal Center, 20612 Laguna Canyon Rd., Laguna Beach CA 92651, USA

Terrance Martin Illinois State Museum Research and Collections Center, 1011 East Ash St., Springfield, IL62703-3500, USA

Thomas Loebel and **Kenneth Farnsworth** Illinois State Archaeological Survey, Prairie Research Institute, University of Illinois, Champaign, IL 61820, USA

Luci Kohn Department of Biological Sciences, Southern Illinois University Edwardsville, Illinois 62026, USA

Brent Buenger Western Archaeological Services, 1600 Dewar Dr., Rock Springs, WY 82901, USA

Abstract

The domestication of dogs likely occurred in Eurasia by 16,000 years ago, with the initial peopling of the Americas potentially happening around the same time. Dogs were long thought to have accompanied the first migrations into the Americas, but conclusive evidence for Paleoindian dogs is lacking. The direct dating of two dogs from the Koster site (Greene Co., Illinois) and a newly-described dog from the Stilwell II site (Pike Co., Illinois) to between 10,190-9,630 cal BP represent the earliest confirmed evidence of domestic dogs in the Americas and individual dog burials anywhere in the world. Analysis of these animals shows Early Archaic dogs were medium-sized and lived active lifestyles, but already exhibited significant morphological variation. Stable isotope analyses suggest diets dominated by terrestrial C₃ resources and substantial consumption of riverine fish.

The domestication and subsequent cultural roles of dogs have been highly debated in the archaeological and genomic literature, especially over the last decade (Germonpré et al. 2009; von Holdt et al. 2010; Larson et al. 2012; Germonpré et al. 2013; Thalmann et al. 2013; Freedman et al. 2014; Drake et al. 2015; Morey and Jeger 2015; Perri et al. 2015; Shipman 2015; Frantz et al. 2016; Perri 2016a; Morey and Jeger 2017). Advances in zooarchaeological, morphometric, and genomic methods have led to a burst of research in the field, but have also engendered disagreement regarding the interpretation of data from investigations into their origins. These debates extend to the earliest appearance of domesticated dogs in the Americas and the circumstances leading to their presence in the region, which are unresolved.

Though it is now widely accepted that all dogs were domesticated from an ancient wolf ancestor (Vila et al. 1997; Freedman et al. 2014), findings diverge on the timing, location, and number of domestication sites. The tentative identification of a number of proposed Paleolithic dogs dating from prior to the Last Glacial Maximum (Sablin and Khlopachev 2002; Germonpré et al. 2009; Ovodov et al. 2011; Germonpré et al. 2012; Germonpré et al. 2015a, 2015b; Germonpré et al. 2017), some up to 40,000 years ago (Camaros et al. 2016), has led to debate regarding the origins of the human-dog relationship (Crockford and Kuzmin 2012; Boudadi-Maligne and Escarguel 2014; Drake et al. 2015; Morey and Jeger 2015; Perri 2016a).

Despite the suggestion of domesticated dogs much earlier in the Paleolithic, a date of around 16,000 cal BP is generally accepted as the timing of domestication, based on secure archaeological and genomic evidence (Axelsson et al. 2013; Freedman et al. 2014; Morey and Jeger 2015; Frantz et al. 2016; Perri 2016a).

Individual domestication locations have been proposed in the Middle East (vonHoldt et al. 2010), Europe (Thalmann et al. 2013), Central Asia (Shannon et al. 2015), and East Asia (Wang et al. 2016), while Frantz et al. (2016) suggested a dual origin in both East Asia and Europe. The possibility of an independent domestication of dogs in the Americas has been raised by some (Koop et al. 2000; Witt et al. 2015), but rejected by others (Leonard et al. 2002; vonHoldt et al. 2010).

The presence of early dogs in the pre-contact Americas is often assumed to be the result of companion animals arriving from across the Bering Land Bridge with migrating Pleistocene human populations (Schwartz 1997; Fiedel 2005; van Asch et al. 2013). Dogs may have assisted migrating groups by transporting goods and people, working as hunting aids, serving as bed-warmers, acting as alarms, warding off predators, and as a food and fur source. A recent analysis of dog remains from eastern Siberia suggests that dogs may have been important for hunting and particularly sled transport in the region up to 15,000 years ago (Pitulko and Kasparov 2017), similar to their present function in some Arctic regions today (Brown et al. 2013).

The earliest human migration into North America south of the ice sheet is proposed via a coastal route by between ~25,000 and 15,000 cal BP (Llamas et al. 2016; Skoglund and Reich 2016; Braje et al. 2017) or via a land route through the Ice Free Corridor by ~15,000 (Munyikwa et al. 2017; Potter et al. 2017). Ancient DNA results suggest ancestral Native American populations split from Siberian populations by 20,000 years ago before moving into eastern Beringia and the Americas (Moreno-Mayar et al. 2017). The earliest archaeological evidence of human presence in the

Americas occurs in both North and South America around 14,500 cal BP (Dillehay et al. 2015; Halligan et al. 2016).

There are a number of large canid remains dating to the late Upper Pleistocene from across Beringia and southern Siberia, many of which are suggested to be Paleolithic dogs (see Germonpré et al. 2017 for a review of the Western Beringian and Siberian specimens). These include canids from Ulakhan Sular (c. 17,200 kya), Dyuktai Cave (c. 17,300-14,100 kya), Afontova Gora-1 (c. 16,900 kya), Verholenskaya Gora (c. 14,900 kya), Berelekh (c. 14,100 kya), Little John (c. 14,000 kya; Easton et al. 2011), McDonald Creek (c. 14,000-12,600 kya; Mueller et al. 2015), Nikita Lake (c. 13,800 kya), Ushki-I (c. 12,800 kya), and Ust'Khaita (c. 12,300 kya). At present, the taxonomy and interpretation of many of these specimens is contested or inconclusive. Others have yet to be evaluated further.

Although the arrival of domesticated dogs with an initial human migration has been the most reasonable explanation for their presence in the Americas, evidence for Paleoindian dogs has proven elusive. Previously, Jaguar Cave (Idaho) was thought to hold the earliest domestic dog remains in the Americas at over 10,000 years old (Lawrence 1967). However, when dated directly, the remains proved to be only 3,000-4,000 years old (Gowlett et al. 1987). Similarly, Beebe (1980) reported early dog remains dating to around 20,000 years ago from Old Crow Basin (Yukon Territory), but later dating demonstrated that this dog is of Late Holocene age (Harington 2003). While there are suggestions of domesticated dogs over 10,000 years old from a few North American sites (Haag 1970; Stanford 1978; Walker and Frison 1982; Grayson et

al.1988; Saunders and Daeschler 1994; Jenkins et al. 2013; Lyman 2013), these canid remains have not benefitted from recent chronological or morphological (re)evaluation.

Fiedel (2005) suggested the lack of dog remains during the Paleoindian period is the result of their ephemeral presence, not their absence. While this is a distinct possibility, the earliest appearance of domestic dogs at Early Archaic sites in the midcontinent (Morey and Wiant 1992; Walker et al. 2005) raises questions regarding their origins and route(s) into the Americas. Tito et al. (2011) reported finding the earliest evidence for dogs in the Americas at Hinds Cave (Texas) - a small bone fragment within a human coprolite. Genomic analysis was performed and the specimen was directly dated to around 9,200 cal BP. Other early examples of domesticated dogs include specimens from Modoc Rock Shelter (c. 8,400 cal BP, Illinois; Ahler 1993), Dust Cave (c. 8,400 cal BP, Alabama; Walker et al. 2005), Rodgers Shelter (c. 8,800 cal BP, Missouri; McMillan 1970), and Koster (c. 9,500 cal BP, Illinois; Brown and Vierra 1983; redated in this study). Together, these specimens constitute the corpus of the earliest confirmed archaeological dog record in the Americas.

The arrival of dogs into the Americas has important cultural and ecological implications. Dogs were the first invasive species (along with humans) and domesticate in the Americas, potentially impacting populations of small mammals through predation, other species of *Canis* through hybridization, and other carnivores through transmission of diseases or competition (Doherty et al. 2017). They may have also contributed to important adaptations in hunting and mobility during the peopling of the Americas and into the Pleistocene-Holocene transition.

Here, we present the identification, zooarchaeological analysis, stable isotope analysis and direct radiocarbon dating of a new isolated dog burial from Stilwell II, an Early Archaic site in the Lower Illinois River Valley. We also present new direct radiocarbon dates and stable isotope results for dogs from the nearby Koster site and three additional Archaic dogs from the region. These dates confirm that the Stilwell II and Koster dogs represent the earliest directly-dated evidence for domesticated dogs in the Americas and the oldest intentional, individually-buried dogs known in the worldwide archaeological record. Other similar individual dog burials appear in hunter-gatherer contexts ~1,000 years later (Perri 2014; Perri 2016b). Importantly, we contribute to an emerging analytical framework for understanding the behavior and life history of these canids. Our analyses (zooarchaeology, paleopathology, morphology, stable isotopes) lend insight into what these dogs looked like, how they lived, and their roles within Early Archaic communities.

Site Backgrounds

The Koster Site

The Koster site (11GE4) is located in a minor tributary valley of the lower Illinois River in Greene County, Illinois (Figure 1). The site is multicomponent and highly stratified, with cultural deposits spanning the Early Archaic to Mississippian, providing a nearly continuous record of Holocene human occupation (Brown and Vierra 1983). The site was excavated continuously over a ten-year period and is one of the most studied sites in the Lower Illinois River Valley (e.g., Butzer 1978; Hajic 1990; Komar and Buikstra 2003).

Three isolated dog burials (cf. Perri 2017) in shallow, well-demarcated pits were identified from Horizon 11, one of the Early Archaic phases at Koster (Figure 2). There is also a fourth burial, likely associated with later period (Hill 1972; Morey and Wiant 1992), and a fifth burial is reported (Neusius 1996), the remains of which are not present in the current Illinois State Museum collection. The skeletons of the three Horizon 11 dogs were complete, articulated, and lacked evidence of butchering or skinning (Morey and Wiant 1992). Given their presence in Horizon 11 and association with a nearby charcoal date (Brown and Vierra 1983), the dogs were attributed to the terminal Early Archaic. Though this date is commonly reported as “8,500 years ago” (e.g., Morey and Wiant 1992: 225), the calibrated age based on the associated charcoal ¹⁴C dates is ~9,500 cal BP. These specimens are often cited as the earliest domesticated dogs and occurrence of intentional dog burials in the Americas (Morey and Wiant 1992; Fiedel 2005; Walker et al. 2005; Lapham 2010; Morey 2010).

The Stilwell II Site

The Stilwell II site (11PK1044) was discovered in 1960 when road grading operations cut through an alluvial fan in Pike County, Illinois, about 35km from the Koster site. Gregory Perino collected lithic and faunal remains from what he described as two living areas composed of a dark layer of soil, 6-inches thick and 20-feet long, exposed at the base of a 14-foot cut bank (Perino 1970:119). He subsequently recovered a dog burial in the northern area of the site, and a human burial in the southern area. The dog burial (Figure 3) was complete and articulated (Perino 1970, 1977). It was excavated and curated at the Illinois State Museum. The faunal remains

collected by Perino and through later excavations by the Illinois State Archaeological Survey include white-tailed deer, turkey, turtle, small birds, vole, squirrel, fish and mussel shell. After the two rescue excavations in 1960 and 1962 Perino published very little about the site and left no field notes or maps. Re-excavation of the site began in 2015 by the Illinois State Archaeological Survey and is ongoing (see Supplementary Information).

Materials and Methods

Zooarchaeology, Morphology, and Paleopathology

The Koster and Stilwell II dogs were analyzed in the zooarchaeology laboratory at the Illinois State Museum's Research and Collections Center, where they are curated. All skeletal specimens were examined in order to note the condition of epiphyseal closure, presence of cut marks, damage by carnivore or rodent gnawing, and exposure to fire. Analysis of shoulder height relies on the regression equations of Harcourt (1974), and body mass estimates use the methods presented by Losey et al. (2014, 2016). Researchers have previously published comprehensive measurement data, burial information, and paleopathology for the Koster dogs (Morey 1992; Morey and Wiant 1992; Morey 2006; Lawler et al. 2016), which is not repeated here. Recent ancient DNA analysis of one Koster specimen has confirmed their status as domesticated dogs from Eurasian stock, likely originating in Siberia (Thalmann et al. 2013, Leathlobhair et al. 2018). Recovery of ancient DNA from the Stilwell II dog has failed thus far.

Though little documentation exists for the site, Perino (1970:119) is clear that the remains of the single Stilwell II dog were a shallow, intentional burial in what he described as the floor of a living area. The only *in situ* photograph of the dog shows an articulated skeleton as an isolated burial (Figure 3), with a northwest-southeast orientation, head facing west. The front legs appear to be tucked partly under the body.

Following von den Driesch (1976), we provide all possible skeletal measurements for the Stilwell II dog and have retaken all possible measurements from the two Koster dogs dated in this study (F2256 and F2357) (Supplementary Table 1). These measurements were compared to a sample of seven Archaic dogs from Iowa and Illinois (Supplementary Table 3). Modern wild canids (*C. latrans*, *C. lupus*) curated in the Illinois State Museum, the University of Kansas Biodiversity Institute, and the East Tennessee Museum of Natural History were also included in osteometric analyses to illustrate the morphological differences between domesticated and wild taxa. 3D models of the Koster F2256 and Stilwell II mandibles are available for download at www.morphosource.org (see Data Availability Statement).

Observations of the appendicular skeleton include overt and incipient pathology. We define incipient pathological changes as very mild or very early changes, not easily visualized by standard radiographic methods and not clarified substantially by standard computed tomography. Each bone was examined directly, supported by magnification as necessary. Microcomputed tomography has been conducted with some of the specimens, as parts of other studies (Lawler et al., 2016). All specimens were photographed. Observations were recorded by location within bone, thus resulting in multiple scores for given joint components (Supplementary Table 2).

Radiocarbon Dating and Stable Isotopes

Small rib fragments (1-2 cm in length) from the Koster and Stilwell II dogs were submitted to the University of Arizona AMS lab (Tucson, AZ) or Rafter Radiocarbon lab (Lower Hutt, New Zealand) for radiocarbon dating. In both cases, collagen was extracted using a modified Longin technique of acid demineralization followed by removal of organic contaminants using a weak basic solution (Longin 1971). Samples were combusted and further purified in a dedicated gas line and converted to graphite targets. These targets were analyzed using the accelerator at the Department of Physics, University of Arizona (USA) and National Isotope Centre, GNS Science (NZ), respectively. All ^{14}C results are calibrated as 2-sigma age ranges with the Intcal13 dataset (Reimers et al. 2013) using Calib 7.1.html (Stuiver et al. 2017).

Bone collagen stable isotope samples followed the same laboratory preparation methods as those prepared for ^{14}C , but were analyzed on a continuous-flow gas-ratio mass spectrometer coupled to an elemental analyzer. At the University of Arizona lab, standardization is based on acetanilide for elemental concentration, NBS-22 and USGS-24 for $\delta^{13}\text{C}$, and IAEA-N-1 and IAEA-N-2 for $\delta^{15}\text{N}$. Precision is better than ± 0.1 for $\delta^{13}\text{C}$ and ± 0.2 for $\delta^{15}\text{N}$. At the Rafter lab, standardization is based on leucine (-22.7‰ for $\delta^{13}\text{C}$, 2.2‰ for $\delta^{15}\text{N}$), and caffeine (-37.9‰ for $\delta^{13}\text{C}$, -7.4‰ for $\delta^{15}\text{N}$). Precision for these measurements is ± 0.3 ‰ for $\delta^{15}\text{N}$ and ± 0.2 ‰ for $\delta^{13}\text{C}$. All $\delta^{13}\text{C}$ results are reported relative to VPDB and all $\delta^{15}\text{N}$ results are reported relative to N-Air. A third Koster dog (222D) from Horizon 11 was also included in the isotopic analyses.

These data are compared to additional Early and Middle Archaic dog samples from Modoc Rockshelter (IL) and Rodgers Shelter (MO), as well as published archaeological dog and human stable isotope data from the Lower Illinois River Valley and American Bottom (Hedman et al. 2002; Hargrave et al. 2006; Fort et al. 2016; Carbaugh et al. in press). A dataset consisting of midwestern wolves (Fox-Dobbs 2007), midwestern deer (Cormie and Schwarcz 1994), and freshwater fish from Lower Illinois River Valley archaeological assemblages dating prior to the local use of maize (Brugam et al. 2017) is also included to illustrate general dietary trends in archaeological dog samples. The modern deer dataset is divided into two groups, representing animals with very little C₄ contribution to the diet (C₃ deer) and those with >10% C₄ contribution to the diet (C₄ deer).

Results

Zooarchaeology, Morphology, and Paleopathology

Aside from faint root etching on several of the long bones, examination of all Stilwell II specimens revealed only two occurrences of gnawing on the bones by small rodents. No cut marks from dispatch wounds (e.g., on the atlas vertebra) or dismemberment (e.g., cuts near articular ends) are present on the skeleton. The dog is an adult of undetermined age and the absence of a baculum from the otherwise well-represented posterior skeleton suggests the animal was a female (see Supplementary Information).

Since it is a relatively complete skeleton, the Stilwell II dog has the potential to provide anatomical insights into the size and morphology of early North American dogs.

It has an estimated shoulder height between 504-517 mm, based on radial (RDgl) and tibial (TAgl) length (Harcourt 1974) (Table 1). Losey et al., recently suggested improved methods for body mass estimation, based on cranio-dental (2014) and limb elements (2016). Application of these regression equations to the Stilwell II dog resulted in widely varying estimates (17-32 kg). Following Losey et al. (2016), we prefer body mass estimates that are based on elements relating directly to locomotion, such as limb elements. Estimates of body mass based on the humerus (distal breadth; HMbd) and radius (proximal breadth; RDbp) are both 17.1 kg (Table 1), similar in mass and build to a small modern English setter. Dogs from the nearby Koster site are slightly shorter (shoulder heights: 439-463 mm) and more lightly built (12-14 kg) (Figure 4).

Mandibular morphology varies significantly between the Stilwell II and Koster dogs (Figure 5). The Stilwell II dog mandible is robust with relatively small carnassial molars and a deep mandibular body. Dog mandibles from the Koster site, however, are more gracile, with large carnassial molars and shallow bodies, relative to their size.

Observations of the Stilwell II dog's axial skeleton included multifocal periodontal-osteal disease and severe tooth wear. The first and second molars exhibit particularly extreme wear (Figure 6) and the right lower canine is worn nearly blunt. Damage of this type depends partly on genetic susceptibility, as in (e.g.) modern small breed dogs, and on diet and habits such as chewing on bones. The dog easily could have experienced several well-recognized complications of chronic oral cavity disease. The rough enlargement of perialveolar mandibular bone below the mandibular arcades signals gingival and periodontal disease. DeBowes and colleagues (1996) showed that multiple organ pathology can be related to oral cavity diseases such as gingivitis and

periodontitis. In particular, significant associations were found between periodontitis and disease of the (a) kidney glomerular and interstitial tissue; (b) myocardium, especially papillary muscle; (c) hepatic parenchyma. The likely explanation is recurring bacteremia of oral tissue origin (Debowes et al. 1996). Without regular dental care, modern domestic dogs commonly develop similar oral pathology, and from the perspective of modern veterinary medicine, the Stilwell II dog would have been very uncomfortable.

Deviations of spinous processes were observed on seven vertebrae. Prevailing opinion has been that domestic dog vertebral spinous process deviations were caused by carrying packs or pulling travois (Darwent and Gililand 2001; Warren 2000; Walker et al. 2005). However, it has been shown recently that thorough differential diagnosis of these features yields multiple possible pathological causes or pseudopathologies (Lawler et al. 2016). Furthermore, the anatomical locations of affected vertebrae are protected by the caudodorsal neck ligament, tendon, and muscle mass (Miller et al. 1979) or lie below the protective transverse plane of the wings of the ilia. Thus, these vertebrae are not susceptible to injury related to carrying packs or pulling travois (Lawler et al. 2016) (Supplementary Table 2). A recent study of arctic foxes supports the notion that vertebral asymmetry can be a part of normal morphological variation in (at least) Canidae (Mustonen et al. 2017).

The limbs yielded observations of normal, incipient and overt pathological changes. The metapodials and phalanges yielded observations of incipient pathology (Supplementary Table 2). The summed changes are consistent with an active life style, and do not differ qualitatively from those that can be seen in modern adult dogs (Lawler and Evans 2016; Mustonen et al. 2017; Lawler et al 2017).

Radiocarbon Dating and Stable Isotopes

Neither the Stilwell II nor the Koster dogs have previously been directly radiocarbon dated. Based on their presence in Horizon 11, three dogs from Koster were associated with five Horizon 11 radiocarbon (^{14}C) assays yielding dates between 8480 ± 110 BP (ISGS-236) and 8130 ± 90 BP (ISGS-1065) (Brown and Vierra 1983), but often cited as 8,500 years ago (e.g., Morey and Wiant 1992). A fourth undated Koster dog likely comes from a later Archaic occupation. Here, we present three new direct ^{14}C dates from the Stilwell II dog and two Koster Horizon 11 dogs (F2256 and F2357) (Table 2). Lyophilized samples from all three dogs had a white, fluffy appearance and carbon:nitrogen (C:N) ratios are within the range of modern mammalian collagen (Tuross et al., 1988), suggesting well-preserved collagen.

Koster dog F2256 dates to 8790 ± 30 BP (10,110-9,680 cal BP), Koster dog F2357 dates to 8820 ± 30 BP (10,130-9,700 cal BP), and the Stilwell II dog dates to 8840 ± 80 BP (10,190-9,630 cal BP). The chronological differences between the Stilwell II and Koster individuals are not statistically significant at the scale of ^{14}C dating. These new dates range several hundred years earlier than previously-associated dates for the Koster dogs, and add another Lower Illinois River Valley dog to the early pre-contact dog record.

The stable isotope values for the Stilwell II dog and three Koster Horizon 11 dogs are presented in Table 2. These data are tightly clustered in isotope space, with an average $\delta^{13}\text{C}_{\text{coll}}$ value of -22.7‰ ($\sigma=0.3$) and an average $\delta^{15}\text{N}_{\text{coll}}$ value of 8.7‰ ($\sigma=0.3$).

Discussion

Morphological Variation in Early North American Dogs

Most morphological work on North American dogs has focused on cranial shape (Morey and Wiant 1992; Morey 1992, 2010; Olsen 1985; Walker et al. 2005); however, measurements on mandibles (Bozell 1988; Walker and Frison 1982) and limb elements (Morey and Aaris-Sorensen 2002) have also been examined. Although highly variable, North American dogs generally exhibit shortened muzzles with accompanying changes to dental and mandibular elements, relative to wild canids. Smaller body size, and the size of certain elements (i.e., carnassial molars) have been attributed to domestication (Morey 2010), though recent work has re-evaluated the usefulness of many so-called domestication markers (Janssens et al. 2016; Ameen et al. 2017; Drake et al. 2017). Unfortunately, crania are fragile and often poorly preserved in the zooarchaeological record. While relatively complete crania are present at the Koster site, the Stilwell II dog is represented only by cranial fragments despite field documentation indicating the presence of a complete skull.

To better understand morphological variability among early midwestern dogs, we use a limited set of mandibular measurements from a larger sample of Archaic midwestern domesticated dogs and modern wild *Canis* spp. (Supplementary Table 3). In this dataset, Archaic midwestern dogs generally have deeper mandibular bodies (i.e., greater height of the mandible behind the carnassial M₁; von den Driesch 1976:60) relative to the length of the carnassial molar (von den Driesch 1976:60; Figure 7). Stilwell II, Simonsen, and one of the Modoc dogs have dog-sized carnassial molars, but relatively deep wolf-like mandibles. Three Koster and two Modoc dogs also have deep

mandibles relative to carnassial size, although they are much smaller specimens. Coyote-dog hybrids (coy-dogs) generally plot near the archaeological dogs in this morphospace, suggesting that hybrid individuals may be difficult to distinguish on the basis of morphology alone. It is also possible that some of the early archaeological dog samples themselves are hybrid individuals, as suggested by recent ancient DNA analysis of one Koster dog (Leathlobhair et al. 2018).

Even this limited sampling of Archaic dogs allows some comparative insight into early dog morphology, both contemporaneously and from several periods at the same site. For example, the three dogs from Modoc Rock Shelter show a significant range of variation in their mandibular height and length of carnassial molar (Figure 7). The largest dog dates to 8,560-8,200 cal BP (Supplementary Table 3), but exhibits intra-individual variation between the left and right mandible (shown via dotted line, Figure 7). Another dog from the site, dating to 5,710-5,330 cal BP, has much smaller molars and a more gracile mandible than that individual. A third undated, likely Archaic, dog falls between these two. Similarly, the two contemporaneous Koster dogs and a third undated, but likely contemporaneous, Koster dog all cluster together. A fourth dog, likely from a later period (Morey and Wiant 1992; Hill 1972), is smaller than those three in both measurements (Figure 7).

Though only a small sample, the distinct differences between the mandibles of the robust Stilwell II dog and the more gracile Koster dogs (Figure 5), from individuals geographically and temporally indistinguishable, suggest there may have been some amount of variation already in the earliest American dogs. This is perhaps unsurprising given the morphological variation seen at sites from similar time periods in eastern

Siberia (Pitulko and Kasparov 2017) and recent ancient DNA analysis which shows at least two distinct ancient American dog haplogroups splitting between 16,400-12,900 years ago (Leathlobhair et al. 2018). The probable female sex of the larger Stilwell II dog suggests the morphological differences are not the result of sexual dimorphism, especially given the similarly gracile directly-dated Koster dogs are both a female (F2256) and a male (F2357) (Morey and Wiant 1992). Similar morphological variation is also seen in the two contemporaneous Middle Archaic dogs from Iowa (Figure 7), with one being more robust like the Stilwell II dog and the other more gracile like the Koster dogs. Though this variation may be the result of morphologically distinct American dog lineages, it may also arise from local admixture with wild canids, such as coyotes and wolves, leading to rapid variation within a more homogenous initial dog population.

Hybridization of Early North American Dogs

Genomic work on wild canid populations has demonstrated that all North American *Canis* spp. have the ability to interbreed, often to a significant degree (Wayne and Jenks 1991; Monzon 2014). Although we analyze these taxa as distinct groups, it is likely that some of these specimens show admixture of different species, even in groups made up of modern museum specimens of “known” taxonomic affinity. For example, a recent ancient DNA analysis of one of the Koster dogs we dated (F2256) found that although the specimen clusters with all other pre-contact North American dog material analyzed (spanning c. 9,000 years), it also shows evidence for potential admixture with a midwestern coyote (Leathlobhair et al. 2018). This may account for the morphological

variation seen between the Koster dogs and the Stilwell II dog, which are otherwise concurrent in space and time.

For these reasons, we consider the present study as merely illustrative of general morphological trends in archaeological *Canis*. Combined genomic and morphological approaches have the potential to answer many lingering questions about North American dog populations. However, these techniques are just beginning to be applied rigorously to questions of early dogs in the Americas.

Environment and Diet

At the landscape scale, a mesic, fire-sensitive woodland would have been present in the Illinois River Valley ~10,000 cal BP (Baker et al. 1992, Nelson et al., 2006). Although C₄ plants were present in low numbers at this time (<22% C₄), they began to dominate upland floras after ~9,000 cal BP with the spread of the tallgrass prairie (Nelson et al. 2006). Within this environment, early Holocene human dietary protein was predominantly acquired from terrestrial and riverine sources (Styles and McMillan 2009) and $\delta^{13}\text{C}$ values would have ranged from -22‰ to -38‰ (average=-26.5‰) (Tieszen 1991, Tieszen and Fagre 1993).

The $\delta^{15}\text{N}$ of bone collagen ($\delta^{15}\text{N}_{\text{coll}}$) in the Midwest is influenced strongly by trophic level fractionation, with a difference of ~3‰ between predators and their prey (Schoeninger and DeNiro 1984, Hedman et al. 2002). Although landscape aridity can also impact the $\delta^{15}\text{N}$ of primary consumers (Heaton et al. 1986), the mesic environment of the Lower Illinois River Valley ~10,000 years ago suggests that aridity would have contributed little to local $\delta^{15}\text{N}_{\text{coll}}$ values. However, seasonality may influence $\delta^{15}\text{N}_{\text{coll}}$

values through the recycling of body tissues due to periodic nutritional stress (Polischuk et al. 2001). Most isotopic studies of human diets in the valley have been focused on the dietary transition of hunting and gathering to maize agriculture (Buikstra et al. 1994; Hedman et al. 2002; Emerson et al., 2005), and tracking the dietary impact of maize, a C₄ grass, on a diet previously dominated by C₃ sources. However, the $\delta^{15}\text{N}$ of human diets has recently received more attention (Hedman et al. 2002, Froehle et al. 2012). Schober (1998, cited in Hedman et al 2002) noted that $\delta^{15}\text{N}_{\text{coll}}$ of Midwestern communities with a maize-dominated diet ($\delta^{15}\text{N}_{\text{coll}} = +9.5\text{‰}$) were not significantly different from co-eval groups who did not rely heavily on domesticates ($\delta^{15}\text{N}_{\text{coll}} = +8.9\text{‰}$).

The Koster and Stilwell II dog isotope values reflect unsurprising results for early Holocene, pre-maize diets in the region. Low $\delta^{13}\text{C}$ values suggest terrestrial C₃ resources, while high $\delta^{15}\text{N}$ values may signal consumption of freshwater resources (Brugam et al. 2017), human feces (Katzenberg 1989) and/or higher overall $\delta^{15}\text{N}$ values in local prey. Early Archaic dog $\delta^{15}\text{N}$ values are significantly greater than the single Early Archaic human value in the region (Kaskaskia Mine, Randolph Co., IL; Hargrave et al., 2006), but more consistent with Middle and Late Archaic human and dog paleodiets (Figure 8). Since these values generally fall outside of the range of modern wolves with a C₃ terrestrial diet, and are within the range of pre-maize freshwater fish from the Illinois River, it is likely that freshwater fish formed the basis for a significant part of the diet in Early Archaic dogs.

At a larger scale, the range of variability in both human and dog $\delta^{15}\text{N}$ values throughout the Holocene is relatively elevated compared to terrestrial herbivores and

carnivores, suggesting that riverine resources were common in diets throughout the region. The primary axis of change throughout the Holocene in both humans and dogs is in $\delta^{13}\text{C}$ values. We interpret this as a general landscape transition to C_4 tallgrass prairie after the Early Archaic (also see Nelson et al. 2006) followed by increasing amounts of maize in human and dog diets during the Woodland and Mississippian periods (Hedman et al. 2002). Future establishment of a local, early Holocene isotopic baseline for the Illinois Valley is needed before we can further understand the role of dogs within the local food web.

Conclusions

The c. 10,000 year-old age of the Stilwell II and Koster dogs introduces an over 4,500 year gap between these earliest dog remains and the proposed initial migration into the Americas. This is consistent with genomic analyses proposing North American dog populations originated around 10,000 cal BP (Witt et al. 2015), though others suggest an earlier split from Eurasian dogs (Thalmann et al. 2013; Leathlobhair et al. 2018). Recent DNA analysis suggests pre-contact American dogs, including those from Koster, share a common ancestor with eastern Siberian dogs around 15,600 years ago and saw an internal population split roughly 1,000 years later (Leathlobhair et al. 2018), though it is not clear on which side of Beringia the latter split occurred. It is possible that the arrival of the first human populations into the Americas predated their access to Eurasian domesticated dogs and thus they arrived without them. In this scenario, dogs may have arrived with later genetically-indistinguishable migrating Siberian groups (as

part of ongoing “migratory dribbles”; Meltzer 2009: 200) before the flooding of the Bering Land Bridge 11,000 years ago (Jakobsson et al. 2017), but were not part of the very first pulse of migration into the Americas.

The earliest New World domesticated dogs appearing in the midcontinent around 10,000 years ago presents a conundrum both temporally and spatially, but the current absence of Paleoindian dogs in the west may be the result of several factors. Earlier dogs in western North America may be going unseen or unrecognized, despite the number of Clovis, WST and earlier sites (Erlandson et al. 2011; Smallwood and Jennings 2014; Stanford and Stenger 2014). Some regions still have few early sites and the ephemeral nature of some sites (e.g., procurement or satellite camps) may constrain the discovery of dog remains (Fiedel 2005; Erlandson et al. 2011). If early dog remains are being encountered, they may not be identified as dogs, particularly given the often limited and poorly-preserved nature of early skeletal material and difficulties in distinguishing early dogs from wolves (Perri 2016a) and coyotes. The few specimens that have been tentatively proposed as Paleoindian dogs (e.g., Haag 1970; Walker and Frison 1982; Grayson 1988) have not been re-evaluated, leaving their taxonomy unclear. These potential dogs are only slightly older than the Stilwell II and Koster specimens, leaving any dogs associated with the earliest human migration in the Americas unaccounted for. Finally, it is possible that domesticated dogs entering the Americas with human groups facilitated rapid movement into the midcontinent, leaving little trace in western North America.

While an *in situ* domestication of North American wolves has been raised as a possibility (Koop et al. 2000; Witt et al. 2015), this has been rejected by several genetic

analyses (Vila et al. 1997; Leonard et al. 2002; vonHoldt et al. 2010; Freedman et al. 2014; Leathlobhair et al. 2018). Some North American archaeological dog specimens do show genetic similarities with North American wolves (Koop et al. 2000; Witt et al. 2015), however this is likely the result of admixture rather than North American wolf domestication. Additional work on ancient American canids, particularly the inclusion of more ancient North American wolf and coyote reference specimens, will further clarify this issue.

Identification of earlier Paleoindian dogs, if they exist, will require distinguishing them from wild canid taxa. This has proven a difficult task, as seen from debates regarding proposed early dogs in the Paleolithic record of Eurasia (Ovodov et al. 2011; Crockford and Kuzmin 2012; Boudadi-Maligne and Escarguel 2014; Drake et al. 2015; Germonpré et al. 2015; Perri 2016a). Differentiation between wild and domestic canids has been based primarily on morphological traits, often requiring well-preserved cranio-dental material. The validity of these traits for distinguishing domestication is also questionable, given the morphological plasticity of *Canis* (Morey and Jeger 2015; Janssens et al. 2016; Ameen et al. 2017; Drake et al. 2017). Substantial introgression between newly-arriving Eurasian dogs and North American wolves and coyotes likely contributed significantly to American dog ancestry as well, as suggested at Koster (Leathlobhair et al. 2018). This potentially extensive introgression, particularly in the case of early coy-dogs (dog x coyote hybrids), may contribute to the misidentification of these specimens in the archaeological record. Though some past research has emphasized apparent introgression between ancient dogs and coyotes or wolves

(Walker and Frison 1982; Valadez et al. 2006), the issue of early hybridization warrants more attention in future studies.

Analysis of ancient DNA is increasingly being used to identify domesticated dogs (Larson et al. 2012; Druzhkova et al. 2013; Frantz et al. 2016), but requires adequate preservation of skeletal material and is subject to debates about the interpretation of results (Savolainen et al. 2002; Ding et al. 2012; Thalmann et al. 2013; Skoglund et al. 2015). Increasingly, techniques that do not rely on ancient DNA preservation or preservation of pristine specimens, such as complete crania, are allowing researchers to document individual life histories of canids, improving chances of identifying individuals in close contact with humans. These techniques include investigating paleopathology and trauma to clarify, for example, pack-loading and mistreatment (Losey et al. 2014; Lawler et al. 2016) and geometric morphometrics (GM) to detect biomechanical differences among canids (Drake et al. 2015; Evin et al. 2016; Drake et al. 2017). Dietary analysis of stable isotopes may also help to identify early canids in close contact with humans (Ewersen et al. 2018). Ultimately, a combination of these methods will best promote the identification of the earliest domesticated dogs (and other domesticated species).

The Stilwell II and Koster dogs were contemporaneous adult, medium-sized dogs with very active lifestyles and surprisingly varied morphologies for their proximity in space and time. Their stable isotope values reflect a C₃-dominated Early Archaic landscape and substantial freshwater fish consumption. Early American dogs likely played key cultural and ecological roles in the movement and adaptation of migrating human populations and their intentional burial suggests they were an important part of

human domesticity in the Americas by 10,000 years ago. Similar intentional dog burials in other temperate hunter-gatherer contexts have been associated with the dog's importance as adaptive hunting tool technology in the face of changing environments and prey during the Pleistocene/Holocene Transition and their subsequent elevated social status (Perri 2014; Perri 2016b). The intentional burial of the Koster and Stilwell II dogs may reflect a similar importance of hunting dogs in the deciduous forested environment of the midcontinent.

The dating of the Stilwell II dog to around 10,000 years ago, coinciding with similar dates for the Koster dogs, adds a further early specimen to the pre-contact dog record and identifies the Lower Illinois River Valley as an important site of early North American domestic dog activity. These new dates extend the presence of North American dogs potentially into the Paleoindian period. They also confirm the Stilwell II and Koster specimens as the earliest securely identified skeletal remains of dogs in the Americas and the earliest examples of intentional, individual dog burials in the worldwide archaeological record¹. Future (re)evaluation of faunal remains from Clovis, Western Stemmed and earlier sites may further identify domesticated dogs in the earlier Paleoindian record, supporting their arrival with the first human migrations into the Americas. Alternatively, the timing and location of these earliest dogs may suggest a later arrival with subsequent early human migrations.

¹Although an individual dog burial has been reported from the Siberian Beringian site of Ushki-1 (Dikov 1979), which dates to around 13,000 years ago (Goebel et al. 2010), by all accounts these remains were identified via photograph in the 1970s and are now lost (Pitulko and Kasparov 2017), having never been confirmed as a dog or directly dated.

Acknowledgements. We thank the Illinois State Museum for access to the faunal collections, the Center for American Archeology for use of the Koster excavation photograph, and Doug Carr and Claire Martin for additional material photographs. We also thank Bonnie Styles, Dee Ann Watt, Mike Wiant, Beckie Dyer, Mike Kolb, Jim Theler, Kris Hedman, and Tom Emerson for their assistance and Ken Ames, Torben Rick, and the anonymous reviewers for their helpful comments on the manuscript. ISAS would particularly like to acknowledge Bob Perino for the generous donation of his father's material from the Stilwell II site to them. Funding was provided by the Illinois State Museum Society, the ETSU Center of Excellence in Paleontology, the Rosemary Cramp Travel Fund and the R. Bruce McMillan Museum Research Internship (A.R.P).

Data Availability Statement.

3D models of the Koster F2256

(http://www.morphosource.org/Detail/SpecimenDetail/Show/specimen_id/10494) and

Stilwell II dog

(http://www.morphosource.org/Detail/SpecimenDetail/Show/specimen_id/10495)

mandibles are freely available on Morphosource.

References Cited

- Ahler, Steven R.
1993 Stratigraphy and radiocarbon chronology of Modoc rock shelter, Illinois. *American Antiquity*, 58(3), 462-489.
- Ameen, Carly, Ardern Hulme-Beaman, Allowen Evin, Mietje Germonpré, Kate Britton, Thimas Cucchi, ... & Dobney, K.
2017 A landmark-based approach for assessing the reliability of mandibular tooth crowding as a marker of dog domestication. *Journal of Archaeological Science*, 85, 41-50.
- Axelsson, Erik, Abhirami Ratnakumar, Maja-Louise Arendt, Khurram Maqbool, Matthew T. Webster, Michele Perloski, Olof Liberg, Jon M. Arnemo, Åke Hedhammar and Kerstin Lindblad-Toh.
2013 The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature*, 495(7441), 360.
- Baker, Richard G., Louis J. Maher, Craig A. Chumbley and Kent L. Van Zant
1992 Patterns of Holocene environmental change in the midwestern United States. *Quaternary Research*, 37(3), 379-389.
- Beebe, B. F.
1980 A domestic dog (*Canis familiaris* L.) of probable Pleistocene age from Old Crow, Yukon Territory, Canada. *Canadian Journal of Archaeology= Journal Canadien d'Archéologie Ottawa*, (4), 161-168.
- Boudadi-Maligne, Myriam and Gilles Escarguel
2014 A biometric re-evaluation of recent claims for Early Upper Palaeolithic wolf domestication in Eurasia. *Journal of Archaeological Science*, 45, 80-89.
- Bozell, John R.
1988 Changes in the role of the dog in protohistoric-historic Pawnee culture. *Plains Anthropologist*, 33(119), 95-111.
- Braje, Todd J., Tom D. Dillehay, Jon M. Erlandson, Richard G. Klein, and Torben C. Rick.
2017 Finding the first Americans. *Science* 358, no. 6363: 592-594.

- Brown, Sarah K., Christyann M. Darwent, and Benjamin N. Sacks
2013 Ancient DNA evidence for genetic continuity in arctic dogs. *Journal of Archaeological Science*, 40(2), 1279-1288.
- Brown, James A. and Robert K. Vierra
1983 *What happened in the Middle Archaic?: Introduction to an ecological approach to Koster Site Archaeology* (pp. 165-195). Orlando: Academic Press.
- Buikstra, Jane E., Jerome C. Rose and George R. Milner
1994 A carbon isotopic perspective on dietary variation in late prehistoric western Illinois. *Agricultural Origins and Development in the Midcontinent, Office of the State Archaeologist, University of Iowa, Iowa City*, 155-170.
- Butzer, Karl W.
1978 Changing Holocene environments at the Koster site: A geo-archaeological perspective. *American Antiquity*, 43(3), 408-413.
- Camarós, Edgard, Susanne C. Münzel, Marián Cueto, Florent Rivals and Nicholas J. Conard
2016 The evolution of Paleolithic hominin–carnivore interaction written in teeth: Stories from the Swabian Jura (Germany). *Journal of Archaeological Science: Reports*, 6, 798-809.
- Carbaugh, Aimee E., Amanda Headley and Matthew Fort
in press Human Remains Analysis Results and Interpretation in *The Broglio Site: A Late Middle Archaic Habitation and Mortuary Site in the Big Muddy Watershed*. Research Report No. 49. Illinois State Archaeological Survey, Prairie Research Institute, University of Illinois at Urbana–Champaign.
- Cormie, A. B. and H. P. Schwarcz
1994 Stable isotopes of nitrogen and carbon of North American white-tailed deer and implications for paleodietary and other food web studies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 107(3-4), 227-241.
- Crockford, Susan J. and Yaroslav Kuzmin
2012 Comments on Germonpré et al., *Journal of Archaeological Science* 36,
2009 “Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes”, and Germonpré, Lázkičková-Galetová, and Sablin, *Journal of Archaeological Science* 39, 2012 “Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic”. *Journal of Archaeological Science*, 39(8), 2797-2801.
- Darwent, Christann M. and J. Eric Gililand
2001 Osteological analysis of domestic dogs from burials in Southern Missouri. *Missouri Archaeology*. 62, 149–169.
- DeBowes, Linda J., Derek Mosier, E. Logan, C. E. Harvey, S. Lowry, D. C. Richardson

- 1996 Association of periodontal disease and histologic lesions in multiple organs from 45 dogs. *Journal of Veterinary Dentistry* 13(2):57-60
- Dikov, Nikolay N.
1979 Drevniye kul'tury severo-vostochnoy Azii. Aziya na styke s Amerikoy v drevnosti [Ancient Cultures of Northeast Asia. Asia at the Junction with America in Antiquity], Nauka, Moscow, 352 pp. (in Russian)
- Dillehay, Tom D., Carlos Ocampo, José Saavedra, Andre Oliveira Sawakuchi, Rodrigo M. Vega, Mario Pino, Michael B. Collins et al.
2015 New archaeological evidence for an early human presence at Monte Verde, Chile." *PloS one* 10, no. 11: e0141923.
- Doherty, Tim S., Chris R. Dickman, Alistair S. Glen, Thomas M. Newsome, Dale G. Nimmo, Euan G. Ritchie, Abi T. Vanak, and Aaron J. Wirsing.
2017 The global impacts of domestic dogs on threatened vertebrates. *Biological conservation* 210: 56-59.
- Drake, Abby G., Michael Coquerelle and Guillaume Colombeau
2015 3D morphometric analysis of fossil canid skulls contradicts the suggested domestication of dogs during the late Paleolithic. *Scientific Reports*, 5.
- Drake, Abby G., Michael Coquerelle, Pavel A. Kosintsev, Olga P. Bachura, Mikhail Sablin, Andrei V. Gusev, Lacey S. Fleming and Robert J. Losey
2017 Three-dimensional geometric morphometric analysis of fossil canid mandibles and skulls. *Scientific Reports*, 7(1), 9508.
- Easton, Norman A., Glen R. Mackay, Patricia B. Young, Peter Schnurr and David R. Yesner
2011 Chindadn in Canada? Emergent evidence of the Pleistocene transition in southeast Beringia as revealed by the Little John Site, Yukon. *From the Yenisei to the Yukon: Interpreting Lithic Assemblage Variability in Late Pleistocene/Early Holocene Beringia*, 289-307.
- Emerson, Thomas E., Kristin M. Hedman and Mary L. Simon
2005 Marginal horticulturalists or maize agriculturalists? Archaeobotanical, paleopathological, and isotopic evidence relating to Langford Tradition maize consumption. *Midcontinental Journal of Archaeology*, 30(1), 67-118.
- Erlandson, Jon M., Torben C. Rick, Todd J. Braje, Molly Casperson, Brendan Culleton, Brian Fulfrost, Tracy Garcia, Daniel A. Guthrie, Nicholas Jew, Douglas J. Kennett, Madonna L. Moss, Leslie Reeder, Craig Skinner, Jack Watts, Lauren Willis
2011 Paleoindian Seafaring, Maritime Technologies, and Coastal Foraging on California's Channel Islands. *Science*, 331.
- Ewersen, Jörg, Stefan Ziegler, Britta Ramminger and Ulrich Schmölcke

- 2018 Stable isotopic ratios from Mesolithic and Neolithic canids as an indicator of human economic and ritual activity. *Journal of Archaeological Science: Reports* 17 (2018): 346-357.
- Fiedel, Stuart J.
2005 Man's best friend—mammoth's worst enemy? A speculative essay on the role of dogs in Paleoindian colonization and megafaunal extinction. *World Archaeology*, 37(1), 11-25.
- Fort, Matthew A., Kristin M. Hedman and Stanley H. Ambrose
2016 Stable Isotope Analysis of Diet in a Sample of Human and Mammal Bone in *The Tree Row Site: A Late Archaic Habitation and Mortuary Site in the Central Illinois Valley*. Illinois State Archaeological Survey, Prairie Research Institute.
- Fox-Dobbs, Kena, J.K. Bump, R.O. Peterson, D. L. Fox, P.L. Koch
2007 Carnivore-specific stable isotope variables and variation in the foraging ecology of modern and ancient wolf populations: case studies from Isle Royale, Minnesota, and La Brea. *Canadian Journal of Zoology*, 85(4), 458-471.
- Frantz, Laurent A., Victoria E. Mullin, Maud Pionnier-Capitan, Ophélie Lebrasseur, Morgane Ollivier, Angela Perri, Anna Linderholm, Valeria Mattiangeli, Matthew D. Teasdale, Evangelos A. Dimopoulos, Anne Tresset, Marilyne Duffraisse, Finbar McCormick, László Bartosiewicz, Erika Gál, Éva A. Nyerges, Mikhail V. Sablin, Stéphanie Bréhard, Marjan Mashkour, Adrian Bălăşescu, Benjamin Gillet, Sandrine Hughes, Olivier Chassaing, Christophe Hitte, Jean-Denis Vigne, Keith Dobney, Catherine Hänni, Daniel G. Bradley, Greger Larson
2016 Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science*, 352(6290), 1228-1231.
- Freedman, Adam H., Ilan Gronau, Rena M. Schweizer, Diego Ortega-Del Vecchyo, Eunjung Han, Pedro M. Silva, Marco Galaverni, Zhenxin Fan, Peter Marx, Belen Lorente-Galdos, Holly Beale, Oscar Ramirez, Farhad Hormozdiari, Can Alkan, Carles Vilà, Kevin Squire, Eli Geffen, Josip Kusak, Adam R. Boyko, Heidi G. Parker, Clarence Lee, Vasisht Tadigotla, Adam Siepel, Carlos D. Bustamante, Timothy T. Harkins, Stanley F. Nelson, Elaine A. Ostrander, Tomas Marques-Bonet, Robert K. Wayne and John Novembre
2014 Genome sequencing highlights the dynamic early history of dogs. *PLoS Genetics*, 10(1), e1004016.
- Froehle, Andrew W., Corina M. Kellner and Margaret J. Schoeninger
2012 Multivariate carbon and nitrogen stable isotope model for the reconstruction of prehistoric human diet. *American Journal of Physical Anthropology*, 147(3), 352-369.
- Germonpré, Mietje, Mikhail V. Sablin, Rhiannon E. Stevens, Robert E.M. Hedges, Michael Hofreiter, Mathias Stiller and Viviane R. Després

- 2009 Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes. *Journal of Archaeological Science*, 36(2), 473-490.
- Germonpré, Mietje, Mikhail V. Sablin, Viviane Després, Michael Hofreiter, Martina Lázničková-Galetová, Rhiannon E. Stevens, Mathias Stiller
2013 Palaeolithic dogs and the early domestication of the wolf: a reply to the comments of Crockford and Kuzmin (2012). *Journal of Archaeological Science*, 40(1), 786-792.
- Germonpré, Mietje, Martina Lázničková-Galetová and Mikhail V. Sablin
2012 Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. *Journal of Archaeological Science*, 39(1), 184-202.
- Germonpré, Mietje, Mikhail V. Sablin, Martina Lázničková-Galetová, Viviane Després, Rhiannon E. Stevens, Mathias Stiller, M. and Michael Hofreiter
2015 Palaeolithic dogs and Pleistocene wolves revisited: a reply to Morey (2014). *Journal of Archaeological Science*, 54, 210-216.
- Germonpré, Mietje, Martina Lázničková-Galetová, Robert J. Losey, Jannikke Rääkkönen, and Mikhail V. Sablin
2015 Large canids at the Gravettian Předmostí site, the Czech Republic: the mandible. *Quaternary International*, 359, 261-279.
- Germonpré, Mietje, Sergey Fedorov, Petr Danilov, Patrik Galeta, Elodie-Laure Jimenez, Mikhail Sablin and Robert J. Losey
2017 Palaeolithic and prehistoric dogs and Pleistocene wolves from Yakutia: Identification of isolated skulls. *Journal of Archaeological Science*, 78, 1-19.
- Goebel, Ted, Sergei B. Slobodin, and Michael R. Waters
2010 New dates from Ushki-1, Kamchatka, confirm 13,000 cal BP age for earliest Paleolithic occupation. *Journal of Archaeological Science*, 37(10), 2640-2649.
- Gowlett, John A., Hedges, R. E. M., Law, I. A., & Perry, C.
1987 Radiocarbon dates from the Oxford AMS system: Archaeometry datelist 5. *Archaeometry*, 29(1), 125-155.
- Grayson, Donald K., Paul W. Parmalee, R. Lee Lyman, and Jim I. Mead
1988 Danger Cave, Last Supper Cave, and Hanging Rock Shelter: the faunas. *Anthropological papers of the AMNH*; v. 66, pt. 1.
- Haag, William G.
1970 Dog remains from Hogup Cave. *Univ. Utah Anthropol. Papers*, 84, 273-274.
- Hajic, Edwin R.
1990 *Koster site archaeology I: stratigraphy and landscape evolution* (No. 8). Center for Amer Archeology Press.

- Halligan, Jessi J., Michael R. Waters, Angelina Perrotti, Ivy J. Owens, Joshua M. Feinberg, Mark D. Bourne, Brendan Fenerty et al.
2016 Pre-Clovis occupation 14,550 years ago at the Page-Ladson site, Florida, and the peopling of the Americas." *Science advances* 2, no. 5: e1600375.
- Harcourt, Ralph A.
1974 The dog in prehistoric and early historic Britain. *Journal of Archaeological Science*, 1(2), 151-175.
- Hargrave, Eve A., Kristin M. Hedman, and Rebecca Wolf
2006 Isolated Human Burial at the Kaskaskia Mine Site (11R687), Randolph County, Illinois. Transportation Archaeological Research Reports No. 104
- Harington, Charles R. (Ed.).
2003 *Annotated bibliography of Quaternary vertebrates of northern North America: with radiocarbon dates*. University of Toronto Press.
- Heaton, Tim H.E., John C. Vogel, Gertrud von La Chevallerie, and Gill Collett
1986 Climatic influence on the isotopic composition of bone nitrogen. *Nature* 322: 822-824
- Hedman, Kristin, Eve A. Hargrave, and Stanley H. Ambrose
2002 Late Mississippian diet in the American Bottom: stable isotope analyses of bone collagen and apatite. *Midcontinental Journal of Archaeology*, 237-271.
- Hill, Frederick C
1972 *A Middle Archaic dog burial in Illinois*. Foundation for Illinois Archaeology. Evanston.
- Jakobsson, M., Pearce, C., Cronin, T.M., Backman, J., Anderson, L.G., Barrientos, N., Björk, G., Coxall, H., De Boer, A., Mayer, L.A. and Mörrth, C.M.
2017 Post-glacial flooding of the Bering Land Bridge dated to 11 cal ka BP based on new geophysical and sediment records. *Climate of the Past*, 13(8), p.991.
- Janssens, Luc, Inge Spanoghe, Rebecca Miller, and Stefan Van Dongen
2016 Can orbital angle morphology distinguish dogs from wolves? *Zoomorphology*, 135(1), 149-158.
- Jenkins, Dennis L., Loren G. Davis, Thomas W. Stafford, Jr., Paula F. Campos, Thomas J. Connolly, Linda Scott Cummings, Michael Hofreiter, Bryan Hockett, Katelyn McDonough, Ian Luthé, Patrick W. O'Grady, Mark E. Swisher, Frances White, Bonnie Yates, Robert M. Yohe II, Chad Yost, Eske Willerslev
2013 Geochronology, Archaeological Context, and DNA at the Paisley Caves. In *Paleoamerican Odyssey* 32: 485-510.
- Komar, Debra and Jane E. Buikstra
2003 Differential diagnosis of a prehistoric biological object from the Koster (Illinois) site. *International Journal of Osteoarchaeology*, 13(3), 157-164.

Koop, Ben F., Maryann Burbidge, Ashley Byun, U. Rink, and Susan J. Crockford
2000 Ancient DNA evidence of a separate origin for North American indigenous dogs. *BAR International Series*, 889, 271-286.

Lapham, Heather A.

2010 A Baumer Phase Dog Burial from the Kincaid Site in Southern Illinois. *Illinois Archaeology: Journal of the Illinois Archaeology Survey*, 22(2).

Larson, Greger, Elinor K. Karlsson, Angela Perri, Matthew T. Webster, Simon YW Ho, Joris Peters, Peter W. Stahl, Philip J. Piper, Frode Lingaas, Merete Fredholm, Kenine E. Comstock, Jaime F. Modiano, Claude Schelling, Alexander I. Agoulnik, Peter A. Leegwater, Keith Dobney, Jean-Denis Vigne, Carles Vilà, Leif Andersson and Kerstin Lindblad-Toh

2012 Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences*, 109(23), 8878-8883.

Lawler, Dennis F.

2017 Differential diagnosis in archaeology. *International Journal of Paleopathology* 19: 119-123.

Lawler Dennis F., Evans RH.

2016 Evaluation of femoral head and neck new bone from a grey wolf (*Canis lupus lupus*): When is it pathology? *Journal of Veterinary Anatomy* 9(1):39-46.

Lawler, Dennis F., Chris Widga, David A. Rubin, Jennifer A. Reetz, Richard H. Evans, Basil P. Tangredi, Richard M. Thomas, Terrance J. Martin, Charles Hildebolt, Kirk Smith, Daniel Leib, Jill E. Sackman, James G. Avery, Gail K. Smith

2016 Differential diagnosis of vertebral spinous process deviations in archaeological and modern domestic dogs. *Journal of Archaeological Science* 9, 54-63.

Lawler DF, Widga C, Smith GK.

2017 Observations of the acetabulum and proximal femur of the dire wolf. *Journal of Veterinary Anatomy* 10(1) :73-83.

Lawrence, Barbara

1967 Early domestic dogs. *Zeitschrift für Säugetierkunde*, 32(1), 44-59.

Leathlobhair, Máire Ní, Angela R. Perri, Evan K. Irving-Pease, Kelsey E. Witt, Anna Linderholm, James Haile, Ophelie Lebrasseur, Carly Ameen, Jeffrey Blick, Adam R. Boyko, Selina Brace, Yahaira Nunes Cortes, Susan J. Crockford, Alison Devault, Evangelos A. Dimopoulos, Morley Eldridge, Jacob Enk, Kevin Gori, Shyam Gopalakrishnan, Vaughan Grimes, Eric Guiry, Anders J. Hansen, Ardern Hulme-Beaman, John Johnson, Andrew Kitchen, Aleksei K. Kasparov, Young-Mi Kwon, Pavel A. Nikolskiy, Carlos Peraza Lope, Aurélie Manin, Terrance Martin, Michael Meyer, Kelsey Noack Myers, Mark Omura, Jean-Marie Rouillard, Elena Y. Pavlova, Paul Sciulli, Mikkel-Holger S. Sinding, Andrea Strakova, Varvara V. Ivanova, Christopher

Widga, Eske Willerslev, Vladimir V. Pitulko, Ian Barnes, M. Thomas P. Gilbert, Keith M. Dobney, Ripan S. Malhi, Elizabeth P. Murchison, Greger Larson and Laurent A. F. Frantz

2018 The Evolutionary History of Dogs in the Americas. *Science*.

Leonard, Jennifer A., Robert K. Wayne, Jane Wheeler, Raúl Valadez, Sonia Guillén, and Carles Vila.

2002 Ancient DNA evidence for Old World origin of New World dogs. *Science*, 298(5598), 1613-1616.

Llamas, Bastien, Lars Fehren-Schmitz, Guido Valverde, Julien Soubrier, Swapan Mallick, Nadin Rohland, Susanne Nordenfelt, Cristina Valdiosera, Stephen M. Richards, Adam Rohrlach, Maria Inés Barreto Romero, Isabel Flores Espinoza, Elsa Tomasto Cagigao, Lucía Watson Jiménez, Krzysztof Makowski, Ilán Santiago Leboeiro Reyna, Josefina Mansilla Lory, Julio Alejandro Ballivián Torrez, Mario A. Rivera, Richard L. Burger, Maria Constanza Ceruti, Johan Reinhard, R. Spencer Wells, Gustavo Politis, Calogero M. Santoro, Vivien G. Standen, Colin Smith, David Reich, Simon Y. W. Ho, Alan Cooper and Wolfgang Haak

2016 Ancient mitochondrial DNA provides high-resolution time scale of the peopling of the Americas. *Science Advances*, 2(4), e1501385.

Longin, Robert

1971 New method of collagen extraction for radiocarbon dating. *Nature*, 230(5291), 241.

Losey, Robert J., Benjamin Osipov, Rajitha Sivakumaran, Tatiana Nomokonova, Evgenii V. Kovychev, and Natalia G. Diatchina

2014 Estimating body mass in dogs and wolves using cranial and mandibular dimensions: application to Siberian canids. *International Journal of Osteoarchaeology*, 25(6), 946-959.

Losey, Robert J., K. McLachlin, T. Nomokonova, K. Latham and L. Harrington

2016 Body mass estimates in dogs and North American gray wolves using limb element dimensions. *International Journal of Osteoarchaeology*, 27(2), 180-191.

Lyman, R. Lee

2013 Paleoindian Exploitation of Mammals in Eastern Washington State. *American Antiquity* 78(2): 227-247.

McMillan, R. Bruce

1970 Early canid burial from the western Ozark highland. *Science*, 167(3922), 1246-1247.

2006 (editor) Records of Early Bison in Illinois. Illinois State Museum, Scientific papers, volume XXXI. Springfield, IL.

Meltzer, David J.

- 2009 *First peoples in a new world: colonizing ice age America*. Univ of California Press.
- Miller, Malcolm E., Howard E. Evans, H.E. and George C. Christensen
1979 *Miller's Anatomy of the Dog*. 2nd Ed. Philadelphia, WB Saunders Co.
- Monzón, J., R. Kays and D. E. Dykhuizen
2014 Assessment of coyote–wolf–dog admixture using ancestry-informative diagnostic SNPs. *Molecular Ecology*, 23(1), 182-197.
- Moreno-Mayar, J. Víctor, Ben A. Potter, Lasse Vinner, Matthias Steinrücken, Simon Rasmussen, Jonathan Terhorst, John A. Kamm et al.
2018 Terminal Pleistocene Alaskan genome reveals first founding population of Native Americans. *Nature* 553, no. 7687 (2018): 203.
- Morey, Darcy F.
1992 Size, shape and development in the evolution of the domestic dog. *Journal of Archaeological Science*, 19(2), 181-204.

2006 Burying key evidence: the social bond between dogs and people. *Journal of Archaeological Science*, 33(2), 158-175.

2010 *Dogs: domestication and the development of a social bond*. Cambridge University Press.
- Morey, Darcy F. and Kim Aaris-Sørensen
2002 Paleoeskimo dogs of the eastern Arctic. *Arctic*, 44-56.
- Morey, Darcy F. and Rujana Jeger
2015 Paleolithic dogs: Why sustained domestication then?. *Journal of Archaeological Science: Reports*, 3, 420-428.

2017 From wolf to dog: Late Pleistocene ecological dynamics, altered trophic strategies, and shifting human perceptions. *Historical Biology*, 29(7), 895-903.
- Morey, Darcy F. and Michael D. Wiant
1992 Early Holocene domestic dog burials from the North American Midwest. *Current Anthropology*, 33(2), 224-229.
- Mueller, Melissa, Ted Goebel, Julie Esdale and Kelly Graf
2015 Archaeology of the Terminal Pleistocene McDonald Creek Site, Central Alaska. Presented at The 80th Annual Meeting of the Society for American Archaeology, San Francisco, California.
- Munyikwa, Kennedy, Tammy M. Rittenour, and James K. Feathers.
2017 Temporal constraints for the Late Wisconsinan deglaciation of western Canada using eolian dune luminescence chronologies from Alberta. *Palaeogeography, Palaeoclimatology, Palaeoecology* 470: 147-165.

- Mustonen. Anne-Mari, Dennis F. Lawler, Leena Ahola, Tarja Koistinen, Liisa Jalkanen, Jaakko Mononen, Marja-Leena Lamidi, and Petteri Nieminen
2017 Skeletal pathology of farm-reared obese juvenile blue Foxes (*Vulpes lagopus*). *Journal of Veterinary Anatomy* 10(2) :51-74.
- Nelson, David M., Feng Sheng Hu, Eric C. Grimm, B. Brandon Curry, and Jennifer E. Slate
2006 The influence of aridity and fire on Holocene prairie communities in the eastern Prairie Peninsula. *Ecology* 87(10): 2523-2536.
- Neusius, Sarah
1996 Koster Site. *The Oxford Companion to Archaeology*. Oxford University Press.
- Olsen, Stanley J.
1985 *Origins of the domestic dog: the fossil record*. Univ of Arizona Press.
- Ovodov, Nikolai D., Susan J. Crockford, Yaroslav V. Kuzmin, Thomas FG Higham, Gregory WL Hodgins, and Johannes van der Plicht
2011 A 33,000-year-old incipient dog from the Altai Mountains of Siberia: evidence of the earliest domestication disrupted by the Last Glacial Maximum. *PLoS One*, 6(7), e22821.
- Perino, Gregory
1970 The Stilwell II Site, Pike County, Illinois. *Central States Archaeological Journal*, 118-122.

1977 Points and barbs: an editorial. *Central States Archaeological Journal*, 99-100.
- Perri, Angela
2014 *Global Hunting Adaptations to Early Holocene Temperate Forests: Intentional Dog Burials as Evidence of Hunting Strategies*. PhD Dissertation. Department of Archaeology, Durham University.

2016a A wolf in dog's clothing: initial dog domestication and Pleistocene wolf variation. *Journal of Archaeological Science*, 68, 1-4.

2016b Hunting dogs as environmental adaptations in Jomon Japan. *Antiquity* 90(353): 1166-1180.

2017 A Typology of Dog Deposition in Archaeological Contexts. *Economic Zooarchaeology: Studies in Hunting, Herding and Early Agriculture*. Oxbow Books, Oxford.
- Perri, Angela R., Geoffrey M. Smith and Marjolein D. Bosch
2015 Comment on "How do you kill 86 mammoths? Taphonomic investigations of mammoth megasites" by Pat Shipman. *Quaternary International*, 368(11).

- Pitulko, Vladimir V. and Aleksey K. Kasparov
2017 Archaeological dogs from the early Holocene Zhokhov site in the eastern Siberian arctic. *Journal of Archaeological Science: Reports*, 13, 491-515.
- Polischuk S., K. Hobson K and M. Ramsay
2011 Use of stable-carbon and -nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. *Canadian Journal of Zoology* 79, 499–511.
- Potter, Ben A., Joshua D. Reuther, Vance T. Holliday, Charles E. Holmes, D. Shane Miller, and Nicholas Schmuck
2017 Early colonization of Beringia and northern North America: chronology, routes, and adaptive strategies." *Quaternary International* 444 (2017): 36-55.
- Reimer, Paula J., Edouard Bard, Alex Bayliss, J. Warren Beck, Paul G. Blackwell, Christopher Bronk Ramsey, Caitlin E. Buck, Hai Cheng, R Lawrence Edwards, Michael Friedrich, Pieter M Grootes, Thomas P Guilderson, Hafliði Hafliðason, Irka Hajdas, Christine Hatté, Timothy J Heaton, Dirk L Hoffmann, Alan G Hogg, Konrad A Hughen, K Felix Kaiser, Bernd Kromer, Sturt W Manning, Mu Niu, Ron W Reimer, David A Richards, E Marian Scott, John R Southon, Richard A Staff, Christian S M Turney and Johannes van der Plicht
2013 IntCal13 and MARINE13 radiocarbon age calibration curves 0-50000 years calBP. *Radiocarbon* 55(4).
- Sablin, Mikhail and Gennady Khlopachev
2002 The earliest Ice Age dogs: evidence from Eliseevichi. *Current Anthropology*, 43(5), 795-799.
- Saunders, Jeffrey J. and Edward B. Daeschler
1994 Descriptive analyses and taphonomical observations of culturally-modified mammoths excavated at "The Gravel Pit," near Clovis, New Mexico in 1936. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1-28.
- Schober, Teresa
1998 Reinvestigation of Maize Introduction in West-Central Illinois: A Stable Isotope Analysis of Bone Collagen and Apatite Carbonate from Late Archaic to Mississippian Times. Master's Thesis, University of Illinois at Urbana-Champaign, Urbana, Illinois.
- Schoeninger, Margaret J. and Michael J. DeNiro
1984 Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochimica et Cosmochimica Acta*, 48(4), 625-639.
- Schwartz, Marion
1998 *A history of dogs in the early Americas*. Yale University Press.

- Shannon, Laura M., Ryan H. Boyko, Marta Castelhana, Elizabeth Corey, Jessica J. Hayward, Corin McLean, Michelle E. White, Mounir Abi Said, Baddley A. Anita, Nono Ikombe Bondjengo, Jorge Calero, Ana Galov, Marius Hedimbi, Bulu Imam, Rajashree Khalap, Douglas Lally, Andrew Masta, Kyle C. Oliveira, Lucía Pérez, Julia Randall, Nguyen Minh Tam, Francisco J. Trujillo-Cornejo, Carlos Valeriano, Nathan B. Sutter, Rory J. Todhunter, Carlos D. Bustamante and Adam R. Boyko
2015 Genetic structure in village dogs reveals a Central Asian domestication origin. *Proceedings of the National Academy of Sciences*, 112(44), 13639-13644.
- Shipman, Pat
2015 How do you kill 86 mammoths? Taphonomic investigations of mammoth megasites. *Quaternary International*, 359, 38-46.
- Skoglund, Pontus and David Reich
2016 A genomic view of the peopling of the Americas. *Current Opinion in Genetics & Development*, 41, 27-35.
- Smallwood, Ashley M. and Thomas Jennings (Eds.).
2014 *Clovis: on the edge of a new understanding*. Texas A&M University Press.
- Stanford, Dennis J.
1978 The Jones-Miller site: An example of hell gap bison procurement strategy. *Plains Anthropologist*, 23(82), 90-97.
- Stanford, Dennis J., Alison Stenger, James M. Adovasio, and David R. Pedler
2014 *Pre-clovis in the Americas: International Science Conference Proceedings Held at the Smithsonian Institution, Washington, DC*. CreateSpace Independent Publishing Platform.
- Stuiver, M., Paula J. Reimer and R. W. Reimer
2017 CALIB 7.1 [WWW program] at <http://calib.org>, accessed 2017-7-12
- Styles, Bonnie W. R. Bruce McMillan
2009 Archaic faunal exploitation in the Prairie Peninsula and surrounding regions of the midcontinent. *Archaic societies: diversity and complexity across the midcontinent*, 39-80.
- Thalmann, Olaf, Beth Shapiro, Pin Cui, Verena J. Schuenemann, Susanna K. Sawyer, D. L. Greenfield, Mietje B. Germonpré, Mikhail V. Sablin, F. López-Giráldez, X. Domingo-Roura, Hannes Napierala, H-P. Uerpmann, D. M. Loponte, A. A. Acosta, L. Giemsch, Ralf W. Schmitz, Brian Worthington, Jane E. Buikstra, A. Druzhkova, A. S. Graphodatsky, Nikolai D. Ovodov, N. Wahlberg, Adam H. Freedman, R. M. Schweizer, K.-P. Koepfli, Jennifer A. Leonard, Matthias Meyer, Johannes Krause, Svante Pääbo, R. E. Green, Robert K. Wayne
2013 Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science*, 342(6160), 871-874.

- Tieszen, Larry L.
1991 Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. *Journal of Archaeological Science*, 18(3), 227-248.
- Tieszen, Larry L. and Tim Fagre
1993 Effect of diet quality and composition on the isotopic composition of respiratory CO₂, bone collagen, bioapatite, and soft tissues. In *Prehistoric human bone* (pp. 121-155). Springer, Berlin, Heidelberg.
- Tito, Raul Y., Samuel L. Belknap, Kristin D. Sobolik, Robert C. Ingraham, Lauren M. Cleeland, and Cecil M. Lewis
2011 Brief communication: DNA from early Holocene American dog. *American Journal of Physical Anthropology*, 145(4), 653-657.
- Tuross, Noreen, Marilyn Fogel and P. E. Hare
1988 Variability in the preservation of the isotopic composition of collagen from fossil bone. *Geochimica et Cosmochimica Acta*, 52(4), 929-935.
- Valadez, Raul, Bernardo Rodríguez, Linda Manzanilla, and Samuel Tejada
2006 Dog-wolf Hybrid Biotype Reconstruction from the Archaeological City of Teotihuacan in Prehispanic Central Mexico. *Dogs and People in Social, Working, Economic or Symbolic Interaction*, 121-131.
- van Asch, Barbara, Ai-bing Zhang, Mattias CR Oskarsson, Cornelya FC Klütsch, António Amorim, and Peter Savolainen
2013 Pre-Columbian origins of Native American dog breeds, with only limited replacement by European dogs, confirmed by mtDNA analysis. In *Proceedings of the Royal Society B* (Vol. 280, No. 1766, p. 20131142). The Royal Society.
- Van der Merwe, Nikolaas J. and John C. Vogel
1978 ¹³C content of human collagen as a measure of prehistoric diet in woodland North America. *Nature*, 276(5690), 815.
- Vilà, Carles, Peter Savolainen, Jesús E. Maldonado, Isabel R. Amorim, John E. Rice, Rodney L. Honeycutt, Keith A. Crandall, Joakim Lundeberg, and Robert K. Wayne
1997 Multiple and ancient origins of the domestic dog. *Science*, 276(5319), 1687-1689.
- Von den Driesch, Angela
1976 *A guide to the measurement of animal bones from archaeological sites: as developed by the Institut für Palaeoanatomie, Domestikationsforschung und Geschichte der Tiermedizin of the University of Munich* (Vol. 1). Peabody Museum Press.

Von Holdt, Bridgett, John P. Pollinger, Kirk E. Lohmueller, Eunjung Han, Heidi G. Parker, Pascale Quignon, Jeremiah D. Degenhardt, Adam R. Boyko, Dent A. Earl, Adam Auton, Andy Reynolds, Kasia Bryc, Abra Brisbin, James C. Knowles, Dana S. Mosher, Tyrone C. Spady, Abdel Elkahloun, Eli Geffen, Malgorzata Pilot, Wlodzimierz Jedrzejewski, Claudia Greco, Ettore Randi, Danika Bannasch, Alan Wilton, Jeremy Shearman, Marco Musiani, Michelle Cargill, Paul G. Jones, Zuwei Qian, Wei Huang, Zhao-Li Ding, Ya-ping Zhang, Carlos D. Bustamante, Elaine A. Ostrander, John Novembre and Robert K. Wayne

2010 Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature*, 464(7290), 898.

Walker, Danny N. and George C. Frison

1982 Studies on Amerindian dogs, 3: Prehistoric wolf/dog hybrids from the Northwestern Plains. *Journal of Archaeological Science*, 9(2), 125-172.

Walker, Renee B., Darcy F. Morey and John. H. Relethford

2005 Early and Mid-Holocene dogs in Southeastern North America: examples from Dust Cave. *Southeast Archaeology* 24, 83–92

Wang, Guo-Dong, Weiwei Zhai, He-Chuan Yang, Lu Wang, Li Zhong, Yan-Hu Liu, Ruo-Xi Fan, Ting-Ting Yin, Chun-Ling Zhu, Andrei D Poyarkov, David M Irwin, Marjo K Hytönen, Hannes Lohi, Chung-I Wu, Peter Savolainen and Ya-Ping Zhang

2016 Out of southern East Asia: the natural history of domestic dogs across the world. *Cell Research*, 26(1), 21.

Warren, Diane M.

2000 Paleopathology of archaic dogs from the North American Southeast. In: Crockford, Susan, J. (Eds.), *Dogs Through Time an Archaeological Perspective*. BAR International Series 889, pp. 93–104.

Wayne, Robert K. and Susan M. Jenks

1991 Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf *Canis rufus*. *Nature*, 351(6327), 565.

Witt, Kelsey E., Kathleen Judd, Andrew Kitchen, Colin Grier, Timothy A. Kohler, Scott G. Ortman, Brian M. Kemp, and Ripan S. Malhi.

2015 DNA analysis of ancient dogs of the Americas: Identifying possible founding haplotypes and reconstructing population histories. *Journal of Human Evolution*, 79, 105-118.

Supplemental Materials. For supplementary material accompanying this paper, visit [www.journals.cambridge.org/\[Journal\]](http://www.journals.cambridge.org/[Journal]).

Figure 1. Location of the Koster and Stilwell II sites

Figure 2. Excavation of the Koster F2256 dog burial (photograph by Del Baston, courtesy of the Center for American Archeology)

Figure 3. The Stilwell II dog burial *in situ* (photograph by W.L. Wadlow, courtesy of the Illinois State Museum Research and Collections Center)

Figure 4. Relative size of the Stilwell II and Koster dogs.

Figure 5. Comparison of left mandibles from the (top to bottom) Stilwell II, Koster F2357, and Koster F2256 dogs.

Figure 6. Left mandible of the Stilwell II dog showing advanced tooth wear.

Figure 7. Relationship between carnassial length (von den Driesch 1976, measurement 13L) and mandibular body height (von den Driesch 1976, measurement 19) among different *Canis* groups. CS=Cherokee Sewer, IA; MD=Modoc Rock Shelter, IL; KS=Koster, IL (KS1 and 2 included in this study); SM=Simonsen, IA; SW=Stilwell II, IL. Dotted line connects left and right mandibles of the same individual. See Supplementary Table 3.

Figure 8. Early Archaic dog $\delta^{13}\text{C}_{\text{coll}}$ and $\delta^{15}\text{N}_{\text{coll}}$ values, compared to the ranges of modern wolves (Fox-Dobbs et al. 2007), modern deer (Cormie and Schwarcz 1994), and archaeological fish from the Midwest (Brugam et al. 2017). Stable isotope values from Early Archaic (Kaskaskia Mine, N=1; Hargrave et al. 2006), Middle Archaic (Broglia Site, N=16; Carbaugh et al. in press), and Late Archaic (Tree Row Site, N=8; Fort et al. 2015) humans, two Late Archaic dogs from the Tree Row site (Fort et al. 2015), and post-maize human diets (N=64; Hedman et al. 2002) are also included for comparison. All illustrated samples are from the Illinois River Valley or the American Bottom.

Table 1. Shoulder height and body mass estimates of the Koster and Stilwell II dogs.

Table 2. Radiocarbon dates and stable isotope values for early dogs from the Lower Illinois River Valley.