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

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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 probably 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 represents the earliest evidence of domestic dogs in the Americas and individual dog burials in worldwide archaeological record. The over 4,500 year discrepancy between the timing of initial human migration into the Americas and the earliest evidence for domesticated dogs suggests either earlier dogs are going unseen or unidentified or dogs arrived later with a subsequent human migration.

The dog's domestication and earliest uses have been topics of much debate 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 of 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 ancient gray wolf ancestors (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 the Americas 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). 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 modern 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 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 9200 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, analysis, and direct radiocarbon dating of an isolated dog burial from Stilwell II, an Early Archaic site in the Lower Illinois River Valley. We also present new direct radiocarbon dates for two dogs from the nearby Koster site.

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) 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; Boon 2013).

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 ^{14}C 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 Eurasia 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 northeast-southwest orientation, head facing east. 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

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 7.1html (Stuiver et al. 2017).

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. One is a small area (circa 6 x 3 mm) on the caudal surface of the right proximal humeral shaft. The second (circa 5 x 3 mm) is on the plantar surface of the left distal tibial shaft. 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. Contemporaneous 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-periosteal 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 glomerularand 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

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 8500 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 (2.9-3.6; 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.

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 M_1; 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). 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.

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 suggesting 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). 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 migrating Siberian groups (as part of ongoing "migratory dribbles"; Meltzer 2009: 200) via an interior route before 10,000 cal BP, but were not part of the very first pulse of migration into the Americas.

The Bering Land Bridge was flooded by ~11,000 years ago (Jakobsson et al. 2017), but populations may have crossed prior to this period, moving into North America through the Ice Free Corridor and dispersing into the midcontinent, leading to the earliest dog records in this region beginning at ~10,000 years ago. This scenario would posit that earlier domestic dog remains have yet to be found in Alaska, western Canada, the northern Great Plains, the Intermountain West and dispersed near the southern exit of the Ice Free Corridor. Many potential early dog remains fit with these circumstances, including those from McDonald Creek (Alaska; Mueller et al. 2015), Little John (Canada; Easton et al. 2011), Agate Basin (Wyoming; Walker and Frison 1982), Danger Cave (Utah; Grayson 1988), and Hogup Cave (Utah; Haag 1970). Equally, undated canid remains from the Early Archaic layers of Daisy Cave on California's Channel Islands may represent the earliest dog remains from the western coast (Rick et al. 2008).

The earliest New World domesticated dogs appearing in the midcontinent around 10,000 years ago present 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 plethora 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 also date to not much earlier 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.

The foregoing observations raise the question of whether domesticated dogs ever accompanied humans across Beringia. 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 (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 varied morphologies for their proximity in space and time. 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 the late Paleoindian/early Archaic. Similar intentional dog burials in other temperate hunter-gatherer contexts have been associated with the dog's importance as adaptive 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 a site of early North American domestic dog activity. These new dates extend the presence of North American dogs potentially into the Dalton period, a transitional Late Paleoindian-Early Archaic phase in the Midcontinent (Koldehoff and Loebel 2009). They also confirm the Stilwell II and Koster specimens as the earliest dogs in the Americas and earliest examples of intentional, individual dog burials in the worldwide archaeological record[1]. 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.

[1]Although 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.

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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.

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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.

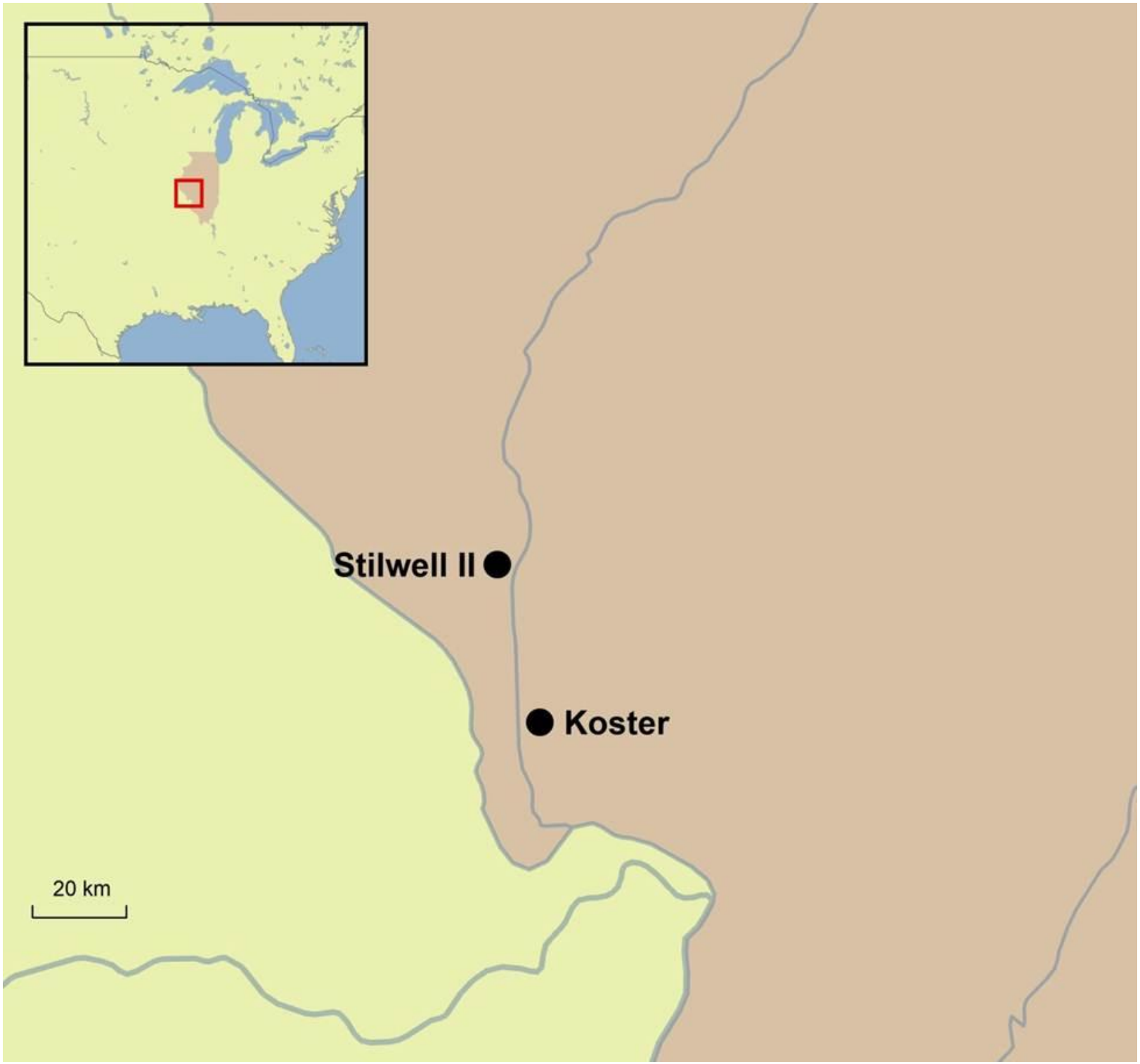
Figure 5. Comparison of left mandibles from the (top to bottom) Stilwell II, Koster F2357, and Koster F2256 dogs.

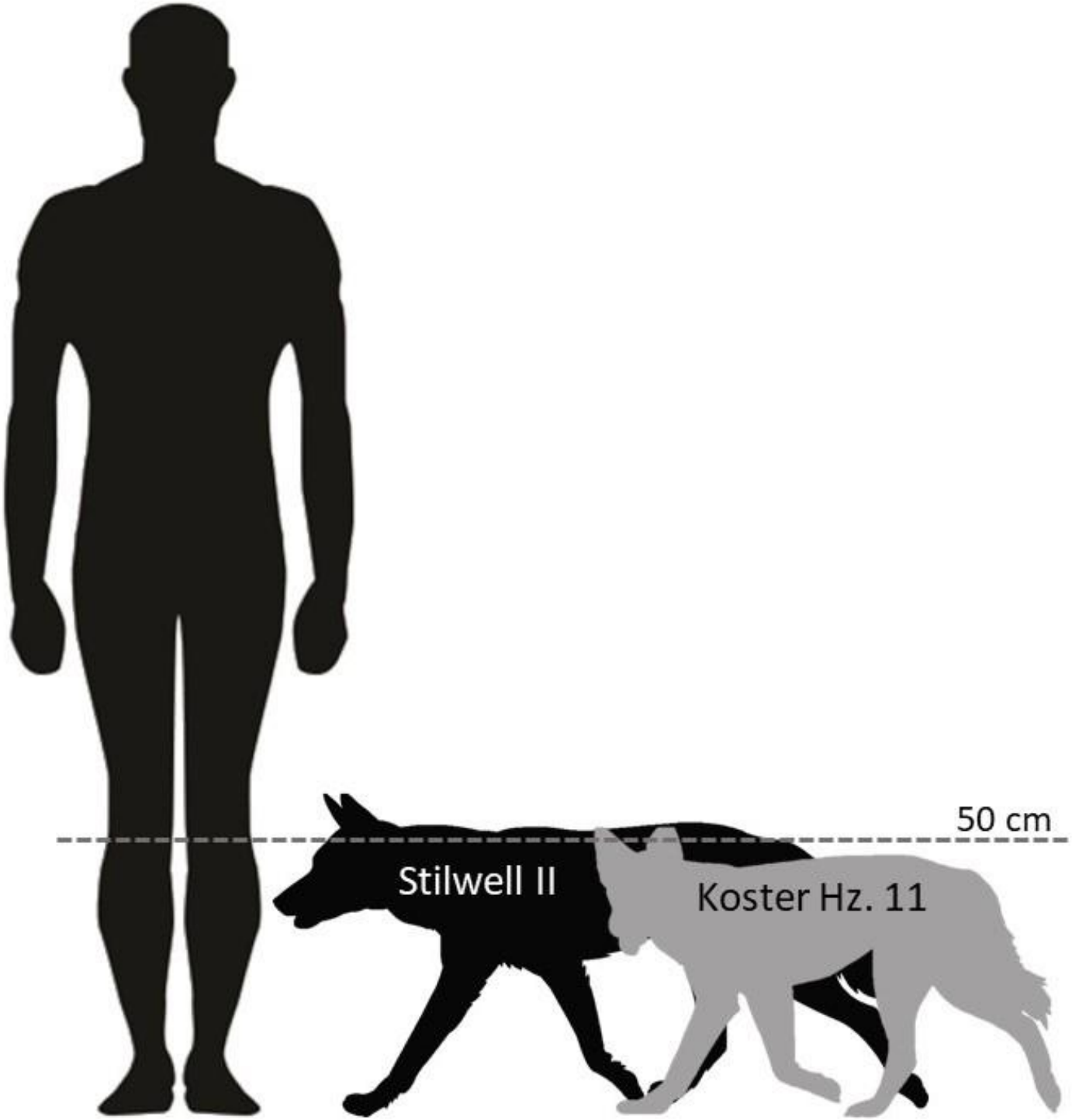
Figure 6. Left mandible of the Stilwell II dog showing advanced tooth wear.

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.

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

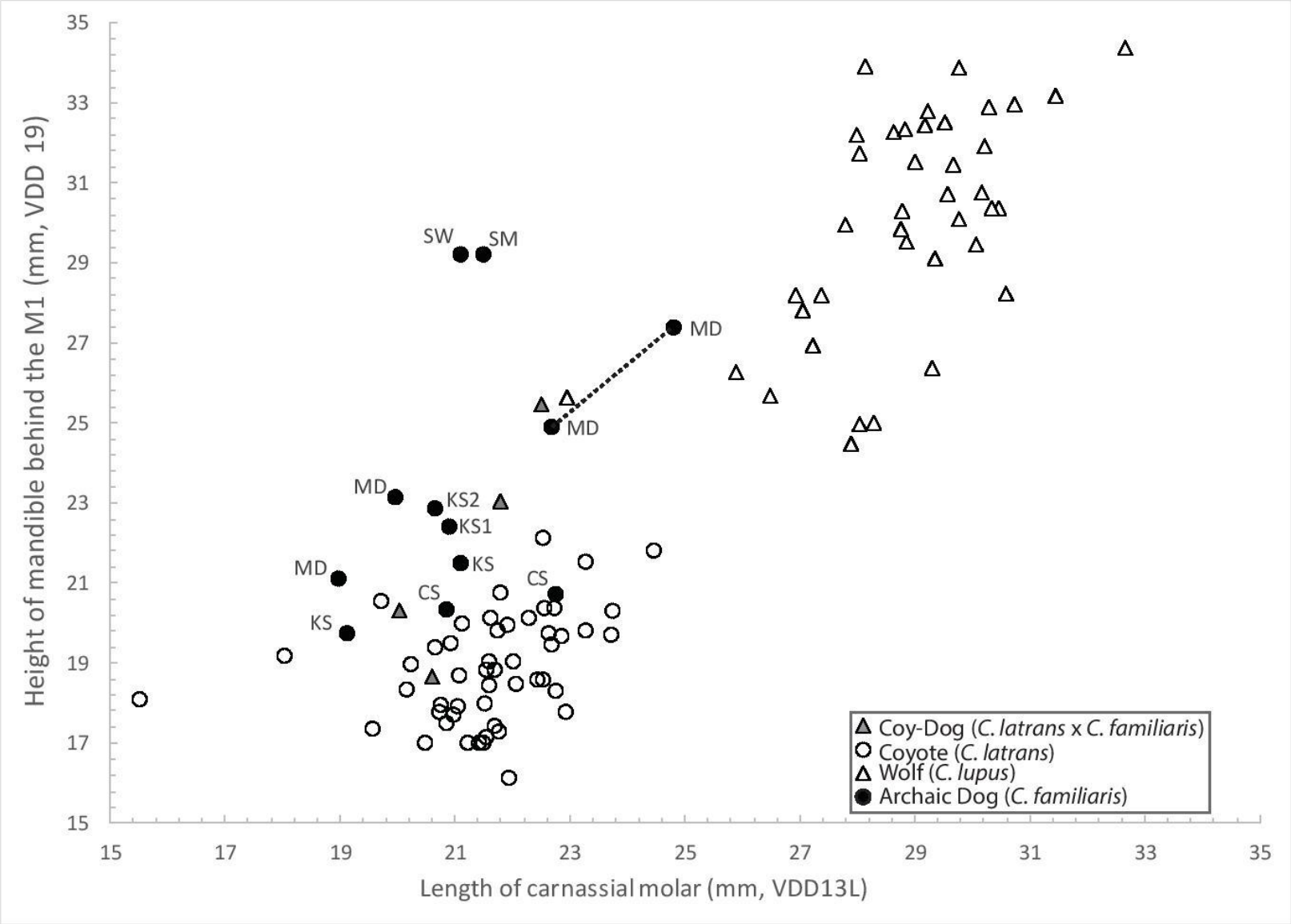
Table 2. Radiocarbon dates and stable isotope values for early dogs from the Lower Illinois River Valley.


Stilwell II
Koster
20 km


50 cm
Stilwell II
Koster Hz. 11

CM

CM


Height of mandible behind the M1 (mm, VDD 19)
Length of carnassial molar (mm, VDD13L)
35
33
31
29
27
25
23
21
19
17
15
15
17
19
21
23
25
27
29
31
33
35
SW
SM
MD
MD
MD
KS2
KS1
KS
MD
CS
CS
KS
Coy-Dog (C. latrans x C. familiaris)
Coyote (C. latrans)
Wolf (C. lupus)
Archaic Dog (C. familiaris)

	Shoulder Height (mm) (Harcourt 1974)		Body Mass (kg) (Losey et al., 2014)		Body Mass (kg) (Losey et al., 2016)	
Measurement	RDgl	TAgl	MR-18	MR-19	HMbd	RDbp
Koster F2256	450.7	439.8	13.4	15.3	12.5	13.6
Koster F2357	463.1	453.0	16.5	16.9	12.8	14.3
Stilwell II	517.2	504.6	22.5	32.3	17.1	17.1

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

Lab No.	Specimen	Material	^{14}C BP	2-sigma, cal BP	C:N
AA101127	Stilwell II dog	Bone collagen	8840±80	10,190-9630	3.4
NZA37136	Koster Horizon 11 (dog F2256)	Bone collagen	8790±30	10,110-9680	3.4
NZA37135	Koster Horizon 11 (dog F2357)	Bone collagen	8820±30	10,130-9700	3.4

Table 2. Radiocarbon dates for early dogs from the Lower Illinois River Valley.

The Stilwell II Site

In 1962, Perino returned to the Stilwell II site and conducted further exploratory excavations, at which time he recovered additional material consisting of broken projectile points, chipped stone tools, lithic debris, and faunal remains. Perino suggested that the site dated to “approximately Dalton times” (1977:99) based on the tool technology. Two of the broken projectile points he recovered were used as type specimens for the Stilwell variant of Kirk corner-notched points (Perino 1970). Perino reported that a bifurcate base point similar to LeCroy or Fox Valley, a Dalton adze, and the base of an Agate Basin point were also recovered during this second dig (Perino 1970, 1977). Perino estimated the Fox Valley and Stilwell points dated to ~7000 BC (1985:136, 365), and the Agate Basin points to ~8300-8000 BC (1985:5), suggesting that more than one occupation component (~1000 years apart) may be associated with the Stilwell II Early Archaic deposits. Agate Basin points are now known to date to between ca. 12,100-11,800 cal BP (Pelton et al. 2017), earlier than Perino’s estimate.

Perino’s observations introduced the possibility that the human burial and dog burial may not be contemporaneous features. Despite Perino’s opinion of the importance of the site, he conducted no further work there and only minor mentions of the site appeared subsequently. No field notes or maps exist, aside from a drawing of the human burial (Farnsworth 2006: 66) and an *in situ* photo of the dog burial (Figure 3). A series of black and white prints and color slides taken during the 1960 roadwork are curated at the Illinois State Museum Research and Collections Center.

The extent of the additional work conducted by Perino in 1962 is unknown, but based on the black and white photos, is assumed to have been focused along the

western cut face. Perino also suspected that the site deposits extended back under the alluvial fan and beneath the road. Perino retained possession of the material from his 1960 and 1962 work, with the exception of the dog and human burials, and some scattered finds of Archaic and Woodland period points from the general area. These were given to Pat Munson who transferred them to the Illinois State Museum.

In 2014, the remaining non-burial material from the site was donated to the Illinois State Archaeological Survey (ISAS) by Perino's son. The donated assemblage contained numerous well-preserved faunal remains, lithic debris, and the broken points and chipped stone tools from the site. These appeared previously in Perino's short published comments on his site work at Stilwell II (Perino 1962, 1977), confirming the origins of the collection.

Included in the lithic assemblage were 309 lithic artifacts plus faunal remains. Lithic debitage (*n* = 271) comprised the bulk of material, dominated by large (1" – 1½" size class) core reduction flakes. Twenty-seven chipped stone tools were also present, including the proximal fragments of two Stilwell points, five biface/preform fragments, one drill/perforator fragment, nine utilized/edge damaged flakes, two chipped stone adzes (with wood use wear polish), one adze preform, six multidirectional cores, and one lanceolate point proximal fragment. Two hammerstones and two faceted groundstone cobbles, one of which is stained with red ochre, complete the assemblage. Seven miscellaneous items were also present, including one fragment of fire-cracked rock (FCR), a coral fossil, a pebble, and three abraded limonite and hematite fragments.

The assemblage is biased toward larger-sized artifacts, likely reflecting a selective collection strategy by Perino. Thus, while it is difficult to interpret the lithic

assemblage, it is clear that occupants of the site were engaged in the procurement and primary reduction of the abundant outcrops of Burlington chert that surround the site. Five artifacts attributed previously to the Stilwell II site in published photographs are extant in the donated assemblage (Perino 1962:48). Other diagnostic points in the collection include the proximal fragment of a lanceolate point resembling an Agate Basin point. The bifurcated base point mentioned by Perino in his 1970 publication is not present.

Faunal remains recovered by Perino include a wide variety of species such as white-tailed deer, small birds, turkey, turtle, fish, and mussel shell fragments that are typical for the Archaic period in this region. A few of the larger specimens show obvious cut marks from butchering, and several modified bone tools are also present.

In 2015, personnel from ISAS visited the Stilwell II location in an effort to relocate the site and evaluate the potential for remaining intact deposits. A topographic map of the site area was generated and 13 bucket augers were excavated along both sides of the road cut. All sediments were screened through ¼” mesh, with the exception of one auger that was retained for flotation processing. Most augers were positive and indicated the presence of lithics, faunal remains, burned earth, and charcoal at depths up to 85 cmbs (limits of testing) along the base of the western cut face. Numerous pieces of debitage (*n* = 92), one perforator fragment, and two utilized flakes were recovered from depths of 20-85 cm during auger testing. Recovered faunal material included 1015 pieces, primarily from the nine-liter flotation sample. Although most of these were too small to identify to species, the assemblage consists primarily of fish

(bowfin, catfish, gar) and squirrels, with some bones being burned. Fragments of vole, eastern cottontail, raccoon, and a possible elk dew claw were identified as well.

Five 2-inch Giddings probe cores were placed across the longitudinal profile of the fan which identified buried paleosols, including anthropogenic deposits, on top of the fan at a depth of 1.5 m, and within an ACb horizon along the roadside at depths of 0.16 m to 1 m (Kolb 2015). A Bw horizon containing artifacts at depths up to 1.5 m is also present, suggesting an even older component at the site. East of the road, the distal fan lies within an active agricultural field with artifacts of varying ages (Archaic-Woodland) exposed on its surface and incorporated into the plow zone. The artifacts from the 2015 work are currently being analyzed, and investigations at the site are ongoing.

The Stilwell II Dog

At or since excavation, transport, and storage, some of the elements which appear intact in the *in situ* 1960 photograph, such as the skull, have collapsed. Inspection of the skeletal material revealed approximately 200 specimens (weighing a total of 678.5 g), 177 of which are identifiable to one individual adult domestic dog. These include 14 cranial fragments, the posterior portions of both mandibles, and 3 isolated teeth; 17 whole and fragmented long bones having closed epiphyses (proximal ends of both humeri and both femurs are missing); 32 vertebral fragments; 55 rib fragments; 47 foot bones (i.e., carpals, tarsals, metapodials, and phalanges); 5 small fragments of scapulae; and 2 incomplete pelves (Supplementary Table 1). A baculum is not present in the inventory, although the posterior skeleton is otherwise well-represented. Therefore, the tentative sex of this individual is female or indeterminate.

The Stilwell II dog is curated at the Illinois State Museum Research and Collections Center.

Six other specimens were found mixed among the dog bones. These include a left pelvis fragment (ilium and acetabulum) from a female white-tailed deer (*Odocoileus virginianus*); left tibial fragments from two gray squirrels (*Sciurus carolinensis*); a left ulna shaft from a medium-sized duck (Subfamily Anatinae); a right femur from a passenger pigeon (*Ectopistes migratorius*); and an anterior carapace fragment (part of a proneural bone) that is most comparable to painted turtle (*Chrysemys picta*).These are likely habitation debris that was included unintentionally with the burial fill.

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Supplementary Table 1. Measurements (mm) of the Stilwell II and Koster dogs, following von den Driesch (1976).

Bone	#vdD	Measurement	Left	Right	Midline
Cranium	#1	Total length			
		Koster F2256			c. 176.5
	#2	Condylobasal length			
		Koster F2256			c. 165.5
	#3	Basal length			
		Koster F2256			158.2
	#4	Basicranial axis			
		Koster F2256			44.9
	#5	Basifacial axis			
		Koster F2256			c. 114.0
	#7	Upper neurocranium length			
		Koster F2256			c. 87.5
	#8	Viscerocranium length			
		Koster F2256			83.0
	#9	Facial length			
		Koster F2256			97.5
	#10	Greater length of the nasals			
		Koster F2256			57.2
	#12	"Snout" length			
		Koster F2256			c. 73.0
		Koster F2357			c. 82.5
	#13	Median palatal length			
		Koster F2256			85.7
	#13a	Palatal length			
		Koster F2256			c. 85.0
	#14	Length of the horizontal part of the palatine			
		Koster F2256			27.8
	#14a	Length of the horizontal part of the palatine			
		Koster F2256			28.0
	#15	Length of the cheekrow teeth ($P^1 – M^2$)			
		Koster F2256	62.6	64.2	
		Koster F2357	62.3	60.6	
	#16	Length of the molar row ($M^1 – M^2$)			
		Koster F2256	17.5	18.7	
		Koster F2357	16.3	18.0	
	#17	Length of the premolar row ($P^1 – P^4$)			
		Koster F2256	48.0	50.0	
		Koster F2357	48.3	46.4	
	#22	Greatest diameter of the auditory bulla			
		Koster F2256	%	21.2	
		Koster F2357	%	22.7	
		Stilwell II	25.1	%	
	#25	Greatest breadth of the occipital condyles			
		Koster F2256			35.1
	#27	Greatest breadth of the foramen magnum			
		Koster F2256			18.8

Bone	#vdD	Measurement	Left	Right	Midline
	#28	Height of the foramen magnum			
		Koster F2256			c. 13.7
	#29	Greatest neurocranium breadth			
		Koster F2256			56.2
		Koster F2357			53.0
		Stilwell II			55.6
	#30	Zygomatic breadth			
		Koster F2256			94.7
	#31	Least breadth of skull			
		Koster F2256			37.7
	#32	Frontal breadth			
		Koster F2256			49.2
	#33	Least breadth between the orbits			
		Koster F2256			34.4
	#34	Greatest palatal breadth			
		Koster F2256			62.0
	#35	Least palatal breadth			
		Koster F2256			c. 33.5
	#36	Breadth at the canine alveoli			
		Koster F2256			35.2
	#38	Skull height			
		Koster F2256			c. 46.0
	#39	Skull height without the sagittal crest			
		Koster F2256			c. 44.0
	#40	Height of the occipital triangle			
		Koster F2256			c. 36.8
Maxillary teeth					
P^4 (carnassial)	#18	Length (L)			
		Koster F2256	18.8	18.3	
		Koster F2357	18.7	18.3	
		Stilwell II	18.5	18.6	
	#18a	Greatest breadth (GB)			
		Koster F2256	11.0	11.1	
		Koster F2357	10.9	10.5	
		Stilwell II	11.0	10.4	
M^1	#20	Length (L)			
		Koster F2256	12.5	11.3	
		Koster F2357	12.6	12.7	
		Stilwell II	12.7	12.4	
		Breadth (B)			
		Koster F2256	14.2	18.2	
		Koster F2357	14.6	14.1	
		Stilwell II	14.2	13.8	
M^2	#21	Length (L)			
		Koster F2256	7.0	7.2	
		Koster F2357	5.7	5.6	
		Stilwell II	6.8	6.9	

Bone	#vdD	Measurement	Left	Right	Midline
		Breadth (B)			
		Koster F2256	9.7	10.0	
		Koster F2357	9.0	8.8	
		Stilwell II	8.9	8.4	
Mandible	#1	Total length			
		Koster F2256	%	126.2	
		Koster F2357	%	122.5	
	#2	Length, angular process to *Infradentale*			
		Koster F2256	%	127.3	
		Koster F2357	124.0	124.0	
	#3	Length from the indentation between the condyle process and the angular process			
		Koster F2256	%	122.0	
		Koster F2357	111.8	111.8	
	#4	Length, condyle process to the aboral border of the canine alveolus			
		Koster F2256	107.6	107.6	
		Koster F2357	%[1]	118.2	
	#5	Length from the indentation between the condyle process and the angular process to the aboral border of the canine alveolus			
		Koster F2256	103.2	103.9	
		Koster F2357	104.4	104.0	
	#6	Length, angular process to the aboral border of the canine alveolus			
		Koster F2256	107.3	109.1	
		Koster F2357	109.0	108.9	
	#7	Length, aboral border of the alveolus of M_3 to aboral border of the canine alveolus			
		Koster F2256	74.0	73.3	
		Koster F2357	72.2	72.7	
	#8	Length of the cheektooth row, P_1 to M_3			
		Koster F2256	(no P_1)	67.4	
		Koster F2357	69.0[2]	68.4	
	#9	Length of the cheektooth row, P_2 to M_3			
		Koster F2256	55.1	63.3	
		Koster F2357	65.2	68.5	
		Stilwell II	46.5	%	
	#10	Length of the molar row, M_1 to M_3			
		Koster F2256	34.2	31.5	
		Koster F2357	33.5	33.3	
		Stilwell II	34.2	35.4	
	#11	Length of the premolar row, P_1 to P_4			
		Koster F2256	(no P_1)	36.7	
		Koster F2357	36.7	37.5	
	#12	Length of the premolar row, P_2 to P_4			
		Koster F2256	32.2	32.8	
		Koster F2357	33.7	33.4	

Bone	#vdD	Measurement	Left	Right	Midline
	#14	Length of the carnassial (M_1) alveolus			
		Koster F2256	21.0	19.6	
		Koster F2357	20.5	21.1	
		Stilwell II	20.7	19.8	
	#17	Greatest thickness of the body (below M_1)			
		Koster F2256	12.1	12.0	
		Koster F2357	10.2	10.4	
	#18	Height of the vertical ramus			
		Koster F2256	47.8	47.7	
		Koster F2357	52.3	53.2	
		Stilwell II	59.9	%	
	#19	Height of the mandible behind M_1			
		Koster F2256	%[1]	21.5	
		Koster F2357	22.2	22.4	
		Stilwell II	29.2	29.3	
	#20	Height of the mandible between P_2 and P_3			
		Koster F2256	19.9	19.6	
		Koster F2357	19.0	18.7	
Mandibular teeth					
M_1 (carnassial)	#13	Length (L)			
		Koster F2256	21.0	21.1	
		Koster F2357	21.5	20.9	
		Stilwell II	21.1	21.3	
		Breadth (B)			
		Koster F2256	8.8	8.7	
		Koster F2357	8.6	8.7	
		Stilwell II	9.3	9.3	
M_2	#15	Length (L)			
		Koster F2256	8.0	8.2	
		Koster F2357	7.5	7.5	
		Stilwell II	8.7	8.6	
		Breadth (B)			
		Koster F2256	6.0	6.0	
		Koster F2357	6.3	6.2	
		Stilwell II	6.9	7.0	
M_3	#16	Length (L)			
		Koster F2256	3.8	3.8	
		Koster F2357	n.p.	3.8	
		Stilwell II	4.9	5.1	
		Breadth (B)			
		Koster F2256	4.0	4.5	
		Koster F2357	n.p.	4.6	
		Stilwell II	4.7	4.6	
Atlas vertebra		Greatest breadth over the wings (GB)			
		Koster F2256			70.4
		Greatest length (GL)			

Bone	#vdD Measurement	Left	Right	Midline
	Koster F2256			33.0
	Greatest breadth of the cranial articular surface (BFcr)			
	Koster F2256			36.6
	Greatest breadth of the caudal articular surface (BFcd)			
	Koster F2256			27.4
	Length of the dorsal arch (LAd)			
	Koster F2256			12.4
	Height (H)			
	Koster F2256			24.5
Axis vertebra	Greatest length of the body (LCDe)			
	Koster F2256			43.7
	Greatest length of the arch (LAPa)			
	Koster F2256			44.8
	Stilwell II			58.5
	Greatest breadth of the cranial articular surface (BFcr)			
	Koster F2256			27.1
	Greatest breadth across the caudal articular surface (BPacd)			
	Koster F2256			25.3
	Smallest breadth of the vertebra (SBV)			
	Koster F2256			20.1
	Height (H)			
	Koster F2256			c. 33.0
	Stilwell II			41.0
Sacrum	Greatest length (GL)			
	Koster F2256			c. 33.2
	Physiological length (PL)			
	Koster F2256			32.1
	Greatest breadth (GB)			
	Koster F2256			40.3
	Greatest breadth of the cranial articular surface (BFcr)			
	Koster F2256			20.1
	Greatest height of the cranial articular surface (HFcr)			
	Koster F2256			9.1
Scapula	Height (H)			
	Koster F2256	110.0	%	
	Smallest length of the scapula neck (SLC)			
	Koster F2256	19.5	20.3	
	Koster F2357	22.1	21.6	
	Greatest length of the glenoid process (GLP)			
	Koster F2256	26.5	26.4	
	Koster F2357	27.5	27.5	
	Length of the glenoid cavity (LG)			
	Koster F2256	22.1	22.3	
	Koster F2357	23.9	23.5	
	Breadth of the glenoid cavity (BG)			
	Koster F2256	16.8	16.5	
	Koster F2357	18.0	18.0	

Bone	#vdD Measurement	Left	Right	Midline
Humerus	Greatest length (GL)			
	Koster F2256	138.7	139.7	
	Koster F2357	142.5	%	
	Greatest breadth of the proximal end (Bp)			
	Koster F2256	26.7	25.8	
	Koster F2357	29.5	28.0	
	Depth of the proximal end (Dp)			
	Koster F2256	36.8	36.8	
	Koster F2357	37.8	37.6	
	Smallest breadth of the diaphysis (SD)			
	Koster F2256	11.0	10.9	
	Koster F2357	10.9	11.5	
	Stilwell II	12.7	12.6	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	28.6	28.7	
	Koster F2357	28.8	29.0	
	Stilwell II	32.3	32.1	
Radius	Greatest length (GL)			
	Koster F2256	135.6	135.5	
	Koster F2357	139.5	%	
	Stilwell II	156.5	157.4	
	Greatest breadth of the proximal end (Bp)			
	Koster F2256	16.3	16.7	
	Koster F2357	16.6	16.5	
	Stilwell II	17.7	17.6	
	Smallest breadth of the diaphysis (SD)			
	Koster F2256	10.2	9.7	
	Koster F2357	10.0	9.8	
	Stilwell II	11.3	11.4	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	21.5	21.7	
	Koster F2357	21.9	%	
	Stilwell II	24.5	23.8	
Ulna	Greatest length (GL)			
	Koster F2256	159.4	158.4	
	Depth across the *Processus anconaeus* (DPA)			
	Koster F2256	21.5	21.4	
	Koster F2357	22.3	22.3	
	Stilwell II	26.2	25.5	
	Smallest depth of the olecranon (SDO)			
	Koster F2256	19.0	18.8	
	Koster F2357	19.1	19.1	
	Stilwell II	22.2	22.2	
	Greatest breadth of the proximal articular surface (BPC)			
	Koster F2256	14.4	14.5	
	Koster F2357	15.3	14.2	

Bone	#vdD Measurement	Left	Right	Midline
	Stilwell II	17.0	16.6	
Metacarpal II	Greatest length (GL)			
	Koster F2256	49.6	49.8	
	Stilwell II	52.9	53.2	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	8.2	8.5	
	Stilwell II	9.7	9.8	
Metacarpal III	Greatest length (GL)			
	Koster F2256	%	58.3	
	Stilwell II	63.8	63.6	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	%	7.7	
	Stilwell II	8.5	8.6	
Metacarpal IV	Greatest length (GL)			
	Koster F2256	%	58.7	
	Stilwell II	64.3	64.0	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	%	7.8	
	Stilwell II	8.7	8.7	
Metacarpal V	Greatest length (GL)			
	Koster F2256	51.1	50.9	
	Stilwell II	55.3	55.9	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	8.3	8.1	
	Stilwell II	8.5	8.5	
Pelvis	Greatest length of one half (GL)			
	Koster F2256	%	125.0	
	Length of the acetabulum including the lip (LA)			
	Koster F2256	%	20.0	
	Stilwell II	23.1	%	
	Length of the acetabulum on the rim (LAR)			
	Koster F2256	%	18.6	
	Stilwell II	21.1	%	
	Length of the symphysis (LS)			
	Koster F2256	%	36.5	
	Smallest height of the ilium shaft (SH)			
	Koster F2256	14.8	14.8	
	Koster F2357	16.5	%	
	Stilwell II	19.1	17.8	
	Smallest breadth of the ilium shaft (SB)			
	Koster F2256	7.3	6.7	
	Koster F2357	7.1	%	
	Inner length of the foramen obturatum (LFo)			

Bone	#vdD Measurement	Left	Right	Midline
	Koster F2256	%	16.8	
Femur	Greatest length (GL)			
	Koster F2256	149.4	148.9	
	Koster F2357	%	148.0	
	Greatest breadth of the proximal end (Bp)			
	Koster F2256	32.3	32.3	
	Koster F2357	35.2	%	
	Greatest depth of the *Caput femoris* (DC)			
	Koster F2256	15.2	15.4	
	Koster F2357	16.9	%	
	Smallest breadth of the diaphysis (SD)			
	Koster F2256	11.4	12.0	
	Koster F2357	11.8	11.9	
	Stilwell II	12.4	12.7	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	28.0	28.5	
	Koster F2357	29.2	29.5	
	Stilwell II	%	30.9	
Patella	Greatest length (GL)			
	Koster F2256			15.7[3]
	Koster F2357			16.2-16.3[3]
	Greatest breadth (GB)			
	Koster F2256			9.6[3]
	Koster F2357			9.7-10.0[3]
Tibia	Greatest length (GL)			
	Koster F2256	147.4	147.2	
	Koster F2357	151.9	%	
	Stilwell II	169.6	170.1	
	Greatest breadth of the proximal end (Bp)			
	Koster F2256	29.6	30.6	
	Koster F2357	31.1	31.5	
	Stilwell II	%	34.1	
	Smallest breadth of the diaphysis (SD)			
	Koster F2256	10.8	10.7	
	Koster F2357	11.5	11.1	
	Stilwell II	12.3	12.7	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	19.8	19.8	
	Koster F2357	20.4	%	
	Stilwell II	20.7	21.2	
Fibula	Greatest length (GL)			
	Koster F2256	%	135.2	

Bone	#vdD Measurement	Left	Right	Midline
Astragalus	Greatest length (GL)			
	Koster F2256	%	24.2	
	Koster F2357	24.1	%	
	Stilwell II	26.5	26.5	
Calcaneus	Greatest length (GL)			
	Koster F2256	41.3	40.8	
	Stilwell II	46.1	45.7	
	Greatest breadth (GB)			
	Koster F2256	16.0	16.0	
	Stilwell II	17.5	17.5	
Metatarsal II	Greatest length (GL)			
	Koster F2256	55.5	55.8	
	Koster F2357	%	58.2	
	Stilwell II	63.1	63.5	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	7.8	7.8	
	Koster F2357	%	7.3	
	Stilwell II	8.1	8.0	
Metatarsal III	Greatest length (GL)			
	Koster F2256	63.1	63.3	
	Koster F2357	%	65.8	
	Stilwell II	72.8	73.1	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	8.0	8.0	
	Koster F2357	%	7.7	
	Stilwell II	8.6	8.5	
Metatarsal IV	Greatest length (GL)			
	Koster F2256	65.0	65.2	
	Koster F2357	%	67.2	
	Stilwell II	75.5	75.1	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	7.7	7.6	
	Koster F2357	%	7.4	
	Stilwell II	8.3	8.0	
Metatarsal V	Greatest length (GL)			
	Koster F2256	%	58.0	
	Koster F2357	%	60.5	
	Stilwell II	65.0	65.0	
	Greatest breadth of the distal end (Bd)			
	Koster F2256	7.5	7.3	
	Koster F2357	%	7.7	
	Stilwell II	8.5	8.0	

[1] No measurement due to abscess on lingual side

[2] Resorbed P_1

[3] Side undetermined

Supplementary Table 2. Skeletal Pathology Observations of the Stilwell II Dog

Appendicular skeleton

Structure		Observations	Normal	Incipient	Pathology
lt[1] scapula glenoid		mild rim lateral articular margin		x	
rt[1] humeral head		periarticular rim			x
rt distal humerus	(cranial)	mild prominent articular margin		x	
“	(medial)	mild rim periarticular margin			x
“	(lateral)	sharp articular margin		x	
“	(caudal)	thickened lateral articular margin			x
lt distal humerus	(cranial)	prominent articular margin		x	
“	(medial)	prominent articular margin toward cranial		x	
“	(caudal)	thickened lateral articular margin		x	
“	(lateral)		x		
rt proximal ulna	(medial)	prominent articular margin rim		x	
“	(cranial)	mild distolateral periarticular prominence		x	
“	(lateral)	prominent anconeal dorsal articular margin & lateral rim			x
lt proximal ulna	(medial)	prominent articular margin rim			x
“	(cranial)	mild distolateral periarticular prominence			x
“	(lateral)	prominent anconeal dorsal articular margin & lateral rim			x
lt proximal radius	(cranial)	periarticular osteophyte rim			x
“	(ulnar)	prominent periarticular margin, sharp ulnar aspect margin			x
rt distal radius	(ulnar)	prominent periarticular margin; rough bone above margin			x
“	(articular)	articular-periarticular margin rim			x
lt distal radius	(cranial)	mild prominent articular margin			x
accessory carpal	(rt, lt)	rough bone surface with normal articulations			2x
rt acetabulum	(fragment)	thickened lateral articular margin; shallow appearance	x		
rt distal femur	(cranial)		x		
“	(caudal)	prominent articular margin	x		
“	(medial)	prominent periarticular margin		x	
“	(lateral)	prominent periarticular margin		x	
rt proximal fibula		fragment	x		
lt proximal tibia	(cranial)	partial	x		
lt distal tibia		prominent articular margin		x	
rt proximal tibia	(cranial)		x		
“	(articular)	mild prominent articular margin			x
“	(caudal)		x		
“	(medial)		x		
“	(lateral)	mild periarticular prominence		x	
rt tibial tarsal	(dorsal)		x		
“	(plantar)	mild prominent articular process lateral		x	
rt 4th tarsal			x		
lt, rt calcaneus		articular margin prominences		2x	
metapodials x13		mild periarticular rough bone		13x	
phalanges x11		rough bone around articulations		11x	

Axial skeleton

Structure	Observations	Normal	Incipient	Pathology
lt maxilla pm3-m2	severe tooth wear; m1root canal exposed			x
lt mandible pm4-m3	severe tooth wear & periodontal/periosteal disease			x
rt mandible pm4-m3	severe tooth wear & periodontal/periosteal disease			x

rib fragments (2)	marks taphonomic or extraction	x	
hyoid (1)		x	
atlas fragment	cranial articular sharp-edged		x
axis	mild lt curve cranial spinous process	requires imaging	
cervical vertebra partial[2]	mild prominent lt cranial articular margin		x
cervical vertebra	mild rt lean spinous process	requires imaging	
cervical vertebra		x	
cervical vertebra		x	
thoracic vertebra	spinous only; rt curve base, lt bow	requires imaging	
lumbar vertebra	spinous process moderate-severe rt lean	requires imaging	
lumbar vertebra partial	spinous process severe rt curve	requires imaging	
lumbar vertebra	spinous process severe rt curve, tip damaged	requires imaging	

[1] lt - left; rt – right
[2] all vertebrae have some taphonomic damage

Supplementary Table 3. Comparative measurements on "length of carnassial M_1" (VDD13L) and "height of mandible behind M_1" (VDD19), following von den Driesch (1976). Abbreviations as follows, SANF=Sanford Museum and Planetarium, Cherokee, IA; ISM=Illinois State Museum, Springfield, IL; KU=University of Kansas Natural History Museum, Lawrence, KS; UA=Stanley J. Olsen Laboratory of Zooarchaeology, Arizona State Museum, Tucson, AZ; ETMNH=East Tennessee State University Museum of Natural History, Johnson City, TN.

Institution	**Locality**	**Catalog No.**	**Graph label**	**Taxon**	**Date**	**VDD13 L (mm)**	**VDD19 (mm)**
SANF	Simonsen, Cherokee Co., IA	#7-2	SM	*Canis lupus familiaris*	Level 3 (7430-7270 cal BP)	21.50	29.22
ISM	Koster, Greene Co., IL	F2256	KS1	*Canis lupus familiaris*	Horizon 11 (10,110-9680 cal BP)	21.10	21.50
ISM	Koster, Greene Co., IL	F2357	KS2	*Canis lupus familiaris*	Horizon 11(10,130-9700 cal BP)	20.90	22.40
ISM	Koster, Greene Co., IL	222D	KS	*Canis lupus familiaris*	Horizon 11 (probably later Archaic period)	19.12	19.74
ISM	Koster, Greene Co., IL	2407	KS	*Canis lupus familiaris*	Horizon 11 (associated date 10,130-9680 cal BP)	20.65	22.86
ISM	Stilwell II, Calhoun Co., IL	SW	SW	*Canis lupus familiaris*	10,190-9630 cal BP	21.10	29.20
ISM	Modoc Rockshelter, Randolph Co., IL	6090	MD	*Canis lupus familiaris*	5710-5330 cal BP	18.97	21.10
ISM	Modoc Rockshelter, Randolph Co., IL	5087	MD	*Canis lupus familiaris*	Archaic, unspecified	19.97	23.13
ISM	Modoc Rockshelter, Randolph Co., IL	dog2 (right)	MD	*Canis lupus familiaris*	8560-8200 cal BP	24.81	27.39
ISM	Modoc Rockshelter, Randolph Co., IL	dog2 (left)	MD	*Canis lupus familiaris*	8560-8200 cal BP	22.67	24.91
SUI	Cherokee Sewer, Cherokee Co., IA	42686	CS	*Canis lupus familiaris*	Horizon I (associated date 7420-7010 cal BP)	22.75	20.74
SUI	Cherokee Sewer, Cherokee Co., IA	38130	CS	*Canis lupus familiaris*	Horizon I (associated date 7420-7010 cal BP)	20.86	20.35
ISM	Redmon, Edgar Co., IL		Coy-Dog	Hybrid (C. l. familiaris x C. latrans)	Modern	22.50	25.45
ISM	Greenview, Menard Co., IL		Coy-Dog	Hybrid (*C. l. familiaris* x *C. latrans*)	Modern	20.59	18.65
ISM	Chatham, Sangamon Co., IL		Coy-Dog	Hybrid (*C. l. familiaris* x *C. latrans*)	Modern	21.80	23.05
ISM	Redmon, Edgar Co., IL	614682	Coy-Dog	Hybrid (*C. l. familiaris* x *C. latrans*)	Modern	20.04	20.31

KU	Cavalier Co., ND	13272	Coyote	*Canis latrans*	Modern (collected 1939)	21.78	20.78
KU	Hemphill Co., TX	7035	Coyote	*Canis latrans*	Modern (collected 1929)	22.28	20.12
KU	Seward Co., KS	12221	Coyote	*Canis latrans*	Modern (collected 1934)	21.74	19.80
KU	Trego Co., KS	5511	Coyote	*Canis latrans*	Modern (collected 1926)	20.48	17.02
KU	Dawson Co., MT	2124	Coyote	*Canis latrans*	Modern (collected 1886)	21.54	17.16
KU	Sully Co., SD	85415	Coyote	*Canis latrans*	Modern (collected 1960)	21.12	19.98
KU	Sully Co., SD	85416	Coyote	*Canis latrans*	Modern (collected 1960)	23.72	19.72
KU	Albany Co., WY	91362	Coyote	*Canis latrans*	Modern (collected 1948)	21.08	18.68
KU	Harding Co., SD	98313	Coyote	*Canis latrans*	Modern (collected 1961-1962)	22.52	18.58
KU	Harding Co., SD	98314	Coyote	*Canis latrans*	Modern (collected 1961-1962)	20.98	17.72
KU	Harding Co., SD	98312	Coyote	*Canis latrans*	Modern (collected 1961-1962)	24.46	21.80
KU	Harding Co., SD	98315	Coyote	*Canis latrans*	Modern (collected 1961-1962)	22.44	18.60
KU	Harding Co., SD	98316	Coyote	*Canis latrans*	Modern (collected 1961-1962)	21.70	17.42
KU	Pennington Co., SD	38124	Coyote	*Canis latrans*	Modern (collected 1946)	21.94	16.14
KU	Pennington Co., SD	101589	Coyote	*Canis latrans*	Modern (collected 1964-1965)	22.52	22.14
KU	Pennington Co., SD	101590	Coyote	*Canis latrans*	Modern (collected 1964-1965)	21.54	18.84
KU	Brule Co., SD	16195	Coyote	*Canis latrans*	Modern (collected 1946)	20.64	19.38
KU	Brule Co., SD	16196	Coyote	*Canis latrans*	Modern (collected 1946)	20.72	17.78
KU	Brule Co., SD	16197	Coyote	*Canis latrans*	Modern (collected 1946)	21.04	17.94
KU	Brule Co., SD	16198	Coyote	*Canis latrans*	Modern (collected 1946)	21.58	19.04
KU	Brule Co., SD	16199	Coyote	*Canis latrans*	Modern (collected 1946)	22.62	19.74
KU	Brule Co., SD	16200	Coyote	*Canis latrans*	Modern (collected 1946)	20.74	17.96
KU	Clay Co., SD	142587	Coyote	*Canis latrans*	Modern (collected 1987)	22.06	18.48
KU	Corson Co., SD	85414	Coyote	*Canis latrans*	Modern (collected 1961)	20.86	17.50
KU	Fall River Co., SD	85419	Coyote	*Canis latrans*	Modern (collected 1961)	19.56	17.36
KU	Fall River Co., SD	85420	Coyote	*Canis latrans*	Modern (collected 1961)	22.68	19.48
KU	Fall River Co., SD	85421	Coyote	*Canis latrans*	Modern (collected 1959)		20.28
KU	Fall River Co., SD	85422	Coyote	*Canis latrans*	Modern (collected 1959)	21.48	17.02
KU	Fall River Co., SD	85423	Coyote	*Canis latrans*	Modern (collected 1959)	22.02	19.06
KU	Hand Co., SD	85417	Coyote	*Canis latrans*	Modern (collected 1961)	21.42	17.02

KU	Hand Co., SD	85418	Coyote	*Canis latrans*	Modern (collected 1961)	20.16	18.34
KU	Harding Co., SD	98309	Coyote	*Canis latrans*	Modern (collected 1961-1962)	21.90	19.94
KU	Harding Co., SD	98310	Coyote	*Canis latrans*	Modern (collected 1961-1962)	21.68	18.82
KU	Harding Co., SD	98311	Coyote	*Canis latrans*	Modern (collected 1961-1962)	21.22	17.02
KU	No Man's Land, OK	2134	Coyote	*Canis latrans*	Modern (collected 1888)	21.60	18.46
KU	Brule Co., SD	16193	Coyote	*Canis latrans*	Modern (collected 1946)	21.52	17.98
KU	Brule Co., SD	16194	Coyote	*Canis latrans*	Modern (collected 1946)	22.72	20.38
KU	Thomas Co., NE	73458	Coyote	*Canis latrans*	Modern (collected 1956-1957)	21.76	17.28
KU	Thomas Co., NE	73459	Coyote	*Canis latrans*	Modern (collected 1956-1957)	23.28	21.54
KU	Thomas Co., NE	73462	Coyote	*Canis latrans*	Modern (collected 1957)	23.26	19.82
UA	Pima Co., AZ	Z1068	Coyote	*Canis latrans*	Modern	20.24	18.96
UA	Pima Co., AZ	Z1075	Coyote	*Canis latrans*	Modern	22.76	18.30
UA	Pima Co., AZ	Z1078	Coyote	*Canis latrans*	Modern	18.04	19.18
ETMNH	Arizona	14309	Coyote	*Canis latrans*	Modern	22.92	17.78
ETMNH	Arizona	6842	Coyote	*Canis latrans*	Modern	15.51	18.09
ETMNH	No data	10276	Coyote	*Canis latrans*	Modern	23.75	20.32
ETMNH	Tennessee	18251	Coyote	*Canis latrans*	Modern	20.92	19.49
ETMNH	No data	251	Coyote	*Canis latrans*	Modern	22.55	20.38
ETMNH	No data	6582	Coyote	*Canis latrans*	Modern	21.62	20.13
ETMNH	Arizona	3017	Coyote	*Canis latrans*	Modern	22.84	19.68
ETMNH	No data	5157	Coyote	*Canis latrans*	Modern	19.72	20.56
UA	Northern Wisconsin	Z5004	Wolf	*Canis lupus lupus*	Modern (collected 1960)	28.86	29.52
ETMNH	Alaska	5256	Wolf	*Canis lupus lupus*	Modern	29.62	35.18
KU	Hidalgo Co., NM	76473	Wolf	*Canis lupus baileyi*	Modern (collected 1953)	25.88	26.26
KU	Kettle River, British Columbia	2143	Wolf	*Canis lupus columbianus*	Modern (collected 1891)	29.78	30.08
KU	Red River, SW Keewatin, Northwest Territories	84886	Wolf	*Canis lupus hudsonicus*	Modern (collected 1943)	28.04	24.96
KU	Anita Bay, Etolin Is., AK	65954	Wolf	*Canis lupus ligoni*	Modern (collected 1953)	30.58	28.22
KU	Anita Bay, Etolin Is., AK	65953	Wolf	*Canis lupus ligoni*	Modern (collected 1953)	29.30	26.36

KU	Clancy township, Nipising District, Ontario	18766	Wolf	*Canis lupus lycaon*	Modern (collected 1947)	27.90	24.48
KU	Sherman Co., KS	2140	Wolf	*Canis lupus nubilus*	Modern (collected 1911)	22.96	25.62
KU	Trego Co., KS	7575	Wolf	*Canis lupus nubilus*	Modern	26.92	28.20
KU	No Mans Land, OK	2138	Wolf	*Canis lupus nubilus*	Modern (collected 1888)	27.38	28.18
KU	No Mans Land, OK	2139	Wolf	*Canis lupus nubilus*	Modern (collected 1888)	26.48	25.66
KU	No Mans Land, OK	2141	Wolf	*Canis lupus nubilus*	Modern (collected 1888)	28.28	25.02
KU	Kettle River, British Columbia	2142	Wolf	*Canis lupus pambasileus*	Modern (collected 1890)	27.06	27.80
KU	Aishihik R., N Canyon, Yukon Territory	21107	Wolf	*Canis lupus pambasileus*	Modern (collected 1947)	27.22	26.94
KU	Southeastern Alaska	145232	Wolf	*Canis lupus pambasileus*	Modern	30.16	30.76
KU	Central Alaska	145233	Wolf	*Canis lupus pambasileus*	Modern	28.04	31.74
KU	McGrath, AK	145234	Wolf	*Canis lupus pambasileus*	Modern	27.78	29.94
KU	East-central Alaska	145235	Wolf	*Canis lupus pambasileus*	Modern	28.62	32.28
KU	Central Alaska	145238	Wolf	*Canis lupus pambasileus*	Modern	28.14	33.92
KU	Central Alaska	145239	Wolf	*Canis lupus pambasileus*	Modern	31.44	33.18
KU	East-central Alaska	145236	Wolf	*Canis lupus pambasileus*	Modern	28.78	30.30
KU	Central Alaska	145237	Wolf	*Canis lupus pambasileus*	Modern	29.78	33.88
KU	Central Alaska	145240	Wolf	*Canis lupus pambasileus*	Modern	29.22	32.78
KU	Central Alaska	145241	Wolf	*Canis lupus pambasileus*	Modern (collected 1967)	29.56	30.72
KU	Central Alaska	145242	Wolf	*Canis lupus pambasileus*	Modern (collected 1966)	32.66	34.38
KU	Central Alaska	145244	Wolf	*Canis lupus pambasileus*	Modern	29.68	31.46

KU	Central Alaska	145245	Wolf	*Canis lupus pambasileus*	Modern	28.76	29.84
KU	Northwestern Alaska	145246	Wolf	*Canis lupus pambasileus*	Modern	28.84	32.32
KU	Northwestern Alaska	145247	Wolf	*Canis lupus pambasileus*	Modern	30.46	30.38
KU	East-central Alaska	145249	Wolf	*Canis lupus pambasileus*	Modern	30.22	31.92
KU	East-central Alaska	145250	Wolf	*Canis lupus pambasileus*	Modern	29.00	31.54
KU	East-central Alaska	145251	Wolf	*Canis lupus pambasileus*	Modern	29.18	32.44
KU	Copper River, Alaska	145252	Wolf	*Canis lupus pambasileus*	Modern (collected 1966)	29.52	32.52
KU	Innoko River, AK	145253	Wolf	*Canis lupus pambasileus*	Modern (collected 1966)	30.34	30.38
KU	Nenana, AK	145254	Wolf	*Canis lupus pambasileus*	Modern (collected 1966)	30.06	29.46
KU	Nenana, AK	145255	Wolf	*Canis lupus pambasileus*	Modern (collected 1966)	30.28	32.88
KU	Nenana, AK	145256	Wolf	*Canis lupus pambasileus*	Modern (collected 1966)	27.98	32.18
KU	Tanana, AK	145257	Wolf	*Canis lupus pambasileus*	Modern (collected 1966)	30.74	32.96
KU	Wahoo Lake, Brooks Range, AK	51561	Wolf	*Canis lupus tundraium*	Modern (collected 1952)	29.36	29.10