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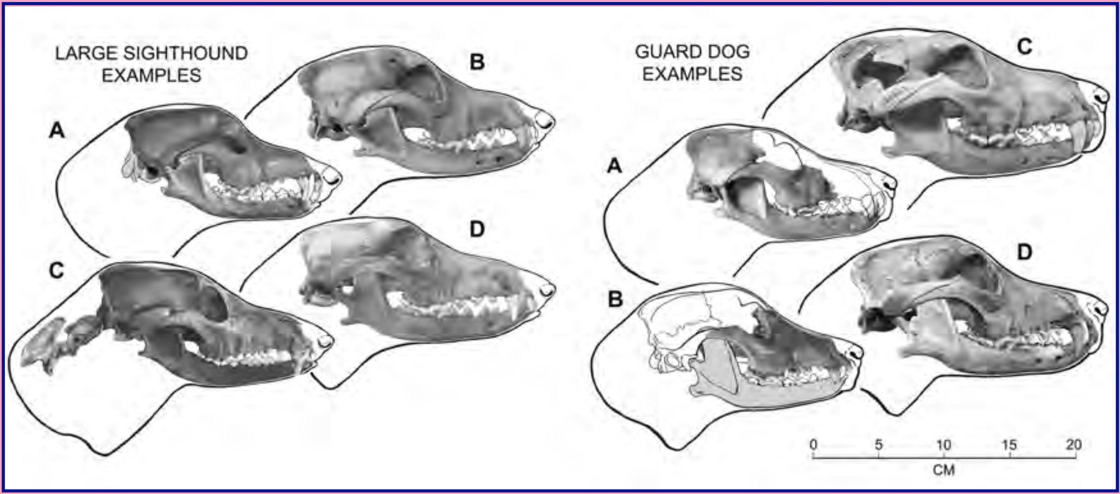

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The dogs of Roman Vindolanda, Part IV: Large sighthounds and guard and utility dogs

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ABSTRACT: In this report we investigate the origin and nature of morphological diversity in domestic dogs utilizing a database of over 1,000 recent and ancient canid skulls and skeletons. Integrated skull–skeleton analysis reveals eight functional groups, giving a clear picture of the extent and kind of morphological diversity produced by dog breeders in Europe, North Africa, and western Asia beginning in the Neolithic and intensifying about 2,100 years ago during the late Iron Age and Roman Era. We report nearly complete associated remains of a large sighthound from Vindolanda, a Roman-era fort–village site in northern England. With this we compare skulls of other sighthounds, and contrast them with remains of guard dogs from Vindolanda and other archaeological sites. The shape of jaw rami, relative size of teeth and state of dental wear, and the size and proportions of postcranial elements are the best differentiators of large dog morphotypes, while most skull parameters are less useful. The central section of the basicranium in ancient sighthounds (parameter Px which measures juvenilization) is little different from wolves, whereas in some modern breeds it is noticeably longer. By contrast, many ancient guard dogs have Px shorter than in wolves and show moderate juvenilization. Gracile sighthounds appear in the archaeological record in the Neolithic, while the earliest robust guard dogs appear later, in Iron Age sites. Building on results of previous work (Bennett & Timm, 2018) we continue to find intriguing similarities between west Asian dog landraces and dog remains from Vindolanda and other Roman-era sites in Western Europe.

KEY WORDS: *CANIS FAMILIARIS*, DOMESTIC DOG, GUARD DOG, JUVENILIZATION, MASTIFF, ROMANO–BRITISH, SIGHTHOUND, VINDOLANDA

RESUMEN: En este informe investigamos el origen y la naturaleza de la diversidad morfológica de los perros domésticos. Utilizamos una base de datos de más de 1,000 esqueletos de cánidos recientes y antiguos. Análisis integrado de cráneo y esqueleto revela 8 grupos funcionales, dando una imagen clara del alcance y el tipo de diversidad morfológica producida por criadores en Europa, África del norte y Asia occidental comenzando en el Neolítico e intensificándose hace unos 2,100 años durante la Edad del Hierro tardía y la época romana. Reportamos restos asociados casi completos de un gran lebrel de Vindolanda, una fortaleza y aldea de la época romana en el norte de Inglaterra. Con esto comparamos cráneos de otros lebreles, y los contrastamos con restos de perros guardianes de Vindolanda y otros sitios arqueológicos. La forma de las ramas de la mandíbula, el tamaño relativo de los dientes y el estado de degaste dental, y el tamaño y las proporciones de los huesos postcraneales son los mejores diferenciadores de los morfotipos de

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perros grandes, mientras que la mayoría de los parámetros del cráneo son menos útiles. La sección central del basicráneo en antiguos lebreles (parámetro Px que mide la juvenilización) es poco diferente al de los lobos, mientras que en razas modernas es notablemente más larga. Por contrario, los perros guardianes de Vindolanda tienen Px más cortos que los lobos y muestran una juvenilización moderada. Gráciles lebreles aparecen en el Neolítico, mientras que los primeros perros guardianes robustos aparecen más tarde, en sitios de la Edad del Hierro. Sobre la base del trabajo anterior (Bennett & Timm, 2018), seguimos encontrando similitudes intrigantes entre las razas locales de perros de Asia occidental y los restos de perros de Vindolanda y otros sitios de la época romano en Europa occidental.

PALABRAS CLAVE: *CANIS FAMILIARIS*, JUVENILIZACIÓN, LEBREL, MASTÍN, PERRO DOMÉSTICO, PERRO GUARDIÁN, ROMANO–BRITÁNICO, VINDOLANDA

INTRODUCTION

The Vindolanda World Heritage archaeological site is a Roman-era fort and village complex located 3 km (2 mi) south of Hadrian's Wall in northern England. From it come abundant well-preserved remains of domestic dogs (*Canis familiaris*). Roman soldiers began inhabiting the site in about 85 CE, and it was occupied, nearly continuously, by Romans and British natives until at least a century after the fall of the Roman Empire in 415 CE. In several previous papers, we reported details of site location, stratigraphy, architectural context, and ethnography along with the abundance and morphological range of the dog remains (Bennett & Timm, 2013, 2016, 2018; Bennett *et al.*, 2016). Excavation methods and history of excavation at this site are detailed in Birley (2003), Blake (2014), and Bennett *et al*. (2016).

MATERIALS AND METHODS

Measurements, Recording, and Calculations

Using digital calipers, we measured 25 parameters in total; 15 on the skull, six on jaw rami, and four on each of the four major long bones (Figures 1, 2). Measurement placement and technique are after Driesch (1976) except as noted in Figures 1 and 2. We make use of on-screen measurements in calculating juvenilization index (see Bennett & Timm, 2018). The PAST freeware package authored by Hammer *et al.* (2001) was used to perform all calculations and analyses.

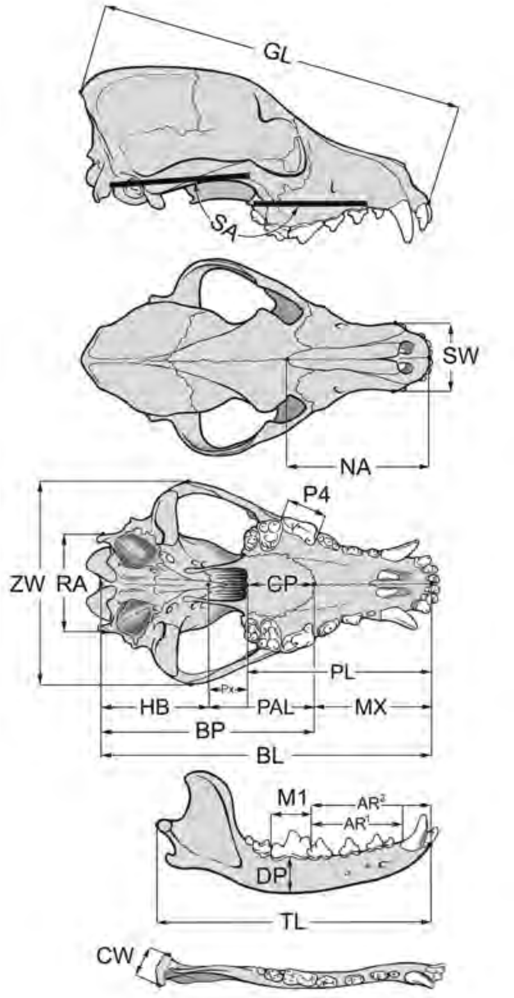

FIGURE 1

Measurements of skull and jaw ramus utilized in this report.

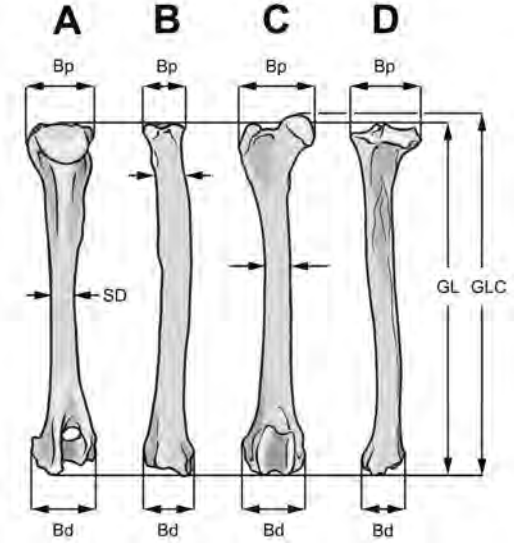

FIGURE 2

Measurements of limb bones; abbreviations and technique after Driesch (1976). A, Humerus; B, Radius; C, Femur; D, Tibia. In calculating limb index, we use Bp for tibia rather than SD.

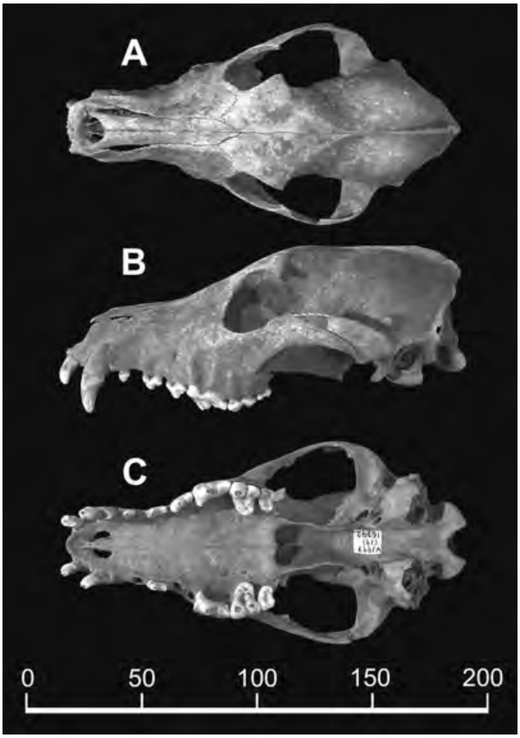

FIGURE 3

Vindolanda sighthound (V1997-19 16742), the "Praetorium dog" from a hypocaust channel of a hot room in the 3rd century praetorium of Stone Fort II [Robin Birley, *pers. comm.*, (2012)]. A, dorsal view; B, left lateral view; C, ventral view. For diagnostic views of other Vindolanda sighthounds, see Supplementary Information document Figs. S1-S4.

Specimens Examined

We report herein eight Vindolanda skulls selected on the basis of large size (condylobasal length (BL) greater than 145 mm). Five specimens exhibit the backsloping occiput, narrow skull, and generally gracile build that are characteristic of sighthounds. Two specimens are more massive in build and are identified as guard dogs (a type of utility dog bred for guarding people, livestock, and property). One specimen (hereinafter "the Praetorium sighthound," V1997-19 16742, Figure 3) is represented by a nearly complete skull and skeleton; the other four skulls identified as large sighthounds can be viewed in the Supplementary Information Document (E/W-111 10155, Figure S1; V04A 861, Figure S2; VH-102 29171, Figure S3; and V04A 863, Figure S4). These specimens have no associated jaws or postcranials but are beautifully preserved and mostly complete, and to them we refer numerous isolated limb bones and jaw rami. The guard dog specimens (V04A 862, Figure 4; LXXII-VI 10158, Figure S5) are both partial skulls; 862 has an associated mandible. To these we refer several isolated limb bones and jaw rami.

The Vindolanda collection contains 37 unassociated dog jaw rami, of which we previously identified 13 as belonging to miniatures or small sighthounds (Bennett & Timm, 2018). Here we refer a further three unassociated jaw rami of a size to fit skulls with BL larger than 145 mm. Of these, two rami are straight and slender and compare well with the rami pertaining to the Praetorium sighthound (Figures 5, 11 and S6–S8). The jaw rami associated with V04A 862 and the isolated jaw LXXII-VI 10158 (Figures 6 and S9–10) are larger and more massive, and pertain to guard dogs.

Extensive comparison of archaeological dog remains with recent wolves and feral and domestic dogs is absolutely crucial to clarifying morphological similarities and elucidating possible relationships. For this report, we examined 717 recent dog skulls representing 111 breeds and feral populations or landraces from 18 different collections worldwide. Of these, 138 are complete or nearly complete skeletons. As outgroup comparisons, we use 167 skulls of five recent kinds of wolves—

North American gray wolves (*Canis lupus*, combined eastern, midwestern, western, and Alaskan wolves); Tuscan wolf (*C. lupus*); Chinese wolf (*C. lupus*); Mexican wolf (*C. lupus baileyi*); and Indian wolf (*C. lupus pallipes*). Of these, 54 are complete skeletons. We also utilized our complete Australian Dingo dataset (*C. familiaris dingo*), comprising some 160 skulls, of which 25 are complete skeletons. New Guinea Singing Dogs (*C. familiaris hallstromi*) are another feral population of interest; we compare nine complete skull–skeleton specimens. We also compare seven late Pleistocene wolf (*Canis lupus*) skulls from the Natural Trap Cave (Martin & Gilbert, 1978; Meachen *et al.*, 2016), along with unassociated postcranials from that site pertaining to at least 29 individuals.

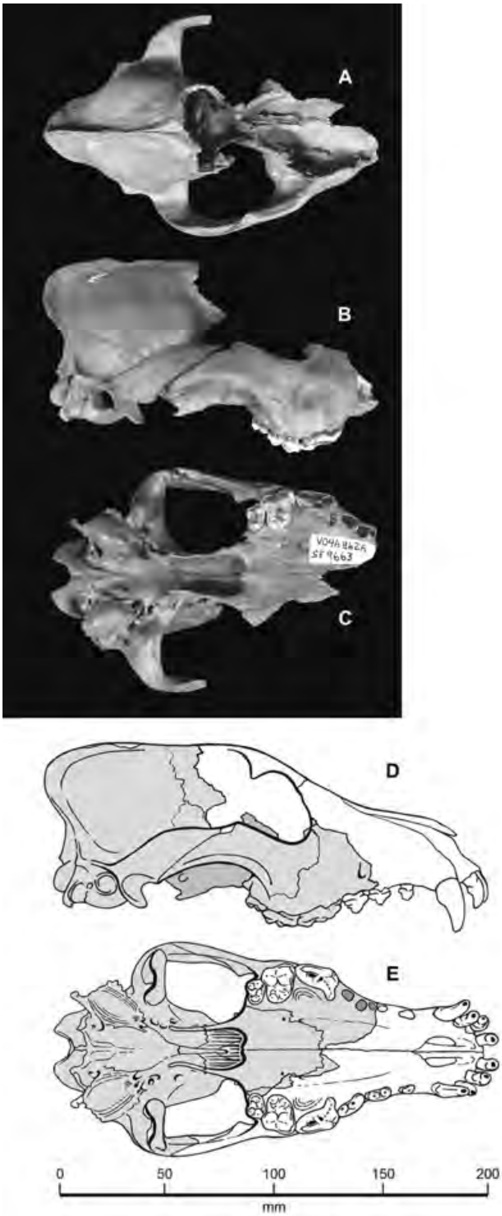

FIGURE 4

Vindolanda guard dog V04A 862. A, dorsal view; B, right lateral view; C, ventral view; D, restoration of lateral aspect; E, restoration of ventral aspect. Skull length restored from the associated complete mandible. For diagnostic views of another Vindolanda guard dog, see Supplementary Information document Fig. S5.

Along with the Vindolanda material (Hambleton, 2003; Bennett, 2005, 2007), we also review 75 dog (*Canis familiaris*) specimens from 22 other Neolithic, Iron Age, Classical Period, Ptolemaic, Roman-era, and 18th-century archaeological sites in Great Britain, Iberia, Egypt, Germany, Italy, Turkey, and Armenia (Reed, 1962, 1983; Luttschwager, 1965; Cram, 1973, 1978; Harcourt, 1974; Van Wijngaarden-Bakker, 1974; Westley, 1975; Bökönyi, 1984; Grant, 1984; Maltby, 1987; Churcher, 1993; Farello, 1995; Clark, 1996, 2006, 2012; Davis, 1997; Bartosiewicz, 2000; De Grossi-Mazzorin & Tagliacozzo, 2000; Manaseryan & Antonian, 2000; Baxter, 2002, 2007, 2009, 2010a, b; Johnstone & Albarella, 2002; MacKinnon & Belanger, 2002; Dunand & Lichtenberg, 2005; Grimm, 2007; Baxter & Nussbaumer, 2009; Phillips *et al.*, 2009; Ayton, 2011; Kitagawa, 2013; Ikram, 2014 and *pers. comm.* (2020); Manaseryan, 2016; Pires *et al.*, 2017; Hourani, 2018). Of these, six are complete skeletons. Because of breakage, the number of specimens utilized in different analyses in this report may differ slightly.

Because we believe that visual comparison is necessary to this and all future work on the origin and nature of morphological diversity in domestic dogs, we present standard diagnostic views of the Vindolanda skulls studied (Figures 3, 4 and S1–S5). Broken skulls and missing teeth are restored from the opposite side or from closest comparable material. We also present precisely scaled lateral views of these skulls with articulated jaw rami and skin outline, comparing them with other specimens of high interest, including eight recent tribally-bred, landrace, or feral dogs; six post-18th century domestic dogs; and five dogs from Roman-era archaeological sites (Figures 5–6 and S6–S10). We also compare the occiputs of the above array of dogs in order to highlight the fact that occipital shape is different in Asian vs. European sighthounds and utility/guard dogs (Figures 7 and S11–S13).

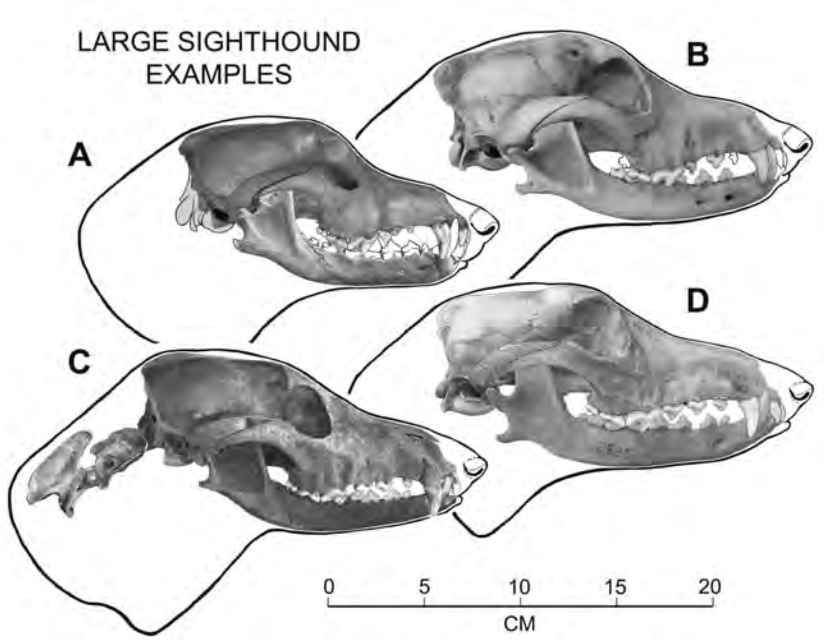

FIGURE 5

Lateral views of articulated skull and jaws; examples of large sighthounds. A, Vindolanda V04A 861 (articulated with jaws that probably go with it, V04A 855). B, FMNH 86835, tribally-bred Afghan hound. C, Vindolanda Praetorium sighthound. D, LACM 22825, “imported Persian hunting dog”, a tribally-bred Saluki. For complete comparative series, see Supplementary Information document Figs. S6–S8.

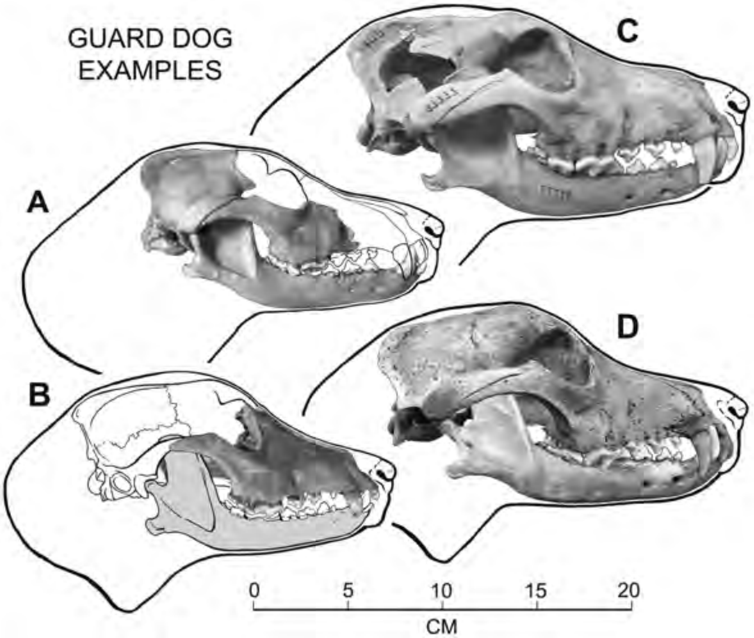

FIGURE 6

Lateral views, articulated skull and jaws of guard dogs, ancient and modern examples. A, Vindolanda V04A 862. B, Vindolanda LXXII-VI 10158. C, FMNH 97777, tribally-bred Kuvasz (skull and jaws reversed). D, LACM 52198, Canaan Dog imported from Israel. For complete comparative series, see Supplementary Information document Figs. S9–S10.

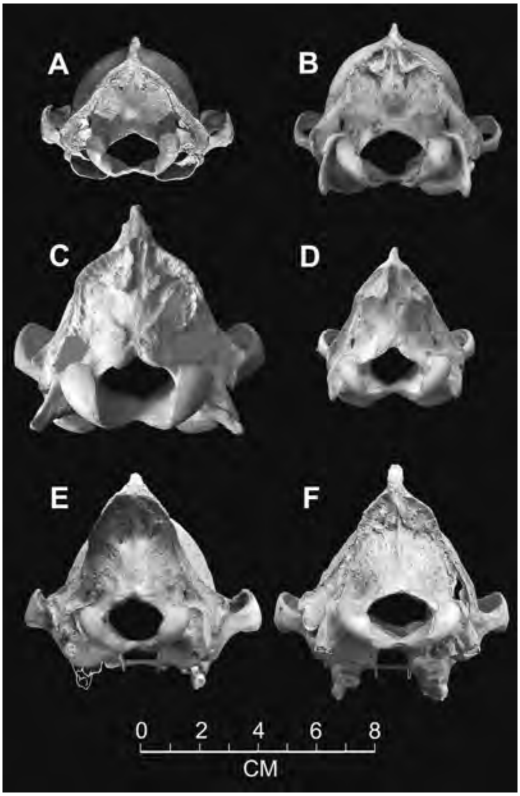

FIGURE 7

Triangular vs. round occiput in large sighthounds and guard dogs. A, Praetorium sighthound. B, FMNH 92896, a landrace Saluki from Khuzistan, Ahwaz, Iran. C, YPM 7345, Irish Wolfhound. D, ANM M-414, Borzoi. E, Vindolanda V04A 862, guard dog. F, FMNH 97777, tribally-bred Kuvasz from W. Azerbaijan. Teeth show in E and F because the skull must be tilted downward considerably to show occiput because of forward slope of occiput and heavy, overhanging lambdoidal crest. For complete comparative series, see Supplementary Information document Figs. S11–S13.

Because the Vindolanda Praetorium sighthound is a well-preserved, nearly complete specimen, in addition to views of the skull and jaws, we present diagnostic views of all recovered limb bones, pelvis, and metapodials, along with vertebrae that are complete or nearly so (Figures S14–S17). Missing parts are restored as above. In addition, we present precisely scaled drawings of humerus, radius, femur, and tibia of all ancient dogs discussed in this report, comparing them with wolves, dingoes, and a standard set of morphologically similar modern dog breeds (Figures S18–S23).

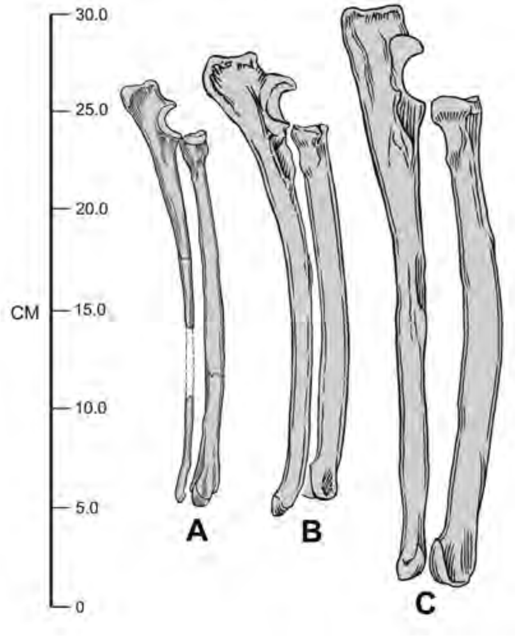

FIGURE 8

Radius and ulna of sighthound and utility/guard dogs in lateral view, showing relative sizes and degree to which the shaft is bowed. A, Vindolanda Praetorium sighthound; radius GL = 188.52 mm. B, Heidelberg–Neuenheim "grosshunde" (after Luttschwager, 1965), radius GL = approx. 190 mm. C, "Varg", from the Saqqara dog tombs [Ikram, *pers. comm*. (2020)], radius GL = approx. 242 mm.

Multivariate Analyses

Bennett *et al.* (2016) give a description of principal component analyses (PCA) used in this series of papers, and our reasons for preferring PCA to discriminant function analysis (DFA) and to canonical variate analysis (CVA).

MTA analysis is a graphic–analytical method in which a ratio, index, or proportional relationship (Y axis) is set against a measurement reflective of body size (X axis) to form a bivariate plot. The two parameters which make up the ratio axis are selected on the basis of high discriminatory power as indicated by the results of principal component analysis. We derive several of the MTAs in this report from our previous PCAs (Bennett *et al.*, 2016). In other cases, we present MTAs based upon parameters considered by Harcourt (1974), Huber (1974), Lüps (1974), Nussbaumer (1978), Baxter (2010 a, b), or Baxter & Nussbaumer (2009) to be most useful.

Successful MTA analysis produces two results: first, within any given analysis there is a diagonal "spread" of bounded polygons (hulls) pertaining to different groups, in other words the groups separate along both the size (X) and ratio (Y) axes. Second, dogs cluster in the same way in all analyses, indicating that groups apparent on paper probably have real-world functional significance. In this report, we present MTA's for five aspects of skull shape, two dealing with features of the jaw, four concerning the major long bones, and one showing degree of juvenilization (Figures 9, 10, 13, 14, 17 and S24–S32). The juvenilization algorithm we presented in previous work concerning small dogs (Bennett & Timm, 2018) is just as useful for understanding developmental characteristics of the skull in large dogs. The algorithm is calculated as (Px × 100)/CP; see Figure 17 and discussion following. These represent most of the same analyses we previously carried out on the small dogs from Vindolanda (Bennett & Timm, 2018), but here we add two more which integrate proportions of the postcranial skeleton ("uphill dog," Figures 18–19) and skull size vs. body size ("aerodynamic dog," Figures 18, 20).

RESULTS

General Morphological Features

Several patterns are evident in all the following MTA analyses of skull shape:

(1) Wolves and dingoes tend to plot toward the center of the Y axis (the axis of proportion); dogs show much greater range.

(2) The Vindolanda specimens and other archaeological dogs are conservative, and like wolves and dingoes tend to plot toward the center of the Y axis range.

(3) Genomic analyses of wolves, dingoes, and modern domestic dogs by Von Holdt *et al.* (2010, using SNP's and haplotypes) and Parker *et al.* (2017, combining genetic distance, migration data, and genome-wide haplotype sharing) classify sighthounds into two groups, European and Asian. The European group contains Irish Wolfhound, Scottish Deerhound, Borzoi, and Greyhound; the Asian group contains Afghan Hound and Saluki. In our purely morphological analyses, we concur with these groupings; however, Greyhound usual-

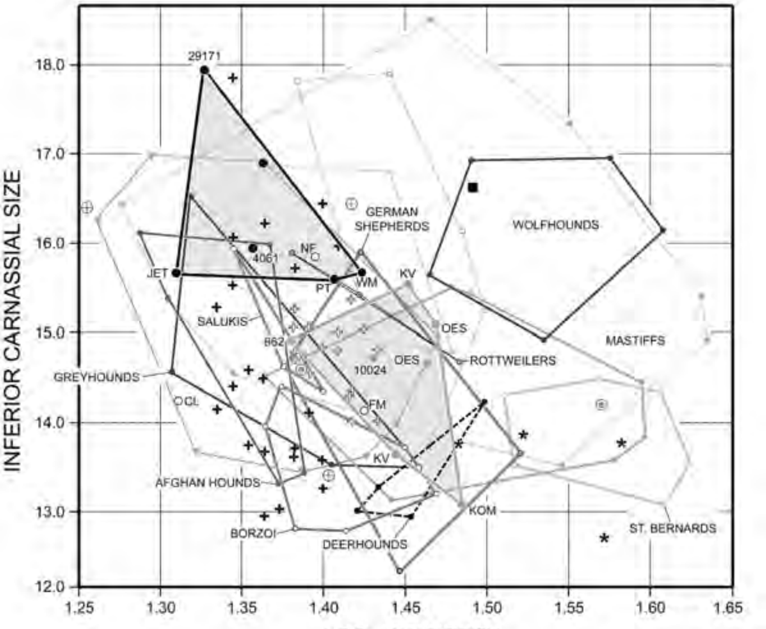

FIGURE 9

MTA analysis of inferior carnassial size, calculated as (M_1 × 100)/TL. Abbreviations: NF = Norfolk Street; FM = Forum dog no. 1 [Baxter, pers. comm. (2015)]; jaw depth of FM estimated from photo). WM = Warmington (measurements courtesy Sheila Hamilton-Dyer, 2019). Symbols: Black plus = Tac Gorsium specimens that are probably large sighthounds. White plus = Tac Gorsium specimens that are probably guard dogs (data from Bökönyi, 1984).

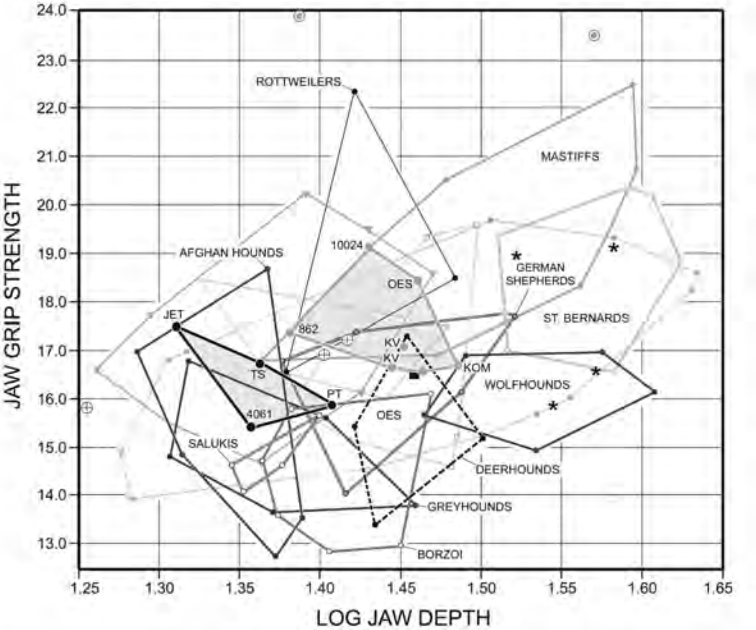

FIGURE 10

MTA analysis of jaw grip strength, calculated as (CW × 100)/TL.

ly plots with the Asian group and it also has the rounded occiput characteristic of that group (Figures 7 and S11).

(4) Von Holdt *et al.* (2010) classify Canaan Dogs with Afghan Hounds and Salukis. We find Canaan Dogs to be morphologically variable, and the breed stud-book recognizes both a more gracile, dingo-like strain and a stouter strain resembling the German Shepherd or Kuvasz (Menzel & Menzel, 1960). We therefore plot Canaan dogs individually rather than incorporating them into hulls.

(5) Ancient guard dogs (hereinafter abbreviated AGD): Genetic studies by Von Holdt *et al.* (2010) and Parker *et al.* (2017) group the Kuvasz and the Hungarian Komondor with "ancient" breeds including the Afghan Hound and Saluki, yet Kuvasz and Komondor are relatively stout-bodied, not gracile sighthounds built for coursing. Old English Sheepdog is another modern breed of robust build that belongs in the AGD group. The AGD group constitutes a subset of utility dogs (Figures 19, 20). Many modern utility dogs (German Shepherds, Mastiffs, Pit Bulls, Rottweilers, Presa Canario) are larger than any Roman-era dog studied.

(6) Ancient large sighthounds (hereinafter abbreviated ALS): The Warmington dog (Schoenebeck *et al.*, 2019) and a skull from Norfolk Lane [Baxter, *pers. comm.* (2015)] plot in the ALS hull along with the Vindolanda Praetorium sighthound and other Vindolanda sighthounds, Salukis, and Afghan Hounds. The Jebel El Teir specimen is a feral Sloughi from Minya Province, Egypt. Charles A. Reed's "tunnel dog", which was collected during the 1960s as part of the Prehistoric Iraq–Jarmo Expedition mounted by the University of Chicago Oriental Institute and the Field Museum of Natural History (Turnbull & Reed, 1974), comes from Tepe Sarab in southern Turkey. It is an intrusion into an older burial mound, but is thought to be at least several hundred years old (Reed, 1962), and in this report we treat it as an archaeological specimen. We identify two subgroups of ALS, those that resemble Afghan hounds vs. those that resemble Salukis (Figures 5 and S6–S8). However, no archaeological dog is exactly like any modern dog breed.

(7) In general, MTA analyses of skull shape are less useful in distinguishing ALS from AGD than are analyses involving the jaw rami or the major long bones. Skull parameters have proven to be much more useful in distinguishing miniature dogs and small sighthounds (Bennett & Timm, 2018).

Analyses of Skull Parameters in ALS and AGD

(1) *Cranial index* (Cephalic index, Skull Shape Index: (ZW × 100)/BL (Figure S24). Harcourt (1974) considered skull index (overall skull shape) to be one of the best morphological discriminators. In our analysis, the hull bounding ALS plots separately from that bounding AGD, but the separation is minimal and the groups could just as well have been plotted as one.

(2) *Snout length* (NA × 100/BL; Figure S25) *and nasal suture.* Harcourt (1974) considered snout length to be nearly as valuable in differentiating dogs as the cranial index. In our analysis, ALS and AGD also plot separately; this reflects the fact that guard dogs have wide snouts while sighthounds have narrow ones (X axis). The range of snout length (Y axis) is much greater in ALS, with the Warmington dog presenting a proportionally shorter snout than any AGD. At the opposite extreme, Vindolanda specimens V04A 863, E/W-111 10155, and the Praetorium sighthound, along with Tepe Sarab, exceed all guard dogs in snout length.

The Warmington dog presents not only a snout short compared to BL, but also a high sutural junction between the nasal, maxillary, and frontal bones (positioned above a line connecting the lower rims of the orbits) (Schoenebeck *et al.*, 2019 fig. 1c). They note that this is rare among sighthounds and a survey of our own database confirms the fact. None of the Vindolanda sighthounds, and indeed no Vindolanda dog skull, has this sutural configuration. We find that such a high placement is also rare in wolves and dingoes, and most frequent in the larger short-snouted modern breeds such as Pugs, Lhasa Apsos, English Bulldogs, and Boxers.

(3) *Snout shape* (SW × 100/NA; Figure S26). In previous work, we found that small dogs from Vindolanda plot almost entirely separately from any wild or feral dog (Bennett & Timm, 2018). Large dogs, however, plot with wolves, dingoes, and similar recent breeds. The ALS group overlaps Afghan Hounds and Greyhounds, while AGD's overlap German Shepherds and Mastiffs. Snout shape in sighthounds is narrow, although not long relative to the overall skull length because the basicranium is also long. In guard and utility dogs, snouts are broader and the snout is also longer in proportion to skull length.

(4) *Mouth Shape* (SW × 100)/PL (Figure S27). Mouth shape has important functional consequences and in large dogs it differs significantly from that in smaller kinds of dogs. Large dogs have much greater grip strength than small ones (see below), and they also have proportionally longer palates. Small Vindolanda dogs as a group cover a narrow range of Y values, from 32–38%. AGD cover a wider range from 57–66%, while ALS range from 48–61% (see Bennett & Timm, 2018 to view all small dog MTA's).

Greyhounds plot separately from Wolfhounds, Deerhounds, and Borzoi but in this analisis their hull is also disjunct from ALS. By contrast, Salukis and Afghan Hounds largely overlap ALS. There is also a small area of overlap with Deerhounds. Kuvasz dogs which usually plot with the guard dog group, in this analysis are broadly disjunct, a reflection of the fact that they have relatively short, wide palates. By contrast, mouth shape in some AGD's is indistinguishable from that of large sighthounds and Afghan Hounds, and as we found with overall skull shape, the two groups could as well have been plotted as one.

(5) *Neck Strength* (RA × 100)/PL (Figure S28). Neck strength is much greater in large dogs than in small ones. Whereas the Vindolanda miniatures and small sighthounds ranged from 43–48% on the ratio axis, ALS and AGD cover a range of from about 75–93%. Salukis and Afghan Hounds plot even higher, while Borzoi range up to 123%.

Analyses of Jaw Ramus and Dentition in ALS and AGD

(1) *Inferior Carnassial Size* (M_1 × 100)/TL (Figure 9). This measure looks at inferior carnassial size relative to jaw length, but inferior and superior carnassial size are coordinate so that what our MTA analyses show concerning the inferior carnassial is also true of the opposing superior tooth. The carnassials of miniature dogs tend to be proportionally large because teeth do not reduce in size at the same rate as the skull (Crockford, 2000a; Clark, 2006; Bennett & Timm, 2018). We find the inverse to be true of large dogs, whose carnassial teeth tend to be small relative to skull size. Teeth are generally uncrowded in larger dogs and there is noticeable interproximal space between premolars, especially in the most dolichocephalic forms (Wolfhounds, Borzoi, ALS, and long-headed modern guard dogs such as Great Danes). Our analysis shows that the

carnassials of ALS are proportionally larger than those of AGD (Y axis), while jaw depth tends to be greater in AGD (X axis).

(2) *Jaw Grip Strength* (CW × 100)/TL (Figure 10). We observed in previous work that breeders seem not to have deliberately attempted to create greater grip strength in small dogs (Bennett & Timm, 2018). Grip strength is of great importance, however, in guard dogs and in many utility dogs, and modern Presa Canarios and some Rottweilers and Mastiffs plot higher for grip strength than any small dog. However, this is not true of AGD's; in proportion to the size of the dog, their grip strength is about the same as that of small dogs from Vindolanda and about the same as wolves.

All large sighthounds have long, shallow jaw rami (Figure 39), and ALS have the weakest grip strength of any group so far studied, although not as weak as some modern Salukis and some Borzois, Greyhounds, Deerhounds, and Afghan Hounds. Modern Wolfhounds are larger dogs than ALS, but by this measure have about the same grip strength, which is at the low end of the wolf range.

(3) *Klinorhynchy and Jaw Shape.* Klinorhynchy is downward angling of the snout relative to the basicranium; airorhynchy is the opposite. We provide series of examples comparing jaw rami of ALS vs. AGD (Figures 11–12). In airorhynchic modern dogs and in modern and ancient types with low degrees of klinorhynchy, the jaw ramus is curved ("rockered"). With greater klinorhynchy, the jaw rami become slightly bowed or straight, and when the dog is "downsnouted" more than about 9 degrees the rami may even be bent downward at the anterior end ("chinned"). We found the range of klinorhynchy among small Vindolanda dogs to vary from 2.4 degrees (incipiently airorhynchic) to 17.5 degrees (strongly downsnouted, equivalent to a modern Scottish Terrier) (Bennett & Timm, 2018). ALS range from 4 to 9 degrees, and consequently have jaw rami that show an undulating underline with at least subtle "chinning". AGD by contrast are straight-headed like wolves, ranging from 0 to 4 degrees of klinorhynchy. Their jaw rami, like those of wolves, are rockered.

(4) Inferior dentition and jaw ramus shape. The inferior teeth of modern large sighthounds are "spaced out" along the jaw, with noticeable interproximal distance between the anterior premolars. In many cases, however, the anterior premolars of AGD's appear spaced out also, due to the fact that their jaws are large overall (or, it may be equally be said that their teeth are small in relation to the length of the ramus, per the observations above). The jaw rami of ALS and AGD differ in their proportions: the anterior part of the jaw, between the carnassial and the canine, is long in ALS, whereas the anterior part of the jaw in AGD's (especially the archaeological members of this group) is proportionally shorter (Figures 11–13). This is a more meaningful classifier than the mere spacing of the teeth (Degerbøl, 1961; Van Wijngaarden-Bakker, 1974).

Sighthounds have relatively shallow jaw rami, whereas those of both ancient and modern guard dogs are deep below the carnassial. Two sub-types of guard dog are evident from examination of jaw rami: one (represented in the Vindolanda collection by V04A-862) has straighter, thinner jaws and most resembles the modern Kuvasz. The other guard dog group presents rami very deep below the carnassial but tapering anteriorly; Vindolanda specimen VI-85 10024 exemplifies this and bears a striking resemblance to Old English Sheepdog. Generally we find that archaeological AGD have heavily worn teeth (wear stages E, F, and G), whereas teeth of ALS are usually much less worn (wear stages A, B, C, D of Horard-Herbin, 2000).

(5) *Relationship of HB length to Slope of the Occiput* (Figure 14). The importance of the development and proportions of the chain of bones which form the dog basicranium was first pointed out by Huber (1974), Lüps (1974), and Nussbaumer (1982). When the posterior basicranium (HB) is long, the condyles are simultaneously pushed backwards to create a backsloping occiput (Bennett, 1980; and see discussion in Bennett & Timm, 2018). When HB is short, the opposite obtains and the occiput is forward-sloping so that the occipital condyles are tucked under the lambdoidal crest.

A bivariate plot of HB against a width dimension of the skull (PW) produces a spread of hulls with little overlap between ALS and AGD. In Figure 14, we have also included the small sighthounds (ASSH) previously reported (Bennett & Timm, 2018) to show that the occiput tends to slope backwards more in small sighthounds than in large ones. Small sighthounds also have more lightly-built skulls with minimal cresting which does not overhang the atlas and axis, whereas ALS have some overhang due to large saggital and lambdoidal crests.

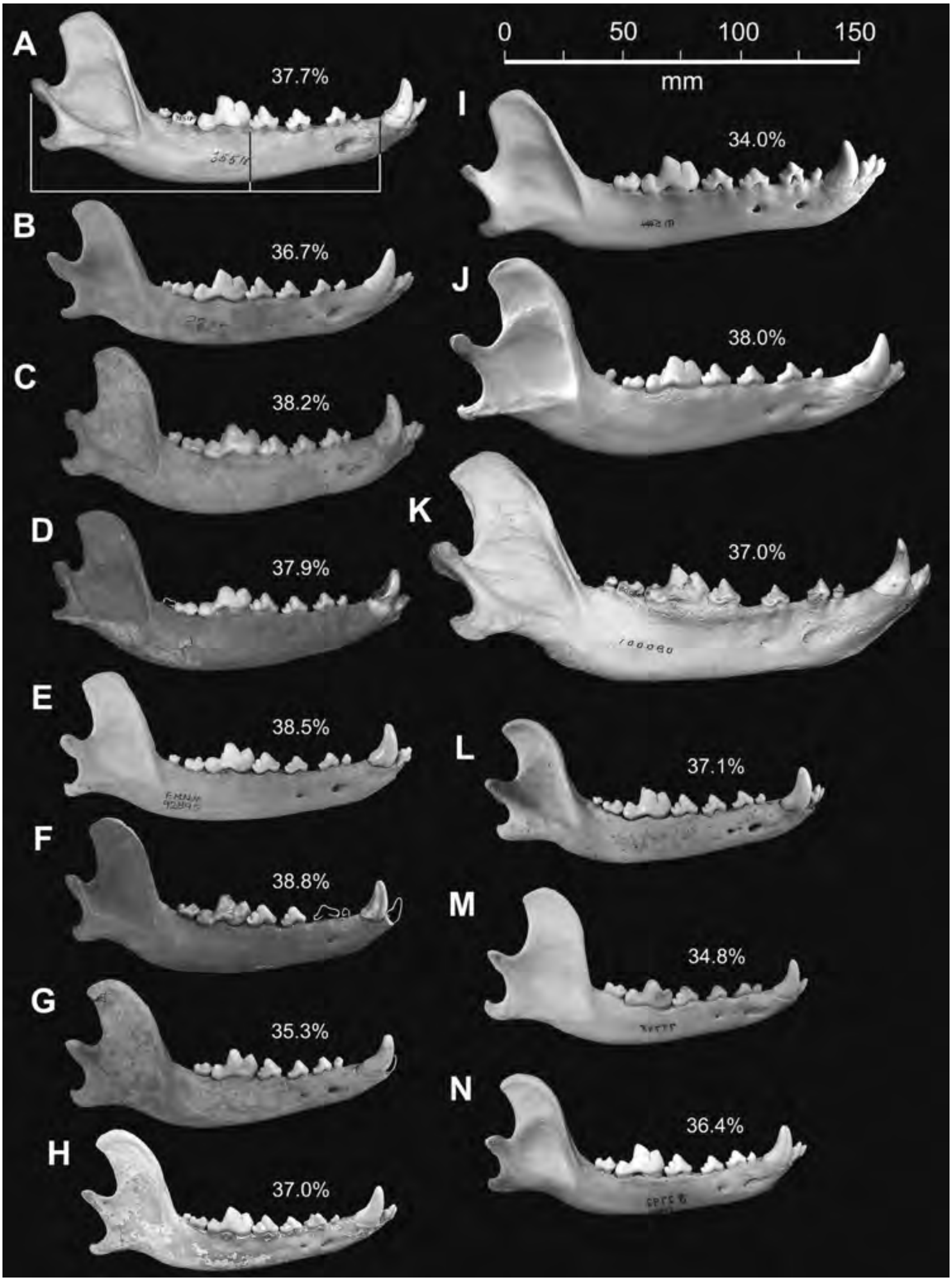

FIGURE 11

Jaw rami of large sighthounds. Percentage length of anterior ramus calculated by (AR[1] × 100)/TL is shown for each; range, 34.0%–38.8%; average, 36.9%.

A, Greyhound AMNH 35511 (canine and P_1 restored from opposite side); GL = 163.84. B, “Imported Persian hunting dog,” LACM 22825 a tribally-bred Saluki; GL = 149.88. C, The Warmington sighthound (Schoenebeck *et al*., 2019); GL = 147.3 (measurements and photo courtesy of Ian Baxter and Sheila Hamilton-Dyer). D, Vindolanda Praetorium sighthound V1997-19 16742; GL = 147.13. E, Landrace Saluki from Kuzistan, Ahwaz, Iran FMNH 92895; GL = 146.17. F, Vindolanda V05-40A 4061, isolated jaw ramus; GL = 139.22. G, “Tunnel dog” from Tepe Sarab, northern Iran FMNH Paleo PM-37/S-I-2A (reversed); GL 138.69. H, Canaan dog from Israel LACM 52197; GL = 128.77. I, Borzoi ANM M-414 (reversed); GL = 175.52. J, Scottish Deerhound YPM 7987; GL 183.67. K, Irish Wolfhound AMNH 100080; GL = 208.23. L, Landrace Saluki from Iraq FMNH 86842; GL = 139.88. M, Feral Sloughi from Jebel El Teir, Egypt FMNH 77745; GL = 131.43. N, Afghan Hound CAS Bandar Collection 2792; GL = 130.10.

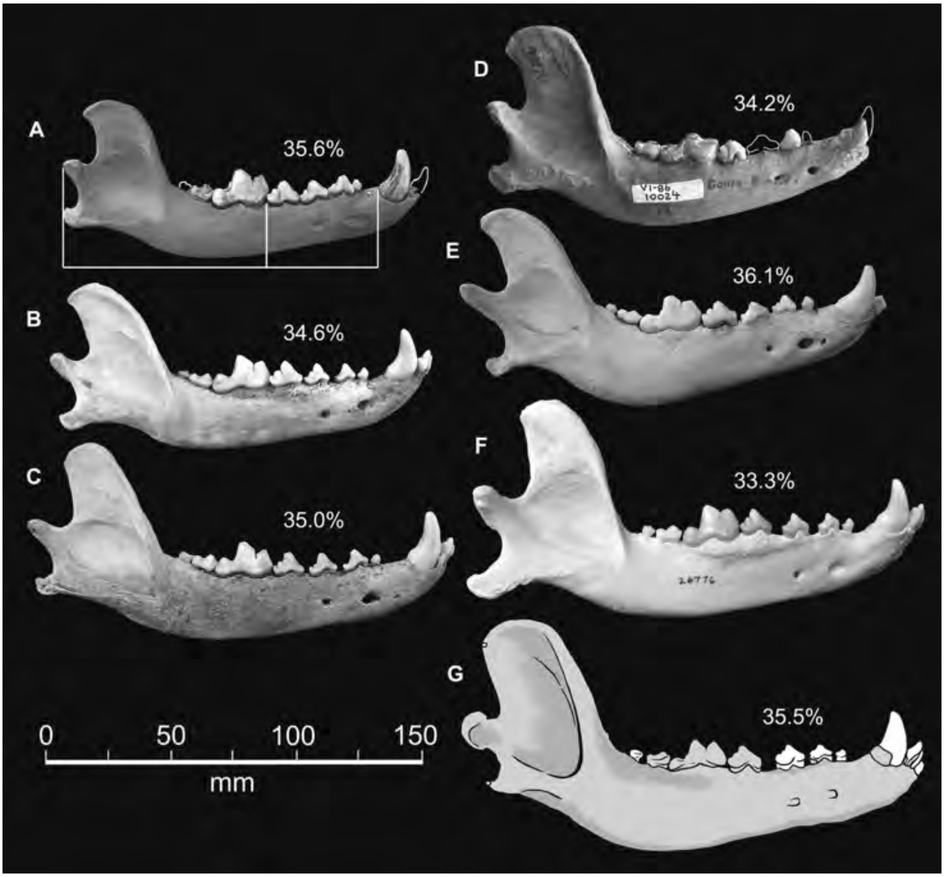

FIGURE 12

Jaw rami of utility and guard dogs. Percentage length of anterior ramus calculated by (AR^1 × 100)/TL is shown for each; range, 33.3–36.1%; average, 34.9%.
A, Vindolanda V04A 862; GL = 141.10. B, Canaan dog LACM 52198; GL = 148.62. C, Tribally-bred Kuvasz FMNH 57252; GL = 166.97. D, Vindolanda VI-86 10024, isolated jaw ramus; GL = 152.89. E, Old English Sheepdog LACM 31099; GL = 166.27. F, Hungarian Komondor CAS 26776; GL = 176.54. G, Drawing made from photo of “Varg,” a large dog from the Saqqara dog tombs in Egypt; GL = 183 [measurements and photo courtesy Sheila Ikram, *pers. comm.* (2020)].

Heavy cresting is characteristic of AGD’s; they tend to have shorter HB and forward-sloping occiputs that are tucked under a large and overhanging lambdoidal crest. Few modern dogs in our database exhibit shorter HB than the AGD group plotted in Figure 14; they include a minority of Boxers, Rottweilers, American Bulldogs, Pit Bulls, Presa Canario, and Pugs—dogs that are all relatively short-faced and incipiently or actually airorhynchic.

(6) *Juvenilization* (Figures 15–17). In this report, we consider dogs with Px proportionally shorter than in wolves to be juvenilized, while those with Px longer than in wolves are the opposite, which may be termed “anti-juvenilized”. To make this clear, we provide both visual comparisons and MTA. A spectrum from long to short Px exists for both ALS and AGD.

Analyses of Major Limb Bones (Figures S18–23 and S29–32).

The long bones most useful for differentiating dog morphotypes are humerus, radius, femur, and tibia. Ancient dogs recovered with associated long bones are of the highest value because they demonstrate the morphology of the whole dog as it was in life. Our analyses are empowered by many modern comparative specimens which, taken together with associated archaeological remains, make it possible to refer isolated limb bone finds with confidence.

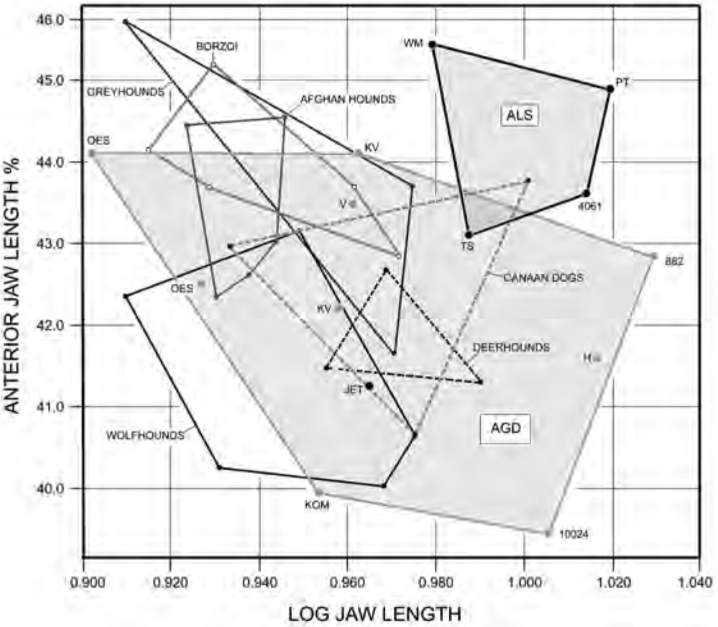

FIGURE 13

MTA analysis of jaw ramus proportions. Anterior jaw length percentages calculated by (AR^2 × 100/TL). AGD's cover a large area but overlap little with ALS. KV = Kuvasz; H = "Grosshunde" from Heidelberg–Neuenheim; JET = feral Sloughi from Jebel El Teir, Egypt; KOM = Hungarian Komondor; TS = "Tunnel dog" from Tepe Sarab; WM = Warmington sighthound; PT = Vindolanda Praetorium sighthound; V = "Varg", large dog from Saqqara dog tombs, Egypt; OES = Old English Sheepdog; numbers are unassociated Vindolanda jaw rami except 842, which is associated with a partial skull.

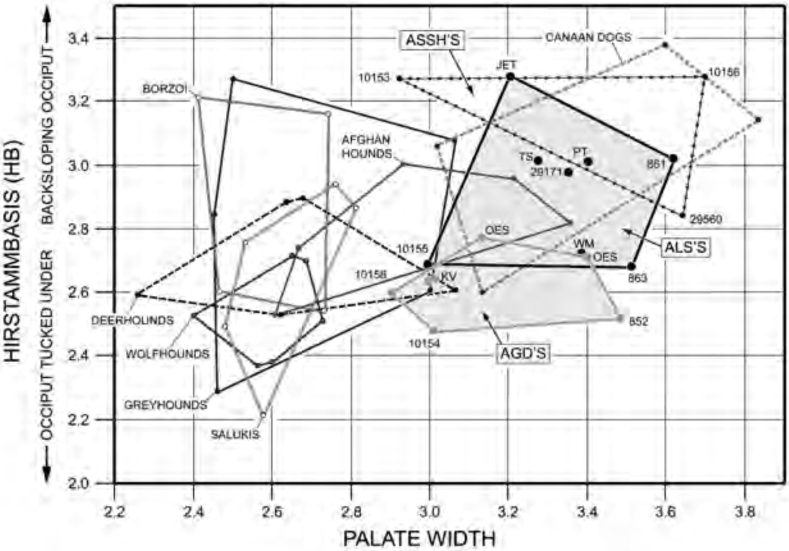

FIGURE 14

Bivariate plot of hirstammbasis (HB) against palate width. Accurate measurement of occipital slope can be made by utilizing screen images of standard lateral views. Before measurement, the skull must first be carefully leveled so that the posterior margin of the alveolus for M2 is on a line with the posterior margin of the canine alveolus. Scales for X and Y axis are in screen units. Note that where cresting is heavy (as in Canaan dogs), the crest may overhang the occipital condyles even when HB is long and the occiput is backsloping. Ancient small sighthounds (ASSH's) have the most backsloping occiputs; AGD's plot at the opposite extreme, with short HB and forward-sloping or "tucked under" occiputs.

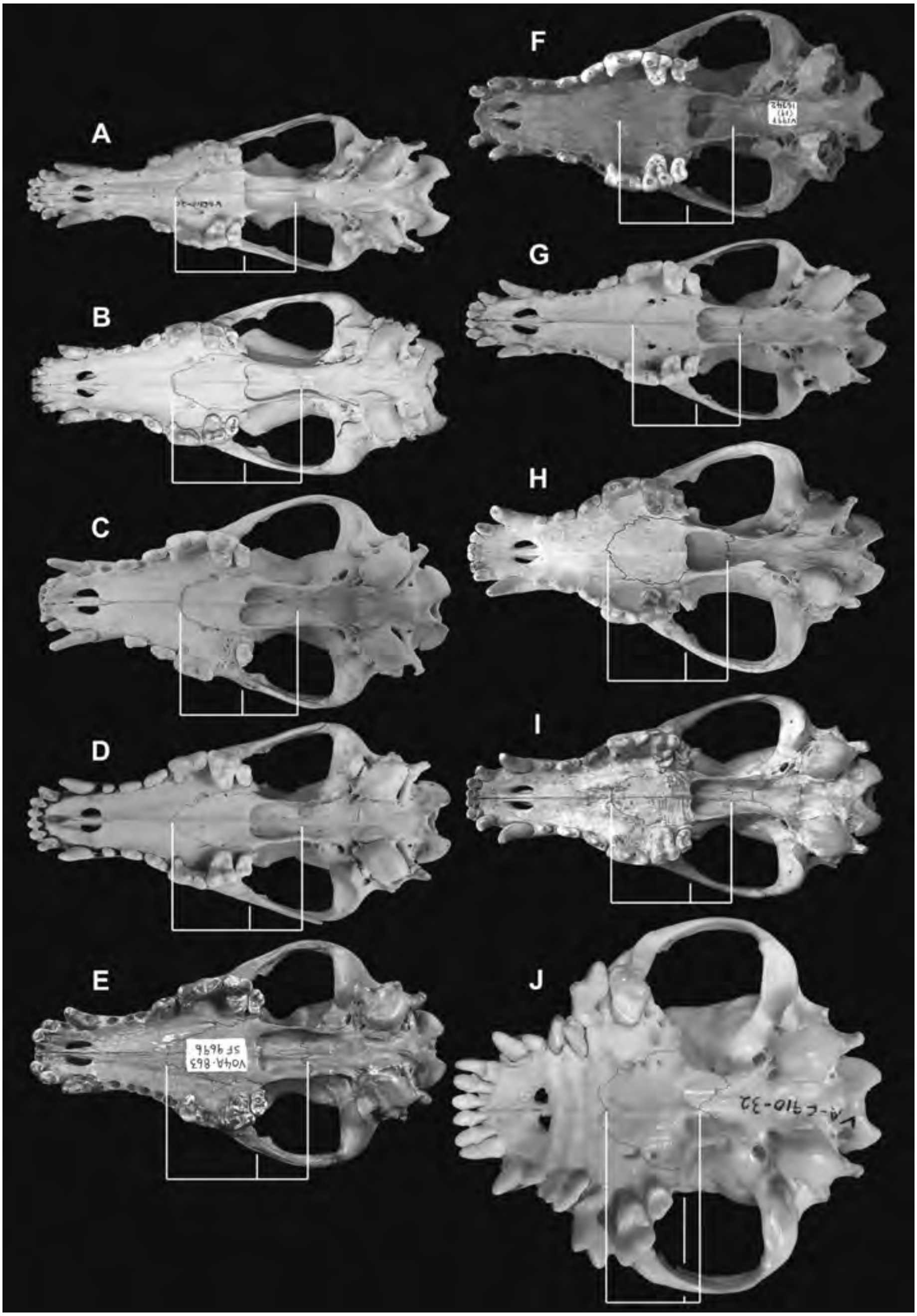

FIGURE 15

Visual comparison showing the spectrum of juvenilization in large sighthounds and a Pekingese. Brackets superimposed on each image show the juvenilization algorithm (Px × 100 compared with CP). Skulls are not to scale, but are reduced to the same BL, and are ordered from longest Px (most "anti-juvenilized") to shortest Px (most juvenilized). Sutures have been highlighted for ease of comparison. None of these dogs (except the Pekingese) is juvenilized compared to the Alaska wolf (Dingo view I and Alaska wolf view H have equal Px length). The Wolfhound (view B) and Borzoi (view A) may be considered strongly "anti-juvenilized".
A, Borzoi WSU C910-20; BL = 218.32. B, Irish Wolfhound AMNH 100080; BL = 249.59. C, Indian wolf (*Canis lupus pallipes*) FMNH 44467; GL = 194.64. D, Tribally-bred Afghan Hound, FMNH 86833; GL = 174.45. E, Vindolanda V04A 863; GL = 146.38. F, Vindolanda Praetorium sighthound V1997-19 16742; GL = 165.82. G, Tribally-bred Saluki FMNH 92896; BL = 183.72. H, Alaska wolf KU 157331; BL = 241.0. I, Australian Dingo ANM S-1885; BL = 181.89. J, Pekingese WSU-VA-C910-32; BL = 76.06.

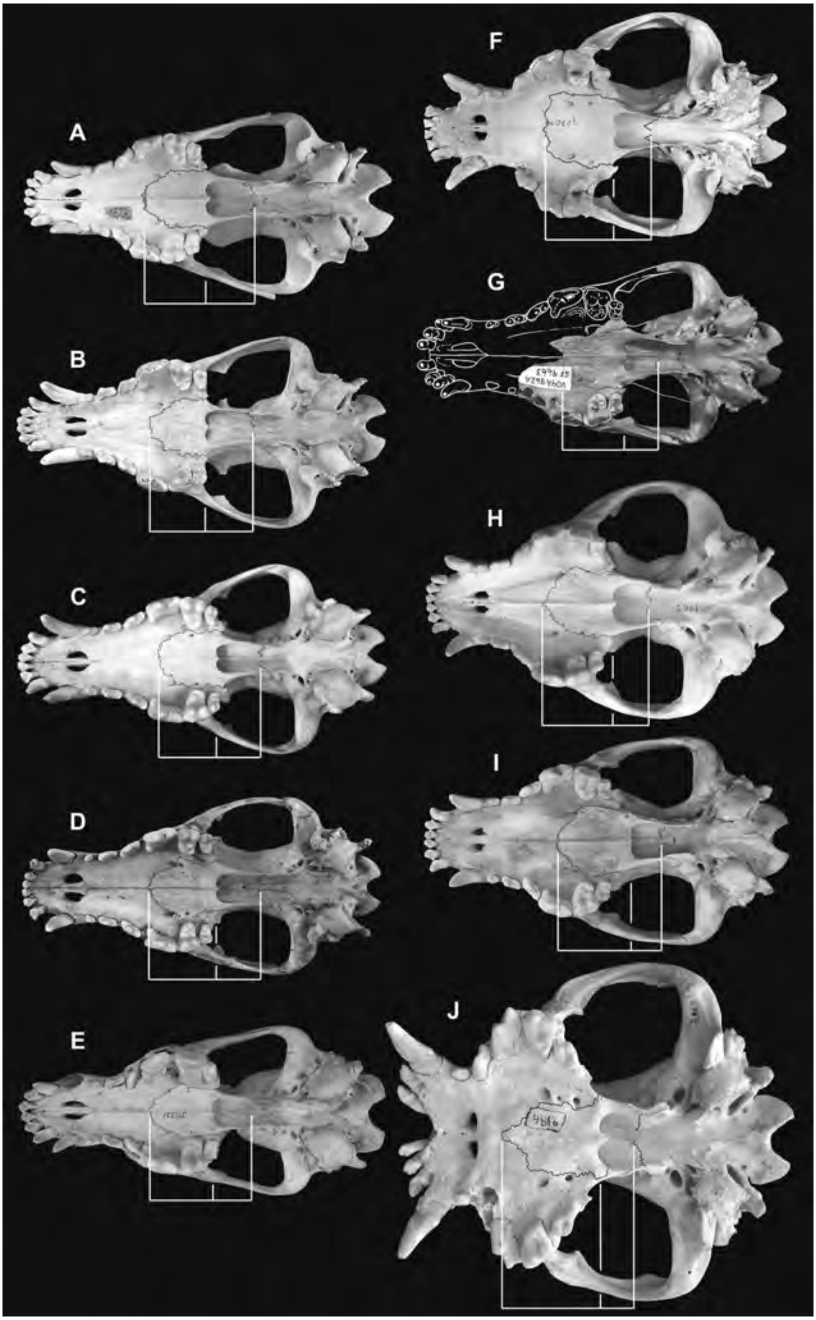

FIGURE 16

Visual comparison showing the spectrum of juvenilization in utility and guard dogs. Brackets superimposed on each image show the juvenilization algorithm (Px × 100 compared with CP). Skulls are not to scale, but are reduced to the same BL, and are ordered from longest Px (least juvenilized) to shortest Px (most juvenilized). Sutures have been highlighted for ease of comparison. Of these large dogs, only the Great Dane (view A), which has Px longer than Eurasian wolves, can be said to be "anti-juvenilized". Many guard and utility dogs have short Px; the Presa Canario and Mastiff (views H and I) are as juvenilized as the English Bulldog (view J).

A, Great Dane MU no. 92; BL = 272.02. B, Mexican wolf MSB 83337; BL = 206.54. C, Chinese Wolf SKU 7360; BL = 197.92. D, Tribally-bred Kuvasz FMNH 57252; BL = 200.7. E, Tuscan wolf QSLD J-11331 (this specimen is a subadult, so juvenilization may be higher than an adult); BL = 179.76. F, Rottweiler CAS 30704; BL = 217.94. G, Vindolanda V04A 862; BL = 192 (estimated from restoration). H, Presa Canario SKU 1489-20875; BL = 156.2. I, Mastiff KU 147390; BL = 191.94. J, English Bulldog YPM 7988; BL = 117.51.

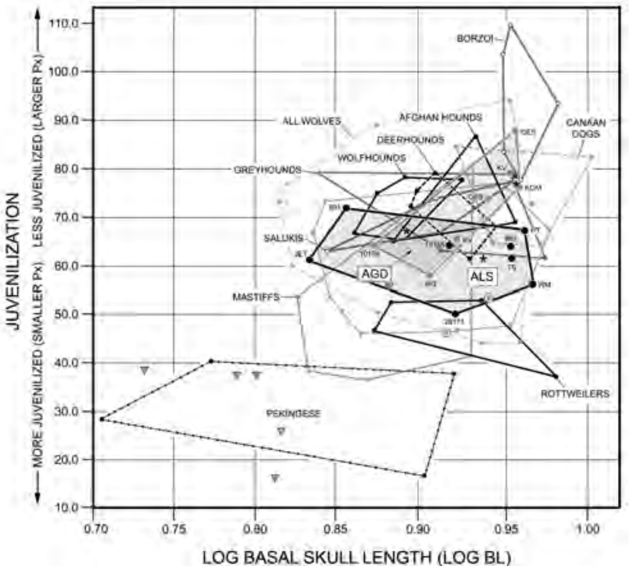

FIGURE 17

MTA chart showing juvenilization. Note that unlike Figures 15 and 16 which show only one representative specimen of each kind of dog, all available specimens are plotted here. There is a good deal of overlap between the ALS and AGD groups because both sighthounds and guard dogs show a spectrum of juvenilization. Borzoi among all sighthounds and Old English Sheepdog among all guard dogs have the longest Px, while Vindolanda 29171 among all sighthounds and Vindolanda 862 among all guard dogs have the shortest Px. Rottweilers, Mastiffs, Presa Canario, and English Bulldogs have the shortest Px of utility dogs, some well down into the Pekingese range. In general, the Vindolanda and other archaeological dogs tend to be more conservative than modern dogs which plot farther toward the extremes. Asterisk symbol = Great Danes; gray triangle, English Bulldogs.

Limb bones are more useful for distinguishing ALS from AGD's than are skulls; the two groups always plot disjunctly. The Wolfhound–Deerhound–Borzoi triad is also always separate from the genetically related Greyhound (Von Holdt *et al.*, 2010; Parker *et al.*, 2017), which plots instead near ALS, Afghan Hound, and Salukis. Canaan Dogs are variable and may plot either with the ALS or the AGD group, or disjunctly.

In addition to MTA analyses (Figures S29–32), we compare archaeological long bones with a standard set of modern breeds (Figures S18–23). We compare humerus and femur for both ALS and AGD's, but there are no images in the literature of radii or tibias of archaeological dogs assignable to AGD, and Vindolanda also happens to have produced none so far.

Limb indexes for archaeological dogs are widely reported, and visual comparison makes the practical meaning clear—ALS are gracile whereas AGD's are robust. In this respect, ALS resemble wolves (their ancestors) and dingoes (their unselected relatives), but AGD's do not (Figure 21). Indexes for all sighthound humeri and femurs average 7.36 and 6.28 respectively, whereas the average for guard dogs is a noticeably more robust 8.72 and 8.02 (Table 1).

Species or Breed	Limb Index Average	Range	Sample Size n = x
HUMERUS Sighthound Comparisons			
North American Wolf (*Canis lupus*)*	7.18	6.33–7.94	n = 19
Indian Wolf (*Canis lupus pallipes*)	7.79	7.22–8.66	n = 4
Mexican Wolf (*Canis lupus baileyi*)	7.97	7.22–8.90	n = 13
Australian Dingo (*Canis familiaris dingo*)	7.32	6.52–8.53	n = 25
Saluki	6.60	6.12–6.87	n = 4
Irish Wolfhound	8.53	——	n = 1
Borzoi	7.86	——	n = 1
Scottish Deerhound	7.31	——	n = 1
Greyhound	6.51	6.40–6.61	n = 2
Afghan Hound	6.5 estimate from photo	——	n = 1
Praetorium Sighthound V1997-19 16742	6.92	——	n = 1
VK–5 10130	7.45	——	n = 1
V06-34A 555	6.8 est	——	n = 1
Warmington	7.78 estimate from photo	——	n = 1
Tepe Sarab	7.83	——	n = 1
Sighthound average	7.36	6.12–8.90	n = 15

HUMERUS Guard Dog Comparisons			
German Shepherd	8.82	8.04–9.89	n = 5
St. Bernard	9.40	9.21–9.59	n = 2
Hungarian Komondor	8.50	——	n = 1
Presa Canario	9.19	——	n = 1
American Mastiff	8.89	8.29–9.49	n = 2
Rottweiler	9.50	——	n = 1
Old English Sheepdog	8.84	——	n = 1
Canaan Dog	7.73	7.07–8.40	n = 2
V04A 994	8.81	——	n = 1
V04A 996	8.16	——	n = 1
Heidelberg Grosshund	8.1 estimate from photo	——	n = 1
GUARD DOG average	8.72	7.07–9.89	n = 11
RADIUS Sighthound Comparisons			
North American Wolf*	8.08	6.77–9.06	n=38
Indian Wolf	7.79	7.30–8.58	n = 3
Mexican Wolf	7.69	6.89–8.41	n = 13
Australian Dingo	7.94	7.02–8.48	n = 25
Saluki	6.64	6.39–7.10	n = 4
Irish Wolfhound	7.99	——	n = 1
Borzoi	6.67	——	n = 1
Scottish Deerhound	7.79	——	n = 1
Greyhound	7.14	7.04–7.24	n = 2
Afghan Hound	7.2 estimate from photo	——	n = 1
Doberman Pinscher	8.37	——	n = 1
Irish Setter	7.07	——	n = 1
Praetorium Sighthound V1997-19 16742	7.23	——	n = 1
V04A 1010	7.47 est	——	n = 1
Warmington	7.2 estimate from photo	——	n = 1
Tepe Sarab	6.66	——	n = 1
SIGHTHOUND average	7.43	6.39–9.06	n = 17
FEMUR Sighthound Comparisons			
North American Wolf*	6.80	5.86–7.93	n = 22
Indian Wolf	7.26	6.72–7.79	n = 4
Mexican Wolf	7.58	6.89–7.92	n = 11
Australian Dingo	6.96	6.45–8.54	n = 25
Saluki	6.08	5.79–6.27	n = 4
Irish Wolfhound	7.06	——	n = 1
Borzoi	6.78	——	n = 1
Scottish Deerhound	6.53	——	n = 1
Greyhound	6.38	6.19–6.57	n = 2
Afghan Hound	6.8 estimate from photo	——	n = 1
Praetorium Sighthound V1997-19 16742	6.40	——	n = 1
VR–104 3158	6.40	——	n = 1
Warmington	6.40 estimate from photo	——	n = 1
Tepe Sarab	6.89	——	n = 1
SIGHTHOUND average	6.28	5.86–8.54	n =15
FEMUR Guard Dog Comparisons			
German Shepherd	7.57	7.08–8.40	n = 5
St. Bernard	8.85	8.66–9.04	n = 2
Hungarian Komondor	7.65	——	n = 1
Presa Canario	8.09	——	n = 1
American Mastiff	7.48	7.05–7.92	n = 2
Rottweiler	8.57	——	n = 1
Old English Sheepdog	8.17	——	n = 1
Canaan Dog	6.94	6.43–7.45	n = 2
II85–E7A 2841	8.90	——	n = 1
GUARD DOG average	8.02	6.43–9.04	n = 9
TIBIA Sighthound Comparisons			
North American Wolf*	18.87	17.00–19.79	n = 18
Indian Wolf	18.76	16.88–19.62	n = 4
Mexican Wolf	21.45	19.32–22.63	n = 11
Australian Dingo	18.89	17.23–20.04	n = 24
Irish Wolfhound	20.24	——	n = 1
Saluki	24.55	23.30–26.16	n = 4
Borzoi	15.87	——	n = 1
Scottish Deerhound	16.99	——	n = 1
Greyhound	18.24	18.09–18.40	n = 2
Afghan Hound	17 estimated from photo	——	n = 1
Vindolanda Sighthound V1997-97 16742	17.45	——	n = 1
VJ–4 10116	17.90	——	n = 1
Warmington	16.88 est from photo	——	n = 1
Tepe Sarab	16.96	——	n = 1
SIGHTHOUND average	17.36	15.87–26.16	n =14

* combined eastern, midwestern, western, and Alaskan wolves.

TABLE 1
Limb Indices: average, range, sample size for four major limb bones.

Integrated Skull–Skeleton or "Whole-Body" Comparisons

(1) *The Uphill Dog* (Figure 19): Utilizing our full database of over 100 archaeological, wild, feral, landrace, and domestic skeletons, we compared the ratio of radius to femur against withers height estimated as an average of humerus, radius, femur, and tibia. This revealed eight functional groups—Asian sighthounds (Sighthound Group 1), European sighthounds (Sighthound Group 2), utility dogs, bulldogs, robust terriers (RT's), small dogs, dwarfs, and miniatures. All ALS and Greyhounds cluster with the Asian sighthound group, while all AGD's cluster with the utility group, of which they constitute a sub-group. There is considerable overlap between the larger utility dogs and Asian sighthounds, and minor overlap between utility and small dogs, and also between small dogs and bulldogs. Of dogs that are below average height, 58 or 89% plot above the line of regression, indicating that they are built more uphill than expected for their withers height. Among dogs that are above

FIGURE 18

Symbol key to dog varieties. Same symbol for each kind of dog is used throughout this report except where specifically noted.

average height, 38 or 77% plot below it, meaning that they are built more downhill than expected for their height.

(2) *The Aerodynamic Dog* (Figure 20): In this analysis, we compare a measure of overall skull size (BL × ZW) to estimated withers height. Sighthounds, especially the Asian sighthounds (Sighthound group 1) plot below the line of regression to a greater degree than other kinds of dogs. ALS plot with this group as they also do in the uphill dog analysis. Of the 98 skeletons analyzed on this chart, 46 (47%) plot on or below the line of regression, meaning that their skulls are at or below the expected volume for their withers height. Of these, 17 (37%) belong to the Asian sighthound group; all of these fall well below the line of regression.

A nearly equal number of utility dogs lie above as below the line of regression (16 and 15, respectively), reflecting the diverse nature of this group (Coppinger & Schneider, 1995). All of the AGD sub-group plot below the line of regression except the very large dog from the Saqqara dog tombs (Ikram *et al*., 2013 and *pers. comm.* 2020). By con-

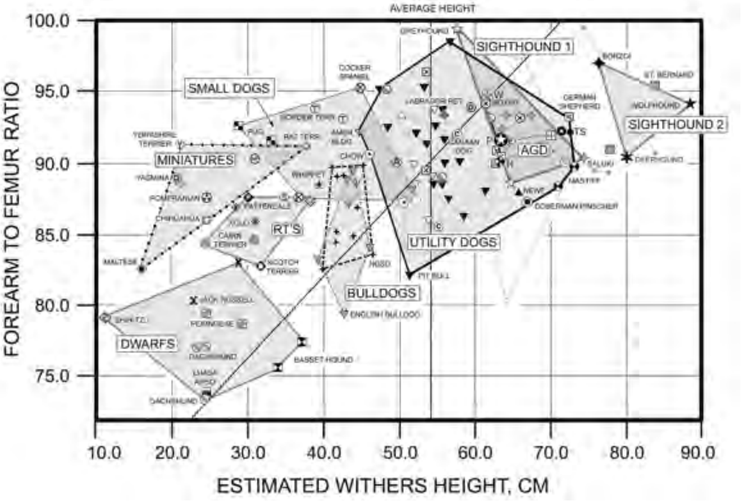

FIGURE 19

The "Uphill dog": MTA analysis. Forearm to femur ratio calculated as (GL radius × 100)/GL femur. Dog varieties are labeled where space permits; for all symbols, refer to Figure 18.

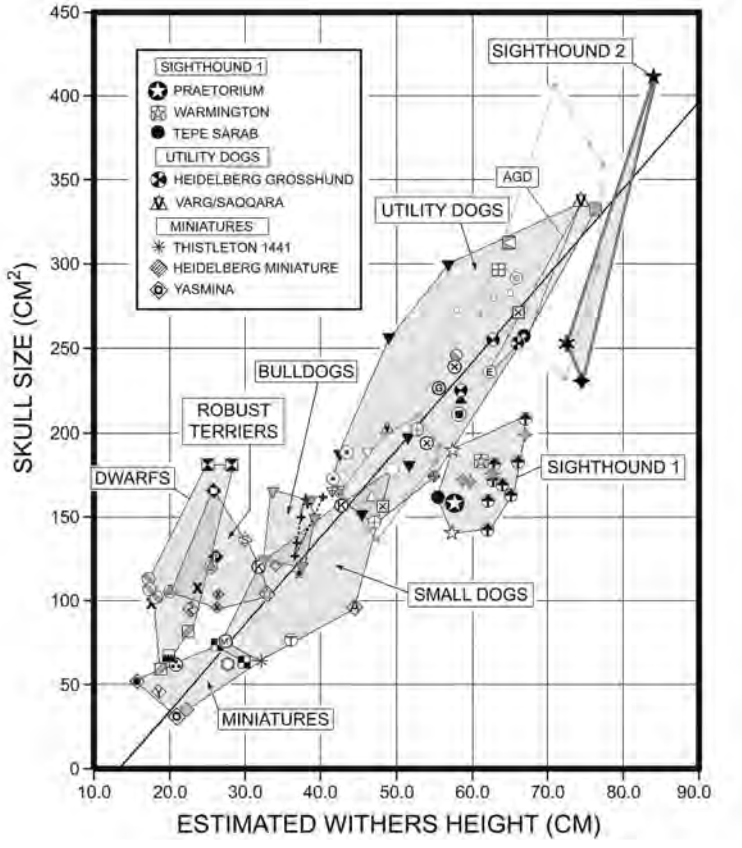

FIGURE 20

The "Aerodynamic dog": bivariate plot of skull size against estimated withers height. Skull size calculated as (ZW × GL). Symbols for all specimens are shown in key Figure 18.

trast, of the 37 dogs belonging to the bulldog, robust terrier, and dwarf groups, a large majority (26 or 70%) plot above the line of regression because their skulls are above the expected volume for their body size.

DISCUSSION

Large Morphological Range

Harcourt's (1974) morphological studies of British dog remains, based as they were on a large sample of archaeological remains from the Paleolithic to the Viking era, are a useful basis for more recent work. Roman-era dogs cover a large size range—data reported for Italy are 26–69 cm in shoulder height (De Grossi-Mazzarin & Tagliacozzo, 2000); Iberia (Colominas, 2016); France 40–62 cm (Méniel, 2001), and Britain, 23–72 cm (Harcourt, 1974; Clark, 1995; Baxter, 2010b). Cram (2000) was the first to demonstrate definite increase in dog diversity beginning in the late Iron Age, and subsequently small dogs have been reported from Neolithic sites (Bâlâşescu *et al.*, 2003; Horard-Harbin *et al.*, 2014), and even from a few pertaining to the Upper Paleolithic (Pionnier-Capitan *et al.*, 2011). At the opposite end of the spectrum, dogs with withers heights upward of 54 cm were present in Britain as early as the Neolithic (Clutton-Brock, 1963; Harcourt, 1974; Clark, 1996; Frantz *et al.*, 2016). Horard-Herbin *et al.* (2014) notes that very large dogs are relatively rare in continental Europe, but nonetheless cites a few finds.

These dogs are also distinct in various bodily proportions both from wolves and from the unselected and very ancient type represented by the Australian Dingo (Lüttschwager, 1965; Corbett, 1995; Salvolainen *et al.*, 2002, 2004; Smith & Litchfield, 2009; Oskarsson *et al.*, 2011; Bennett *et al.*, 2016; Bennett & Timm, 2016, 2018; Fillios & Taçon, 2016; Koungoulous & Fillios, 2020; and see Figure 21). Dogs with morphology specialized for hunting, guarding, coursing, or fighting certainly existed in Britain from the late Iron Age onward (Cram, 1973, 1978, 2000; Harcourt, 1974; Clark, 1995, 2012; Baxter & Nussbaumer, 2009; Phillips *et al.*, 2009; Schoenebeck *et al.*, 2019).

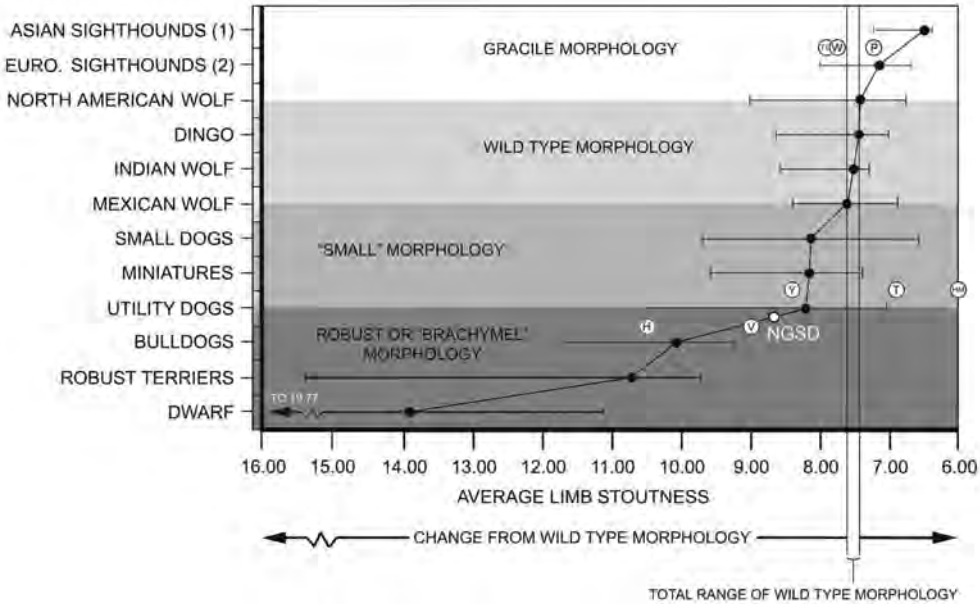

FIGURE 21

Chart showing change from wild type limb morphology in 12 different types of canids. Note that limb indexes for the Dwarf group extend far to the left. Dots represent averages from our dataset, lines give the range. Abbreviations: NGSD = New Guinea Singing Dogs. TS = Tepe Sarab; W = Warmington; P = Vindolanda Praetorium sighthound; Y = Yasmina (data from MacKinnon & Belanger, 2000); T = Thistleton 1441 (data from Baxter, 2010a, 2010b); HM = Heidelberg miniature (data from Baxter, 2010b); H = Heidelberg "grosshunde" (data from Luttschwager, 1965); V = "Varg" from the Saqqara dog tombs [data from Salima Ikram, *pers. comm*. (2020)].

All Analyses are Not Created Equal

A large database containing skull–mandible and skull–skeleton specimens has proven to be essential for confident placement of archaeological dog remains, especially where these consist of isolated skulls, jaws, or major limb bones. Herein, we use proportional analyses (MTA's and bivariate plots) because they are effective at separating dog morphotypes, interpretation of results is straightforward, and the studies are non-destructive and require no special equipment or expensive software. With the aid of PAST freeware (Hammer *et al.*, 2001) they can also easily be applied in the field.

This does not mean that all such analyses are of equal efficacy in separating dog morphotypes. Measured parameters cannot usefully be selected at random, but rather should be chosen with an eye to their potential to demonstrate functional significance. Some analyses make use of features diagnostic for only some kinds of dog—for example the "bugeye" and "Tweetiebird" MTA's we previously used to aid understanding of small dogs (Bennett & Timm, 2018) do not appear in this report because they are not useful in differentiating ALS from AGD. Neither is keyholing of the foramen magnum discussed here, because it is relatively rare in large dogs.

Analyses of the Skull

Contrary to Harcourt's (1974) results, we find that morphometric analyses of most skull parameters are weaker differentiators of large dogs than are those involving jaw rami and major limb bones. Cranial index, a measure of overall head shape, along with mouth shape and neck strength, are only moderately efficient at distinguishing ALS from AGD. Analysis of snout length and shape reveals that AGD have broader snouts than ALS while also having shorter basicrania, so that the snout constitutes more of the total length of the skull. Conversely, in ALS the basicranium is long, so that the Warmington specimen has a snout not only proportionally shorter than any Vindolanda sighthound, but shorter than any AGD.

The high position of the junction between frontal, maxilla, and nasal bones in the Warmington dog (Schoenebeck *et al.*, 2019) is not a cause, but may be a reflection, of its relatively short snout. This feature also appears in a very large dog of Neolithic date from Staines Road Farm (Clark, 1996), suggesting that a high placement of the junction might have been more common earlier in time; we find that it is rare in modern breed dogs as well as dingoes and wolves.

There is a causative and functionally meaningful relationship between the length of the base of the braincase (hirstammbasis, HB (Fig. 1) (Lüps, 1974) and the slope of the occiput that has proven to be useful to differentiate both dogs and equines (Bennett, 1980). Sighthounds are the only modern dogs that have backsloping occiputs. The occiput in small sighthounds slopes more strongly backwards than in large sighthounds; small sighthounds also have minimal cresting (Bennett & Timm, 2018). The skulls of large Asian sighthounds also have only moderate cresting and rounded braincase shape in rear view (Figures 7 and S11). Occiputs of the big European sighthounds, however, show heavy cresting which defines a rugose triangular or sub-rectangular shape and which largely blocks the braincase from view (Figure S12). Guard dogs, both ancient and modern, have heavy cresting and likewise a wolf-like, triangular shape to the occiput in rear view (Figures 7 and S13).

A backsloping occiput predicts greater length in the axis and atlas and a more open resting angle between the skull and neck bones, yielding a more wide-open throatlatch, particularly evident when the animal is running (Bennett, 1980; Clark, 2012; Bennett & Timm, 2018). Since in mammals inspired air must pass through the pharynx before it can get to the lungs, a wide-open throatlatch is of obvious functional advantage to a dog intended for chasing game. Guard dogs are not cursorial, but are bred instead for massiveness and strength. Their occiputs are tucked under heavy lambdoidal cresting on a relatively large skull, which gives plenty of space for the attachment of powerful neck muscles.

Analyses of Jaw Shape and Dental Wear

Sighthounds, both ancient and modern, present jaw rami that are shallow and straight or slightly bowed, while those of AGD are deep and rockered (Figures 11, 12). This is a direct consequence of degree of klinorhynchy vs. airorhynchy (Bennett & Timm, 2018). It is important to note that no known ancient dog is positively airorhynchic, but there are many individuals with zero to only a few degrees of klinorhynchy, and these may be said to be "incipiently airorhynchic" (Phillips *et al*., 2009); into this category fall AGD's. By contrast, when klinorhynchy is measured at 9 degrees or more, the jaw rami are straight or may even be bent downward at the anterior end ("chinned"). Klinorhynchy of from 6 to 15 degrees is characteristic of large sighthounds; modern representatives of this group frequently measure at the high end of this range. Small sighthounds, however, tend to be straight-headed to only slightly klinorhynchic (Bennett & Timm, 2018), indicating that small sighthounds are not merely like females of large sighthounds but rather functionally a completely different kind of dog.

The jaw rami of ALS vs. AGD also differ in their proportions—the anterior part of the jaw, between the carnassial and the canine, is long in ALS, whereas the anterior part of the jaw in AGD's is proportionally shorter (Figures 11–13). Both ALS and AGD show anterior premolars "spaced out" along the jaw, so that the mere spacing of the teeth does not separate these two very different morphotypes. For example, Clark (1996) indexes tooth spacing but wisely does not use it to identify different kinds of large Neolithic dogs. Degerbøl (1961) and Van Wijngaarden-Bakker (1974) both recognize the need to calculate jaw proportions as well as proportional size of the teeth, because it is a combination of both factors that determines whether the teeth will be spaced or crowded.

Tooth wear stage at death (Horard-Harbin, 2000) is consistently greater in Roman-era and Iron Age guard dogs than in large sighthounds from the same time period. It also tends to be greater in the Vindolanda sample. This may indicate that AGD are longer-lived than ALS, or that they were fed a different diet. Baxter (2007) also notices moderate to heavy wear on the teeth of large, robust archaeological dogs and characterizes them as "habitual bone-crunchers". Crockford (2000b) suggests that wear on the molar teeth parallel to the gumline is characteristic of European dogs while Asian dogs show heavy concave wear on the lingual surfaces of molar teeth. Both ALS and AGD from Vindolanda appear to show the European wear pattern. No Vindolanda dog has heavy concave wear on the molar teeth, indeed the molar teeth in all specimens appear a little less worn than the carnassial just in front of them. Heavy tooth wear may also reflect developmental constraints. Just as small dogs have teeth larger than expected for body size because teeth to not miniaturize at the same rate as the skull and jaws (Clark, 2016; Bennett & Timm, 2018), they also do not enlarge as fast as skull size and large dogs thus have smaller than expected teeth. Whether smaller teeth equate to weaker teeth that wear out sooner is unstudied.

Analyses of Major Limb Bones

The ALS and AGD groups plot disjunctly for all four major limb bones (Figures S29–S32), and thus limb bones are very useful for telling these sorts of dog apart. Limb bones of ALS are in fact hard to mistake for any other dog morphotype because they are large in scale as well as slender (Figures S18, S20, S21, S23). Large sighthounds are similar to wolves in this respect; the average limb index for ALS (humerus, radius, and femur combined) is 7.02, while the same average for wolves (all species combined) is only a little larger at 7.57. Guard dogs have noticeably stouter limbs (Figures S19, S22); the average index (humerus and femur combined) is 8.37 (Table 1, Figure 21).

Proportional differences from wolves, whether in skull or skeleton, are likely due to selection; ALS appear to be a direct development in one direction from an original wild-type morphology, while AGD are a development in the opposite direction (Figure 22). Dogs with limb indexes equal to or less than wolves and standing over 54 cm at the withers date back to the Neolithic in Britain; Harcourt (1974) cites one from Nympsfield Long Barrow with estimated height of 62 cm, and Clutton-Brock (1963) mentions a dog from Quanterness, Orkney that stood 55–57 cm. We consider the large and wolf-like Neolithic canid reported by Clark (1996) from Staines Road Farm to be a dog because its upper carnassial, which measures 20.8 mm, is below the wolf threshhold of 22 mm (Bennett *et al.*, 2016). We estimate this skull measured 225 mm from inion to incisivus, big enough to fall within the range of Indian wolves. The Staines Road Farm skull is not only larger but proportionally broader than either the Vindolanda Praetorium or the Warmington dog (Figure 22)—but it is narrower than wolves, so can be regarded as an "incipient" sighthound.

Guard dogs are more different from wolves than are large sighthounds, and their antiquity appears

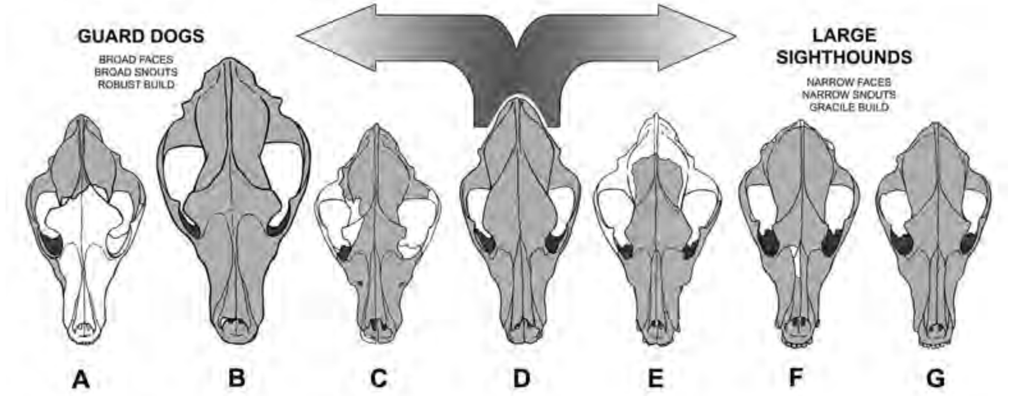

FIGURE 22

Large sighthounds and utility/guard dogs represent departures in opposite directions from an ancestral wolf-like morphology. A, Vindolanda V04A 862, dated to about 250 CE; GL = 240 mm (est). B, "Varg", a guard dog from the Saqqara dog tombs, dated to between 150 BCE and 100 CE; GL = 279 [Salima Ikram, *pers. comm.* (2020)]. C, Guard dog from a "Classical Period" Armenian grave, dated to between 600 BCE–301 CE; GL = 215 (estimated; after Manaseryan, 2016). D, Indian wolf (*Canis lupus pallipes*) FMNH 44469, GL = 242.42. E, a late Neolithic sighthound from Staines Road Farm, GL 225 (estimated; after Clark, 1996). F, the Warmington sighthound, GL = 191, dated to 50–100 CE (after Schoenebeck *et al*., 2019). G, the Vindolanda Praetorium sighthound dated to about 250 CE; GL = 190.00.

to be less. Manaseryan's (2016) big dog from a Classical Period burial site in Armenia may be the earliest known guard dog, with a date somewhere between 600 BCE–301 CE. Kitagawa (2013) reports six specimens above 61 cm, including one standing 72 cm at the withers, from the Roman-era Tomb of the Dogs in Egypt; and Ikram reports a massive specimen of 75 cm estimated shoulder height from the dog tombs at Saqqara that dates to between 150 BCE–100 CE (Ikram, *pers. comm.*, 2020) (Figure 22).

Measures of Overall Build and Functioning

Skulls with associated long bones are indispensable for elucidating relationships among modern and archaeological dogs, because skull and skeleton have frequently been subject to different selective pressure. We find, for example, that ALS have wolf-like skeletons but narrow, un-wolflike skulls, whereas AGD have skeletons noticeably more massive than any wolf but retain (or imitate) a wolf-like skull. Among modern breed dogs, there are many kinds which are brachycephalic; some of them are huge and massive (Presa Canario, French Mastiff, St. Bernard); some are medium-sized and stout (English Bulldog); while some are relatively gracile (Boxer). There are also many dolichocephalic dogs, including not only sighthounds, Great Danes, and Irish Setters, but also achondroplastic forms such as Dachshunds, Welsh Corgis, and Bassett Hounds whose short, thick limb bones are in stark contrast to those of gracile sighthounds.

Overall, our "uphill dog" analysis predicts that taller dogs will have a higher forearm to femur ratio—in other words they are built to stand higher in front, although less so in most cases than might be expected on the basis of size alone. Thus, uphill build is not merely the product of allometry but probably due to selection. The most uphill dogs are also cursorial, and speed in cursorial mammals is enhanced when the forelimbs are long (Hildebrand, 1974; Bennett, 2013). Small dogs by contrast (especially Dwarfs) are built to stand lower in front, although in most cases they are built less downhill than might have been expected on the basis of size alone, once again pointing to selection as a cause. Note that outgroup comparisons (wolves and dingoes whose hulls appear in the background of all of our MTA's) are generally above average in height; they are chase hunters and may be built as much or more uphill than sighthounds.

Sighthounds along with wild and feral chase hunters benefit from having proportionally small, lightweight heads, paralleling the difference between draft horses and racehorses or between lions and cheetahs. Our "aerodynamic dog" analysis indicates overall that larger dogs have larger heads, but cursorial sighthounds much more often plot below the line of regression, indicating that their relatively small heads are the result of selection, not mere allometry. Our analyses (discussed above) show that grip strength in sighthounds is not particularly great; these dogs sacrifice grip strength in favor of aerodynamic functioning. Bulldogs, utility dogs, and robust terriers, which are bred for jaw grip strength, benefit from having relatively large heads and they most often plot above the line of regression. In dwarf dogs, a proportionally large head reflects development mediated by chondrodysplasia which causes their limb bones to thicken and stop growing early, while it does not inhibit the overall growth of the skull (Parker *et al*., 2009).

Our “uphill” and “aerodynamic” analyses both produce the same eight clearly defined clusters. That these analyses compare completely different Y axis parameters yet yield the same results, indicates that the eight clusters have real functional meaning. This is further indicated by results from limb bone and jaw analyses. That these same groups are ancient is shown by the fact that particular archaeological dogs (Praetorium sighthoundhound, Warmington, Heidelberg grosshunde, Yasmina, and Thistleton 1441) plot similarly in each analysis where they appear. It is desirable for zooarchaeologists to think in terms of functional groups rather than breeds, because breed registries and kennel clubs did not exist before the mid-19th century. In this paper, we have endeavored to find terminology for the various groups that does not imply breed affinity or ancestor–descendant relationship. We look to researchers working with DNA to elucidate to what degree our functional groups coincide with or predict genetic similarity or relatedness, and we look forward to seeing our work tested in this way (Larson *et al*., 2012).

Juvenilization in Large Dogs

In our previous work we demonstrated that some recent dog breeds are juvenilized, and that incipient juvenilization (relatively short Px) can be observed in some small dogs of the Roman era and late Iron Age (Bennett & Timm, 2018). However, all juvenilized dogs are not small (for example, the English Bulldog), so size alone does not predict juvenilization.

In the basicrania of juvenilized individuals, the posterior part of the palatine bone (Px) grows very little. In some modern sighthounds and utility dogs by contrast, the palatine bone grows more than is typical of wolves or dingoes. These dogs can be thought of as “anti-juvenilized.” Most ALS are little different from wolves in degree of juvenilization, although dogs that have been subjected to strong selection for large size and/or long heads, such as the Irish Wolfhound and Borzoi, are anti-juvenilized. By contrast, most AGD are juvenilized and juvenilization is evident in both Vindolanda guard dog specimens, V04A 862 and LXXII-VI 10158. Modern breeds, such as the Presa Canario, Mastiff, and English Bulldog, show still greater degrees of juvenilization due to strong selection for shortness of the face, which has in fact affected the entire skull (Drake & Klingenberg, 2008). Juvenilization may also be linked to the development of airorhynchy.

Landrace Dogs of Southwest Asia

We have previously said (Bennett & Timm, 2018) that the west Asian dogs collected by Charles Reed are “of nameless breed but ancient ancestry”—in other words, they represent landraces. A landrace is a population consisting of both fully domesticated and feral animals which is found in a particular geographic area (Zeven, 1998; Casañas *et al*., 2017). Pilot *et al*. (2015) aptly characterize these dogs, which may be owned but which are not permanently restrained, as “free-breeding.” The study of village dogs has highlighted the importance of these populations as a source of genetic health, their morphological and behavioral differences from other populations, and as the source population for southeast Asian and Australian dispersal events (Salvolainen *et al*., 2004; Brown *et al*., 2011; Sacks *et al*., 2013; Shannon *et al*., 2015). Their common characteristic is that, except when they may be temporarily confined by humans, they are not restricted as to mate choice. Tribesmen in many west Asian countries keep dogs in exactly this manner, temporarily controlling the breeding of some with an eye to production of individuals useful for coursing, guarding, fighting, or hunting (Ansari-Renani *et al*., 2013). Dogs are usually let loose at night, and there is rather fluid interchange of breeding stock between different tribes and between domestic and free-roaming subpopulations (Lawrence & Reed, 1983; Shrestha, 2005; Gehring *et al*., 2010; Ansari-Renani *et al*., 2013; Erdogan *et* *al.*, 2013). Casañas *et al.* (2017) observe that "despite being considered by many to be inalterable, landraces have been and are in a constant state of evolution as a result of natural and artificial selection."

In these respects, tribal dog breeding closely parallels tribal horse breeding, although there are now few feral horses (Firouz, 1998, 2015; Erdoğan *et al.*, 2008). Landraces may exist over time spans from a few to many centuries, and they are particularly characteristic of areas bordering the Silk Road from China west to Syria, which produce a rich array of both dog and horse strains (Barisitz, 2017; Erdoğan *et al*., 2008). Firouz (2015) notes that "the unusual richness of many breeds of horses peculiar to Persia has been largely neglected by scholars," and notes that this is "a distinct pity, as the 20th century has seen a decline in horse populations in this area, affecting the general standard of the breeds and causing the total disappearance of some." Landrace dogs have shown a similar pattern; Yilmaz and colleagues have mapped the occurrence of many now-rare Turkish and north Iranian breeds used for guarding, hunting, and fighting (Hughes & Madconald, 2013; Yilmaz *et al.*, 2015; Yilmaz, 2018). The decline in numbers of live animals translates to a dearth of museum specimens, making Charles Reed's Field Museum collection of landrace and tribally-bred dogs and Indian wolves all the more valuable.

Migration of Asian Dogs to Europe

Vindolanda specimens that we have previously studied are morphologically similar either to old breeds or else breeds thought to have originated within a short geographic distance from the Vindolanda site (Bennett & Timm, 2018). Thalmann *et al*. (2013) and Thalmann & Perri (2018) present genetic evidence implying that indigenous, genetically distinct varieties of dogs were already present in Europe before the Neolithic. Studies of dog tracks impressed into tile suggest that dogs at the Vindolanda site were commonly let loose at night, giving them ample opportunity to breed with self-selected mates (Higgs, 2001; Bennett, 2012). Botiqué *et al.* (2017) argue for genetic continuity among European dogs, and it is reasonable that indigenous British dogs would constitute the founder populations for Iron Age and Roman-era breeding. Horard-Herbin *et al*. (2014) concludes that indigenous European dog bloodlines were never entirely replaced. However, there is no question whether new kinds of dog arrived in Europe during the late Neolithic (Salvolainen *et al.* 2013), and we find that dogs from southern Turkey, northern Iran, Azerbaijan, and Iraq consistently present the closest morphological comparisons to Vindolanda specimens (Bennett & Timm, 2018).

Baxter & Nussbaumer (2009), Phillips *et al.* (2009), and Schoenebeck *et al.* (2019) echo our results in finding strong morphological similarities between Romano–British specimens and modern dog breeds whose origins lie in Asia. Horard-Heerbin *et al*. (2014) and Thalmann & Perri (2018) conclude that dogs of paleolithic Europe were probably partially replaced by dogs arriving from the east, and this view is echoed by linguists who note that livestock with novel genetics might have been introduced into Europe, perhaps more than once from the Neolithic onwards, by human populations migrating from the east (Haak *et al*., 2015). Genetic and biogeographic reconstruction of ancestral distributions by Dubleya *et al*. (2015) and Pilot *et al*. (2015) likewise indicate westward expansion of dogs indigenous to East Asia to the Middle East and Europe via Central and West Asia, i.e., along the Silk Road routes (McLaughlin, 2016). In the heyday of the Roman Empire, enormous trading reach was also undoubtedly a factor, so that the Vindolanda dogs or their immediate ancestors may well have been sourced from areas along the Silk Road (Reed, 1961, 1969, 1983; Clark, 2012).

CONCLUSIONS

Integrated skull–skeleton analyses reveal that modern and ancient dogs cluster into eight functional groups which we have labeled European sighthounds, Asian sighthounds, utility dogs, bulldogs, robust terriers, small dogs, dwarfs, and miniatures. The utility dog category is diverse and contains a guard dog subgroup (AGD's). The nearly-complete skeleton of a dog from the 3rd-century Vindolanda Praetorium is that of a large sighthound (ALS) morphologically close to modern Afghan hounds and Salukis. From Vindolanda also come two partial skulls and some isolated limb bones that are large, rugose, and stout and these AGD's resemble the modern Kuvasz and Old English Sheepdog.

Large sighthounds of the late Iron Age and Roman Era are morphologically conservative, differing only moderately from wolves in terms of the length of Px, a measure of juvenilization. Guard dogs differ more, showing definite shortening of Px compared with wolves. Strong selection for developmental and morphological change from wild type (Drake, 2004, 2011; Drake & Klingenberg, 2008) thus appears to have occurred later in time. Likewise, differences in long-bone shape and overall build between wolves and ALS are not very great. AGD's differ more, and archaeological guard dogs, which are found at much lower frequency than dwarf dogs and sighthounds on Iron Age and Roman sites, are probably a later development. Large dogs were present in the European Neolithic, when migration from the east appears to have swamped an earlier, indigenous western European population. This raises the question of whether the Vindolanda dogs represent an amalgam of indigenous and imported bloodlines. We look to future genetic studies to resolve this question.

Extensive morphological comparison carried out in this study enables us to present a clear picture of the extent and kind of morphological diversity produced by west Eurasian and north African breeders at the beginning of domestic dog diversification which began in the Neolithic and intensified during the late Iron Age and Roman Era. Trade and migration are important factors, for where people go their dogs go too. We continue to find intriguing evidence of links between west Asian domestic dog landraces and dogs recovered from Vindolanda and other Iron Age and Roman Era sites in western Europe.

Institutional Abbreviations

AMNH = American Museum of Natural History, New York; ANM = Australian National Museum, Sydney; CAS = California Academy of Sciences, San Francisco; DU = Zooarchaeological collection of the Department of Anthropology, Durham University; FMNH = Field Museum of Natural History, Chicago; HA = Hebrew University of Jerusalem, Israel; KU = University of Kansas Natural History Museum, Lawrence; KSU = Kansas State University School of Veterinary Medicine, Manhattan; LACM = Natural History Museum of Los Angeles County; MSB = Museum of Southwestern Biology, University of New Mexico, Albuquerque; MU = Massey University School of Veterinary Medicine, Palmerston North, New Zealand; MVZ = Museum of Vertebrate Zoology, University of California at Berkeley; QSLD = Queensland Museum of Natural History, Brisbane; SKU = Museum of Osteology, Skulls Unlimited International, Oklahoma City; UCD = Anthropology Department collection, University of California at Davis; UNSM = University of Nebraska State Museum, Lincoln; WSU = Washington State University School of Veterinary Medicine; YPM = Yale Peabody Museum, New Haven, Connecticut.

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This paper is dedicated to the memory of Robin Birley, distinguished scholar, dedicated excavator, inspiring educator, and perceptive scientist.

SUPPLEMENTARY MATERIAL

See supplementary material at https://revistas.uam.es/archaeofauna/article/view/archaeofauna2021_010/suplemmentary.

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SUPPLEMENTARY MATERIAL

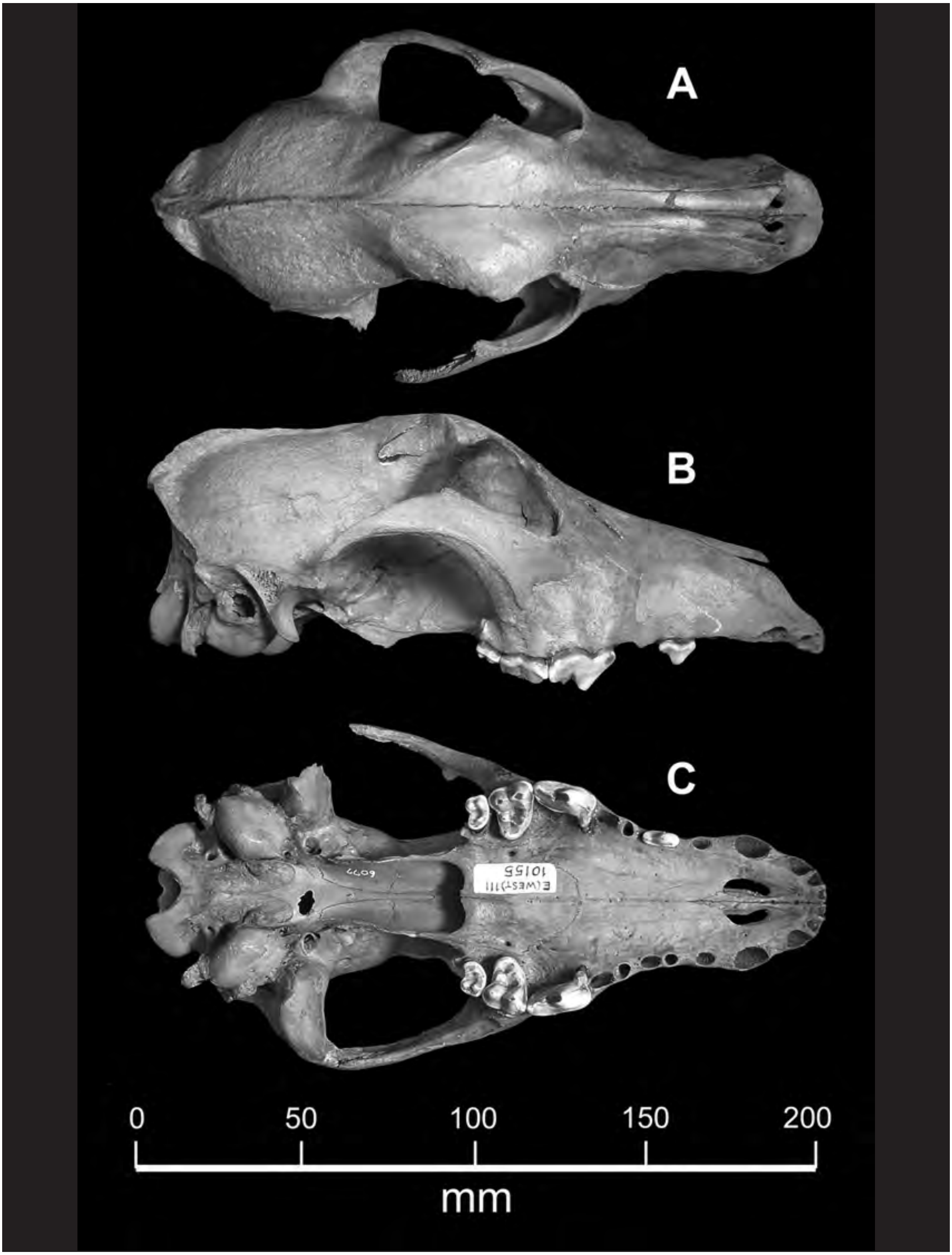

FIGURE S1

Vindolanda sighthound E(W)-111 10155. A, dorsal view; B, right lateral view; C, ventral view.

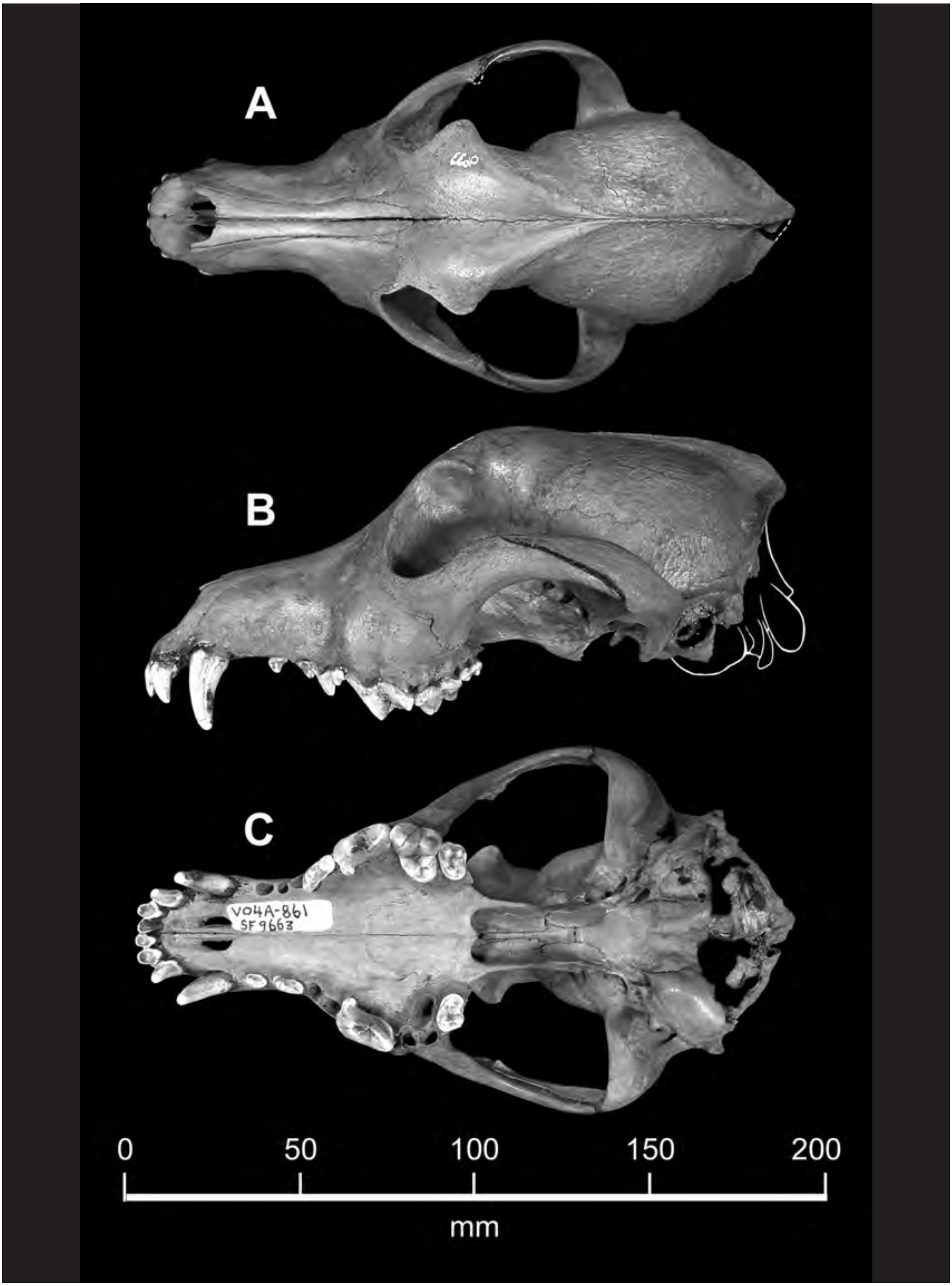

FIGURE S2

Vindolanda sighthound V04A 861. A, dorsal view; B, left lateral view with anterior premolars restored from the opposite side; C, ventral view. Restored portions of occiput shown in white line.

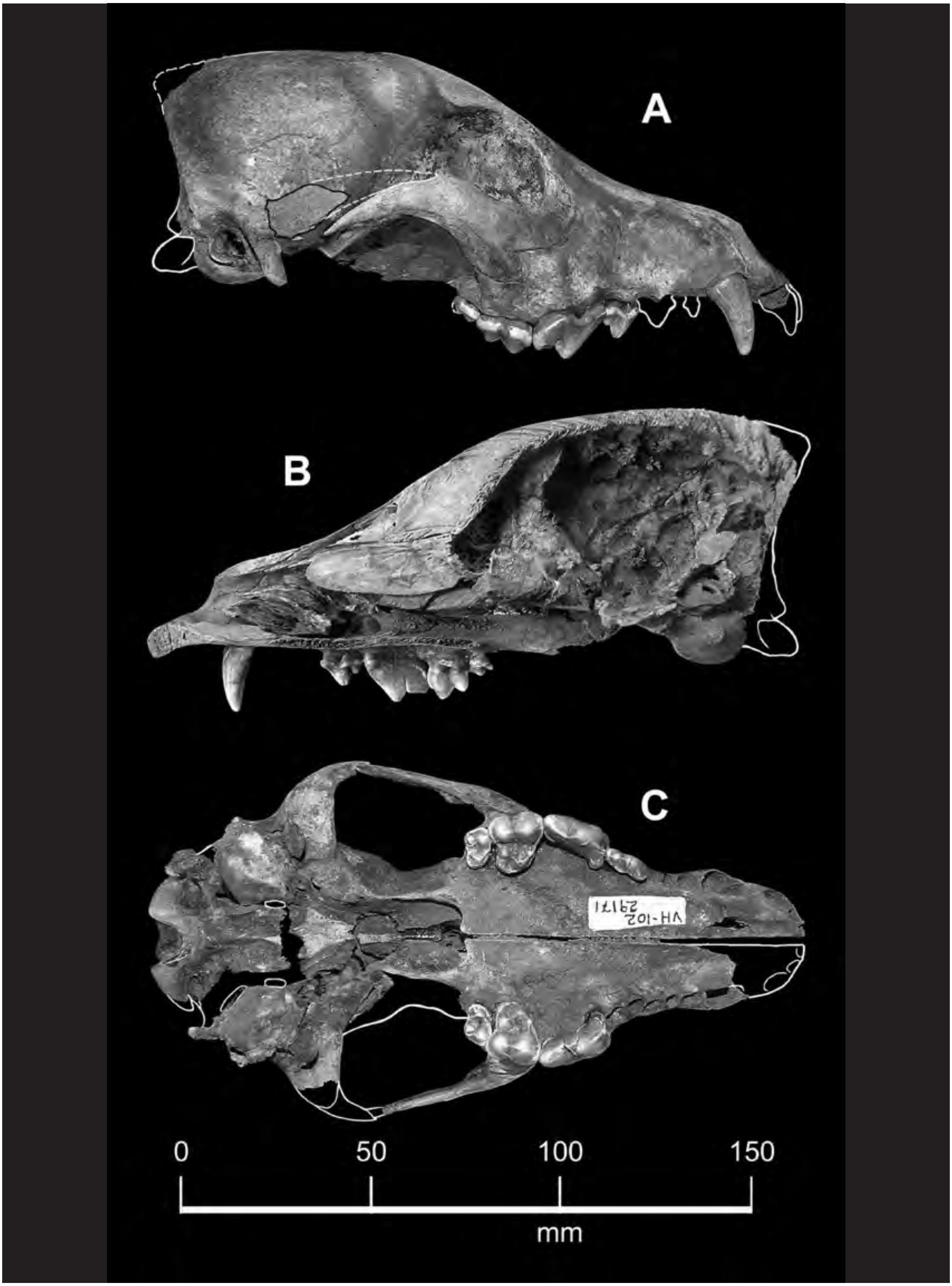

FIGURE S3

Vindolanda sighthound VH-102 29171. A, right lateral view; B, left lateral view showing the internal anatomy of the right half of the skull; C, ventral view.

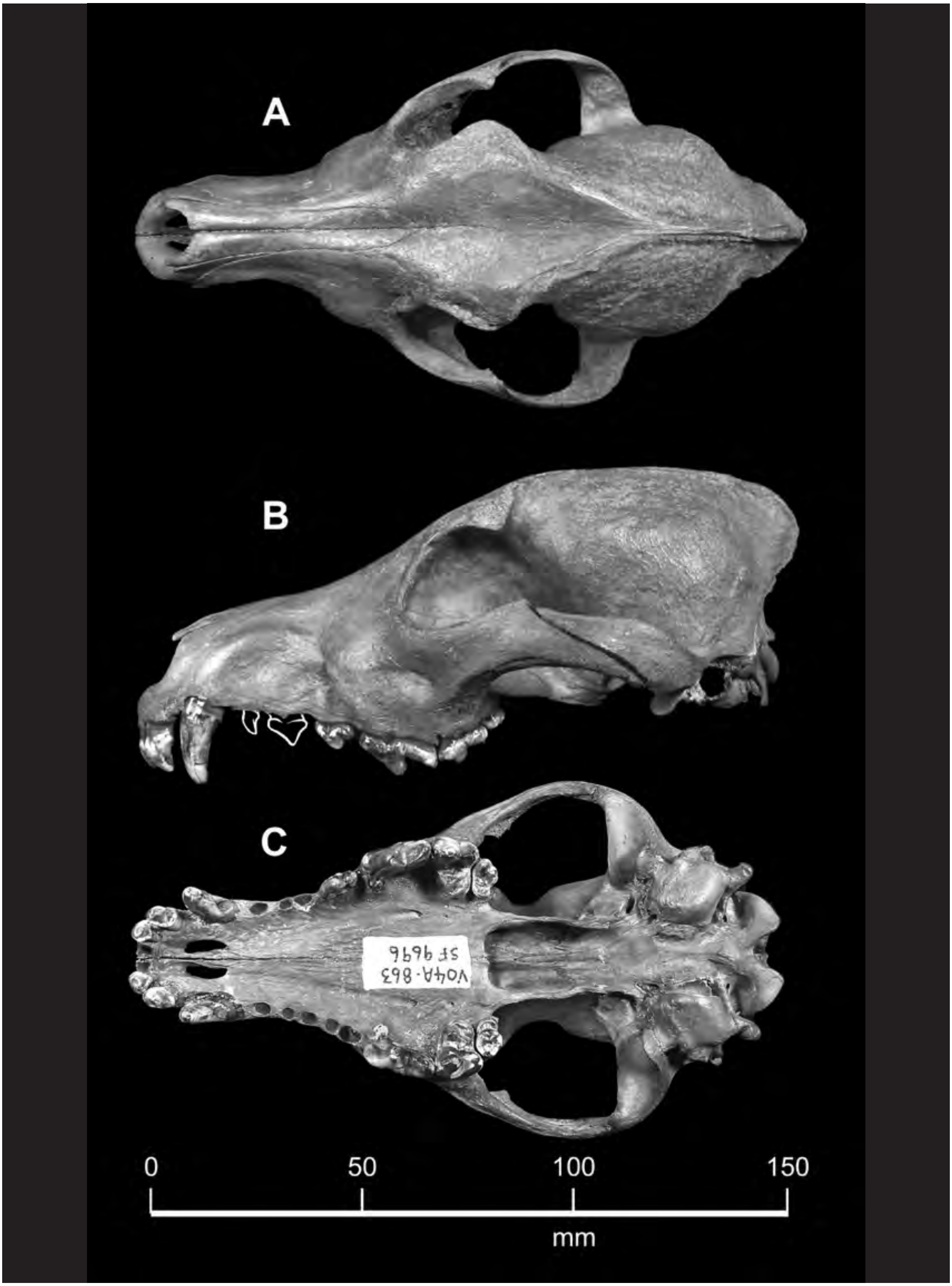

FIGURE S4
Vindolanda sighthound V04A 863. A, dorsal view; B, left lateral view; C, ventral view.

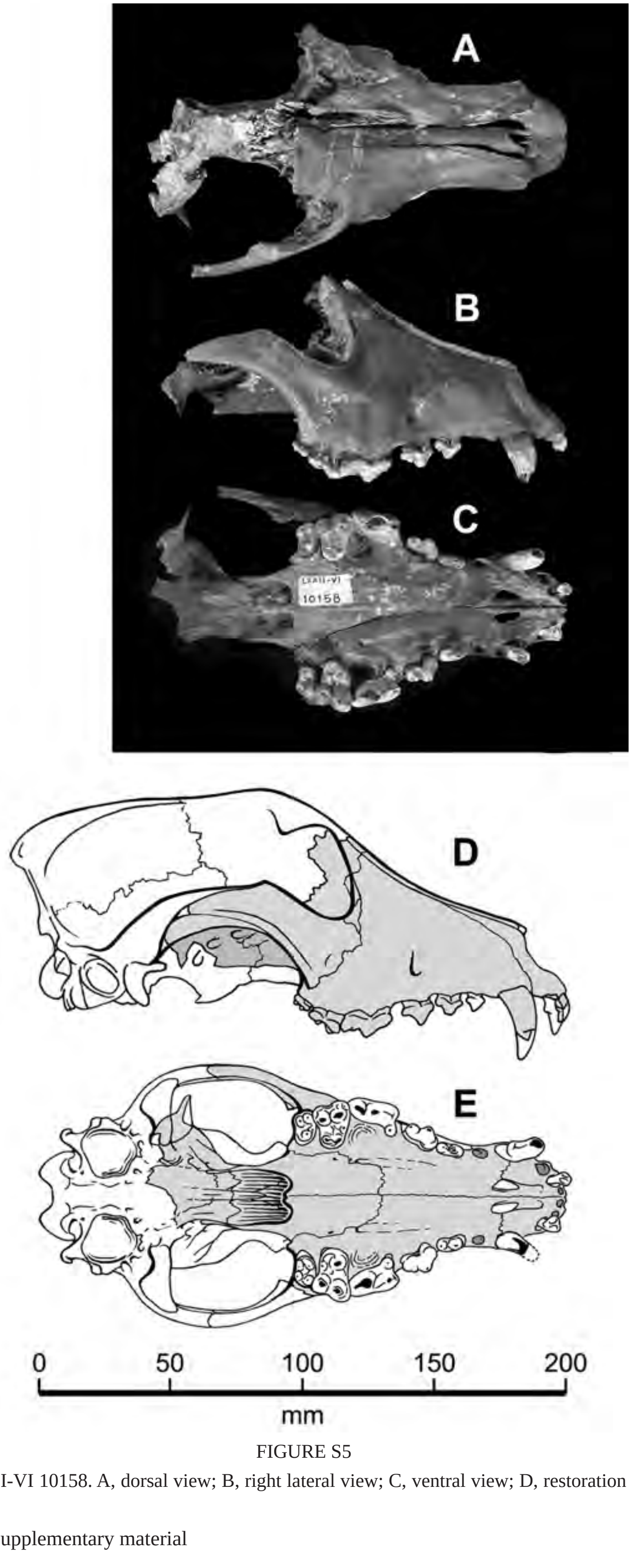

FIGURE S5

Vindolanda guard dog LXXII-VI 10158. A, dorsal view; B, right lateral view; C, ventral view; D, restoration of lateral aspect; E, restoration of ventral aspect.

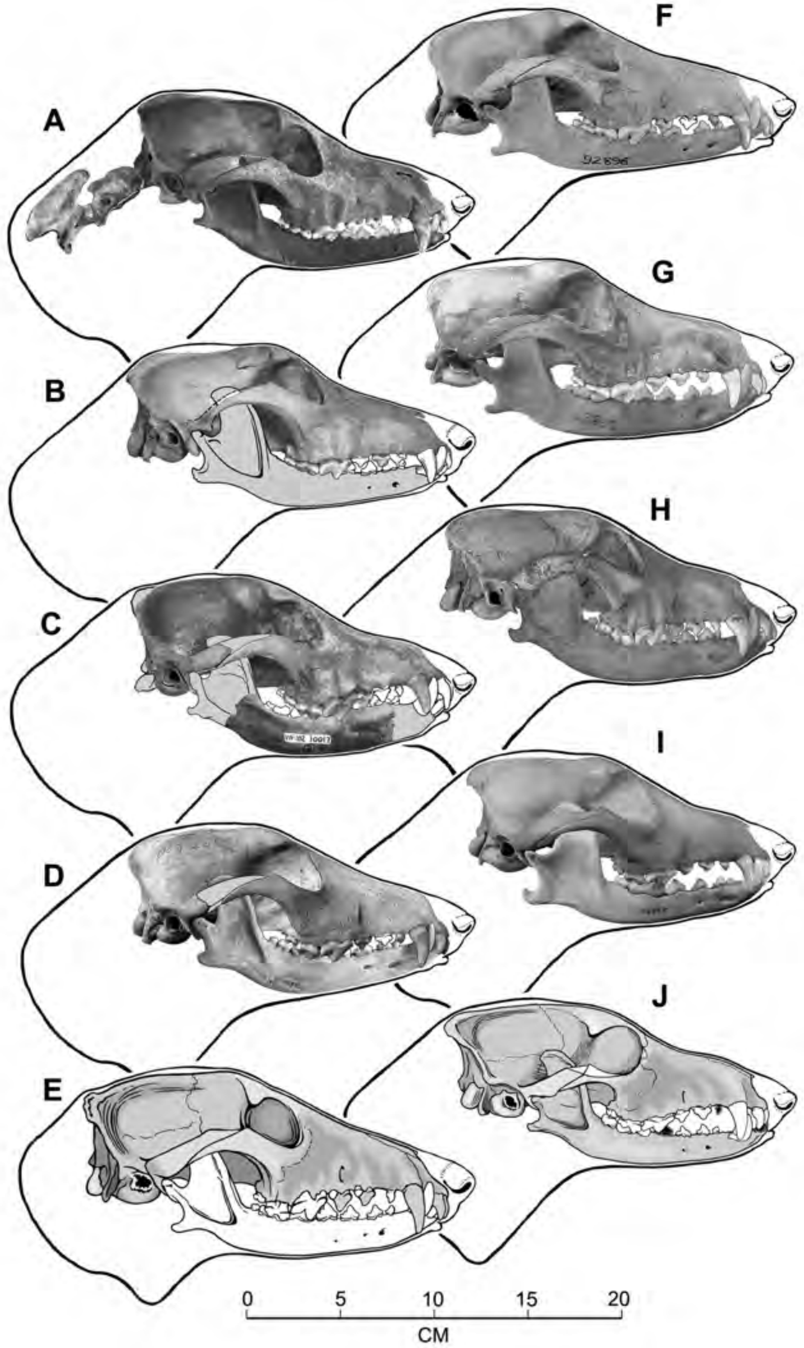

FIGURE S6

Lateral views, articulated skull and jaws of sighthounds; Saluki-like series. A, Vindolanda Praetorium dog. B, Vindolanda E(W)-111 10155. C, VH-102 29171 (articulated with jaws that probably go with it, VH-102 10017). D, ANM-M 18965, Greyhound (jaws reversed but not skull). E, Drawing of skull no. 35 from Gyoma in the Sarmatian Barbaricum of Roman date (after Bokonyi, 1984). F, FMNH 92896, tribally-bred Saluki from Kuzistan, Ahwaz, Iran. G, LACM 22825, “imported Persian hunting dog”, a tribally-bred Saluki. H, Skull from Warmington, England reported by Schoenebeck et al., 2019; photo courtesy Sheila Hamilton-Dyer. I, FMNH 77745, feral Sloughi from Jebel El Teir, Egypt (jaws reversed but not skull). J, Drawing of skull no. 3 from Ein Tirghi, Egypt (after Churcher, 1993).

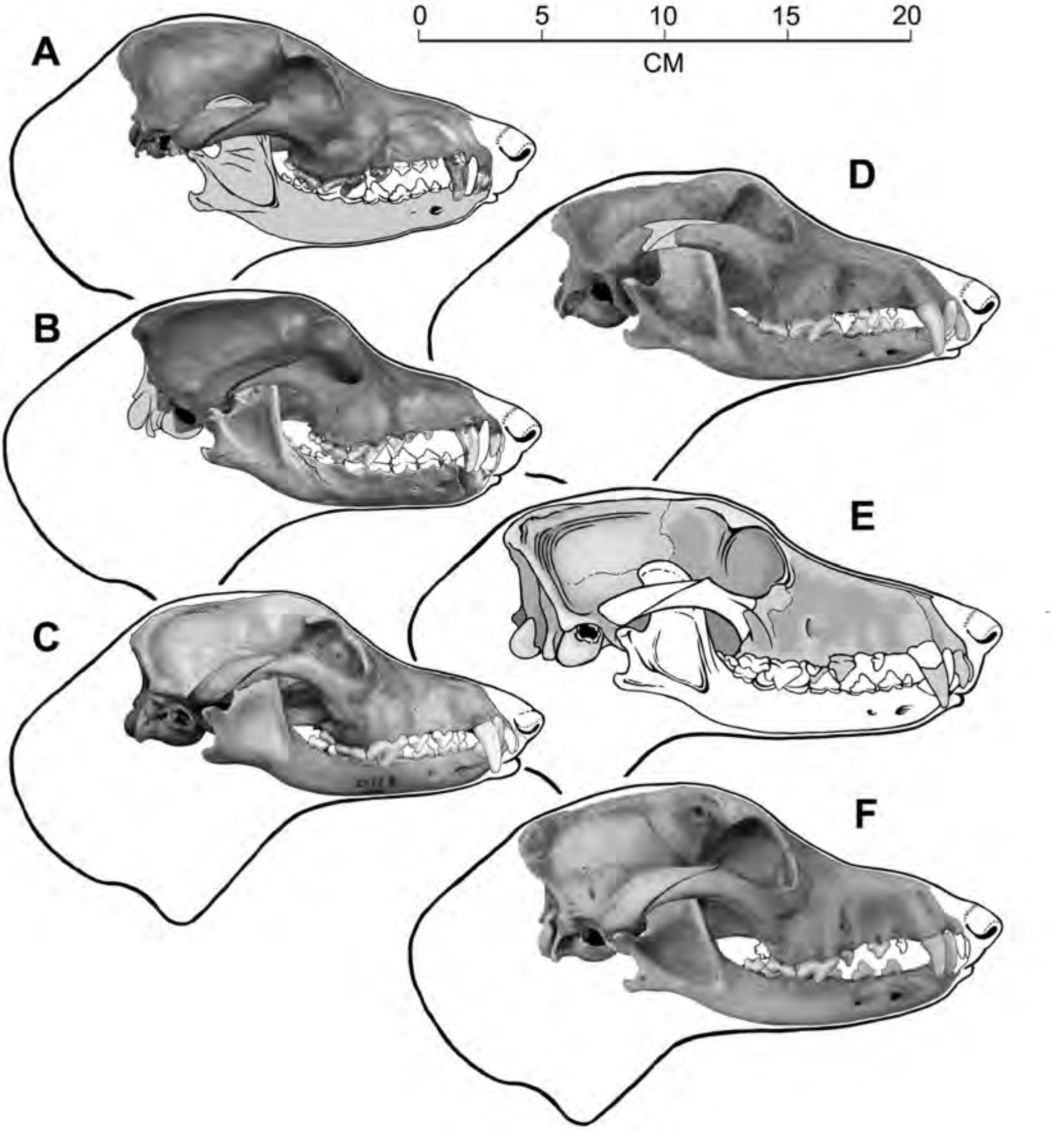

FIGURE S7

Lateral views, articulated skull and jaws of sighthounds; Afghan Hound-like series. A, Vindolanda V04A 863. B, Vindolanda V04A 861 (articulated with jaws that probably go with it, V04A 855). C, CAS 26503, Afghan Hound. D, FMNH Paleo/37/S-I-2A, the “tunnel dog” from Tepe Sarab, northern Iran. E, Drawing of skull no. 30 from Roman Tac Gorsium (after Bökönyi, 1984). F, FMNH 86835, tribally-bred Afghan hound.

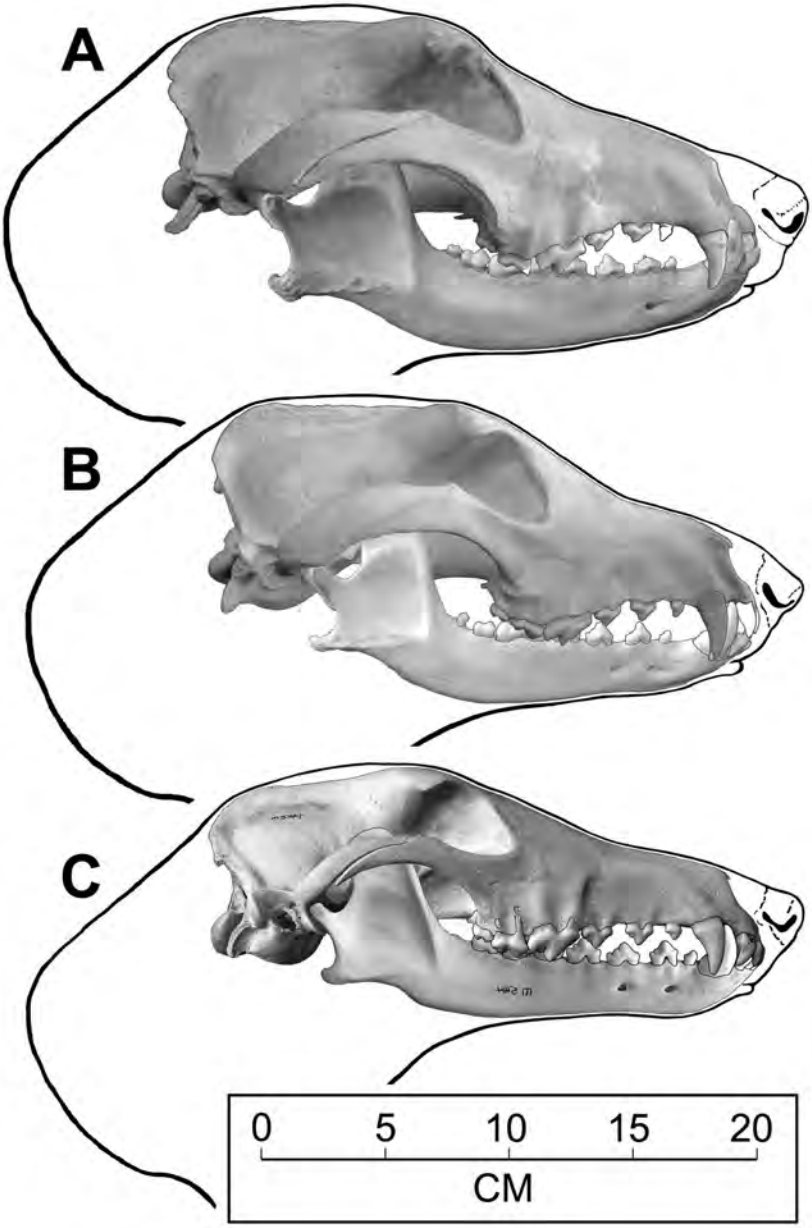

FIGURE S8

Lateral views, articulated skull and jaws of modern European sighthounds. A, YPM 7345, Irish Wolfhound. B, YPM 7987, Scottish Deerhound. C, ANM M-414 Russian Borzoi.

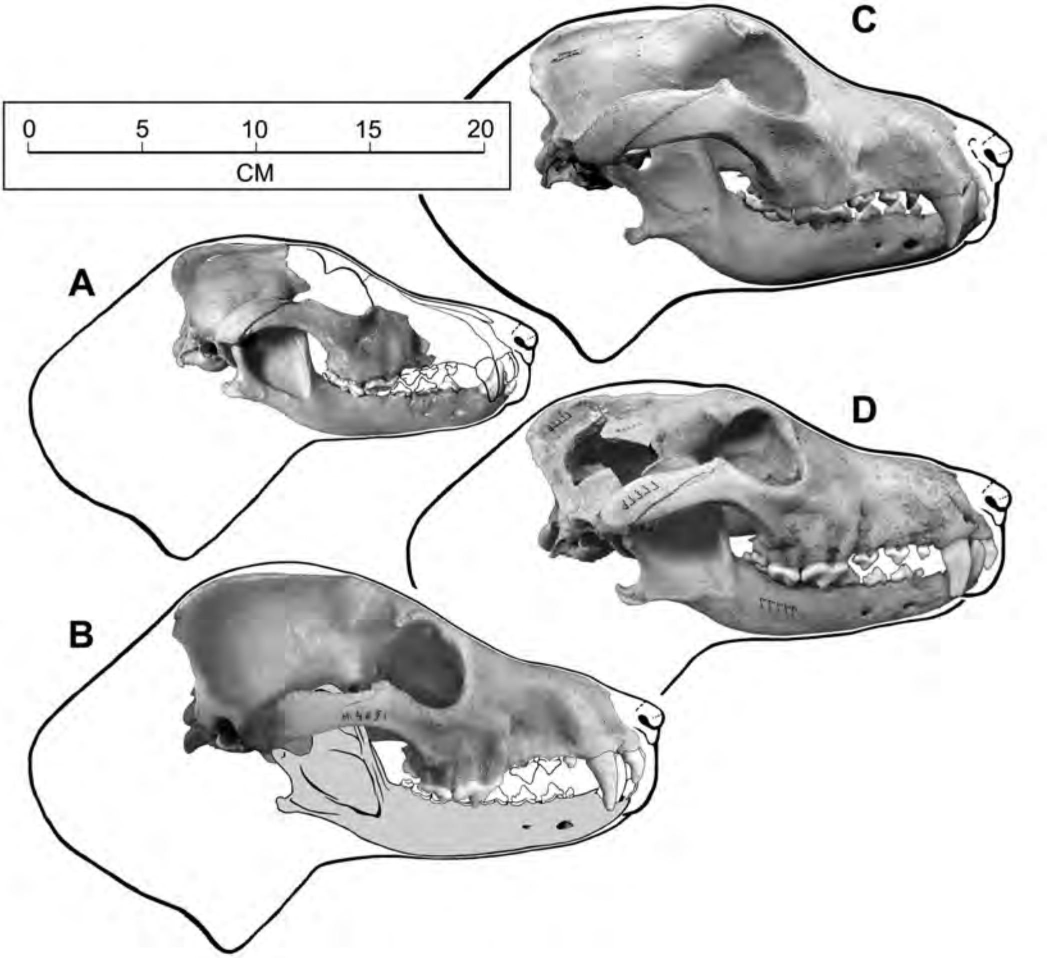

FIGURE S9

Lateral views of articulated skull and jaws of guard dogs, series 1. A, Vindolanda V04A 862. B, HA M-4054, Canaan Dog from original Israeli founder pack (photo courtesy Nimrod Marom). C, LACM 31099, Old English Sheepdog (skull and jaws reversed). D, FMNH 97777, tribally-bred Kuvasz (skull and jaws reversed).

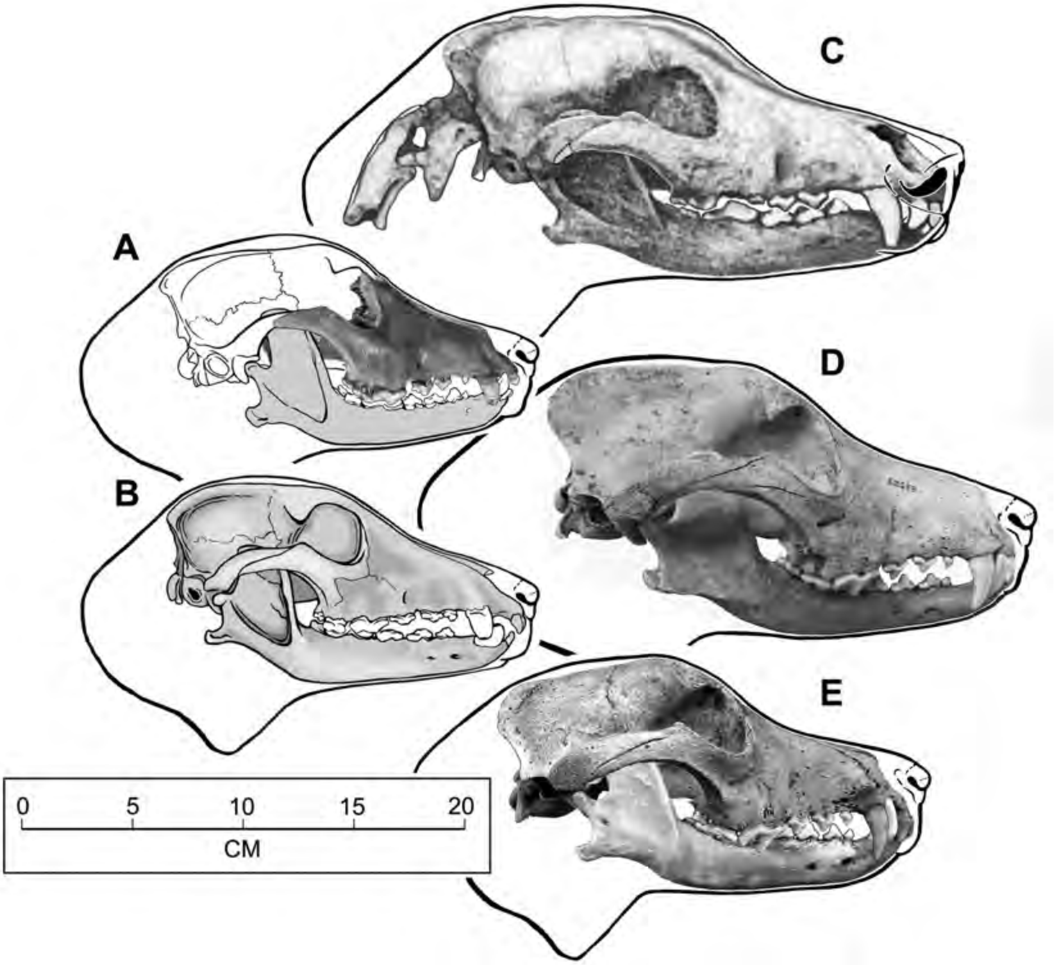

FIGURE S10

Lateral views, articulated skull and jaws of guard dogs, series 2. A, Vindolanda LXXII-VI 10158. B, Ein Tirghi skull no. 4 (after Churcher, 1993). C, "Grosshunde" from Heidelberg–Neuenheim (after Luttschwager, 1965). D, Tribally-bred Kuvasz FMNH 52752 (reversed). E, Canaan dog from Israel LACM 52198.

FIGURE S11

Round shape of occiput in Vindolanda and modern Asian sighthounds. A, Praetorium sighthound. B, V04A 861. C, V04A 863. D, E(W)-111 10155. E, “Tunnel dog” from Tepe Sarab, FMNH Paleo/37/S-I-2A. F, FMNH 77745, feral Sloughi from Jebel El Teir, Egypt. G, FMNH 92896, landrace Saluki from Khuzistan, Ahwaz, Iran. H, LACM 22825, imported Persian hunting dog (tribally-bred Saluki). I, ANM M-18965 Greyhound. J, FMNH 86835, tribally-bred Afghan hound.

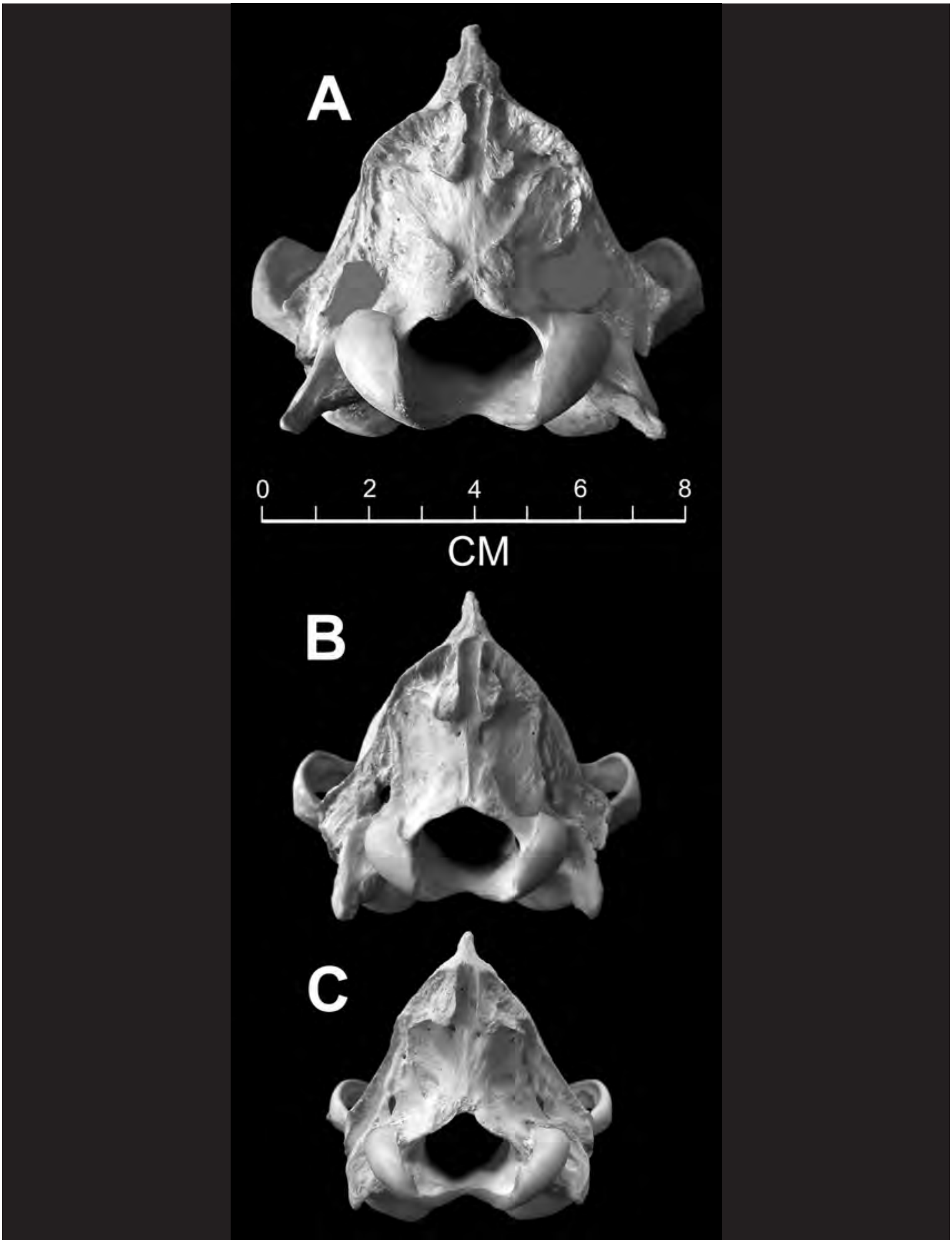

FIGURE S12

Triangular shape of occiput in modern European sighthounds. A, YPM 7345, Irish Wolfhound. B, YPM 7987, Scottish Deerhound. C, ANM M-414, Russian Borzoi.

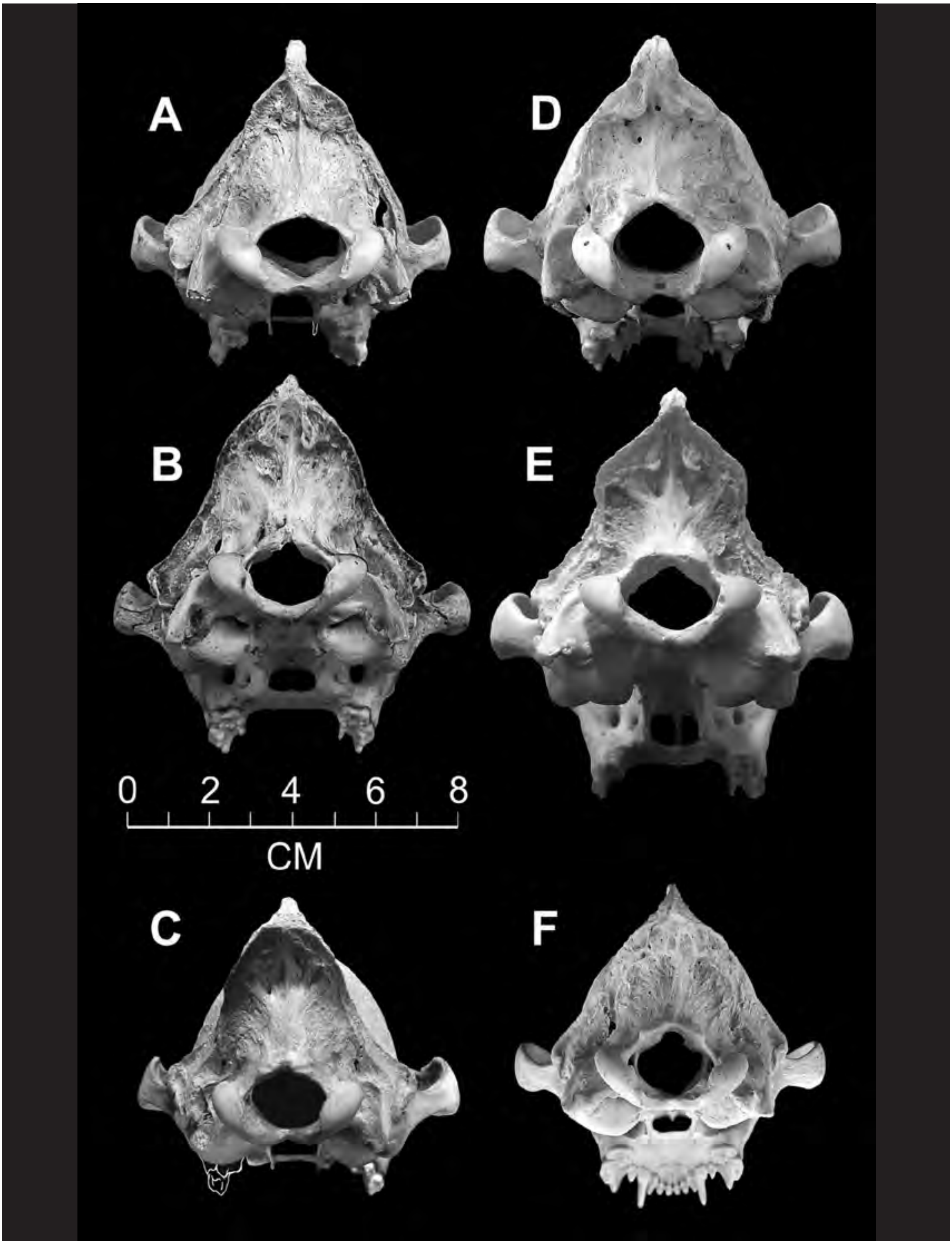

FIGURE S13

Triangular shape of occiput in ancient and modern guard dogs. A, FMNH 97777, tribally-bred Kuvasz from W. Azerbaijan. B, FMNH 57252, tribally-bred Kuvasz. C, Vindolanda guard dog V04A 862. D, LACM 31099, Old English Sheepdog. E, CAS 26776, Hungarian Komondor. F, LACM 52198, Canaan dog imported from Israel. Teeth show because the skull must be tilted downward considerably to show occiput because of forward slope of occiput and heavy, overhanging lambdoidal crest.

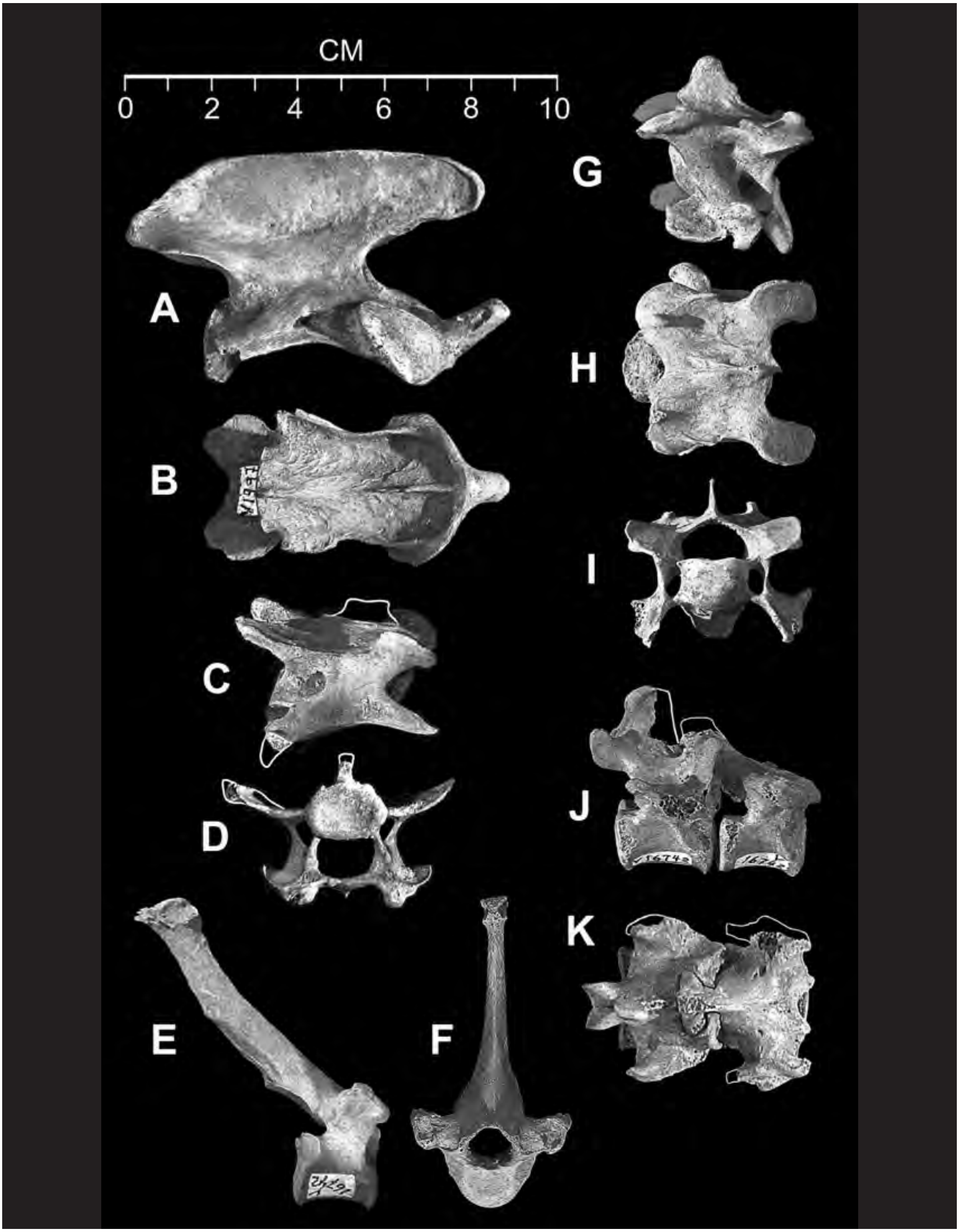

FIGURE S14

Vertebrae pertaining to the Vindolanda Praetorium sighthound, V1997-19 16742. A, Axis vertebra, right lateral view. B, Axis vertebra, ventral view. C, 4th cervical vertebra, right lateral view. D, 4th cervical vertebra, posterior view. E, 4th thoracic vertebra, right lateral view. F, 4th thoracic vertebra, anterior view. G, 6th cervical vertebra, right lateral view. H, 6th cervical vertebra, dorsal view, anterior to right. I, 6th cervical vertebra, anterior view. J, articulated 10th and 11th thoracic vertebrae, right lateral view. K, articulated 10th and 11th thoracic vertebrae, dorsal view, anterior to right.

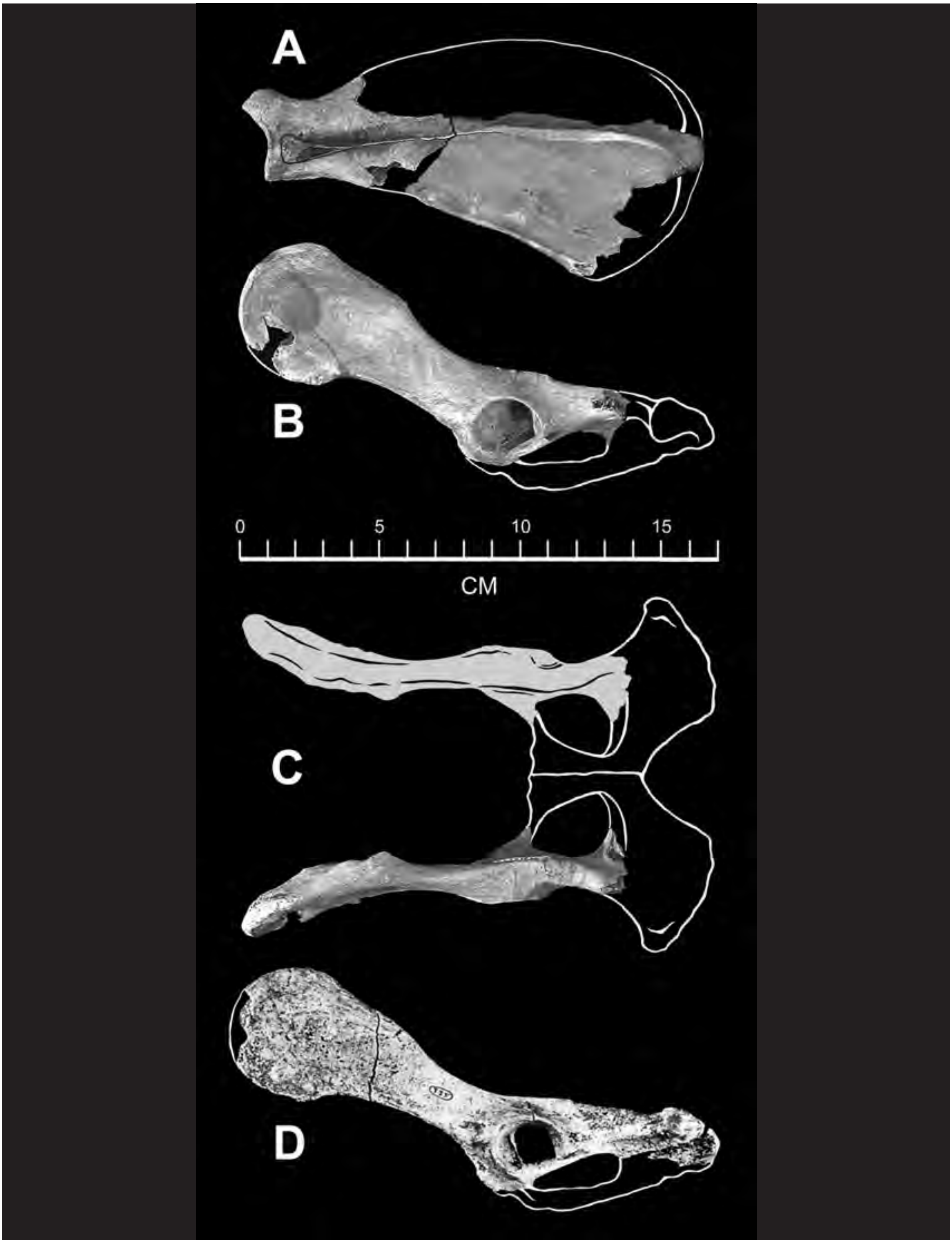

FIGURE S15

Scapula and pelvis. A, Left scapula of Vindolanda Praetorium dog V1997-19 16742 in lateral view; posterior portion behind the break is the opposite side (reversed). B, Left partial ilium of Praetorium dog in lateral view. C, Left partial ilium of Praetorium dog in dorsal view, with restoration of the whole pelvis indicating that the animal is likely a female. D, Left partial ilium of the Heidelberg–Neuenheim "grosshunde" (after Luttschwager, 1965). Note subtle differences in shape of the ilium in an ancient sighthound (B) and an ancient guard dog (D).

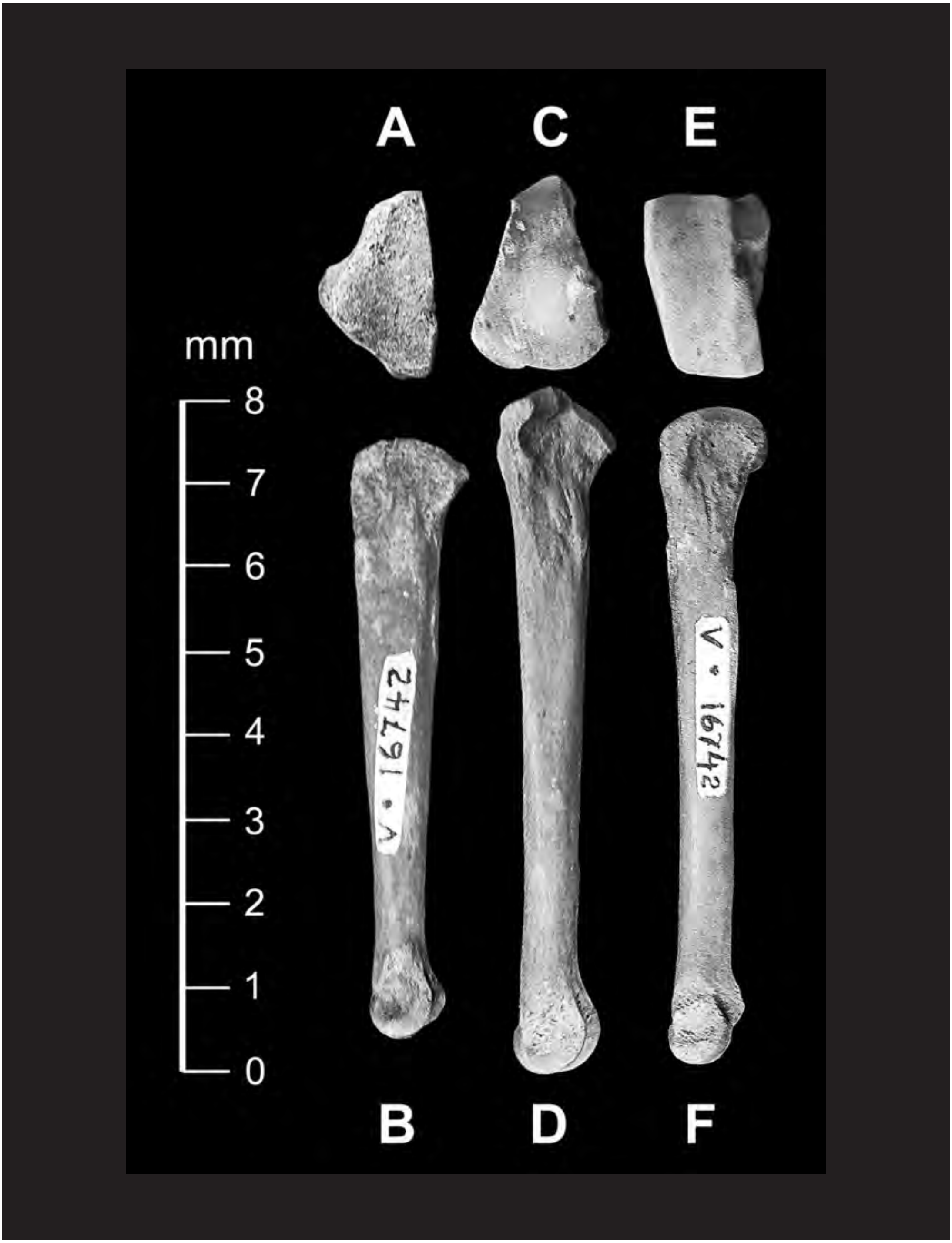

FIGURE S16

Metacarpals pertaining to the Vindolanda Praetorium sighthound. A, Right metacarpal II, dorsal view. B, Right metacarpal II, medial view. C, Left metacarpal III, dorsal view. D, Left metacarpal III, lateral view. E, Left metacarpal IV, dorsal view. F, Left metacarpal IV, lateral view.

FIGURE S17

Metatarsals pertaining to the Vindolanda Praetorium sighthound. A, Left metatarsal II, dorsal view. B, Left metatarsal II, lateral view. C, Left metatarsal III, dorsal view. D, Left metatarsal III, lateral view. D, Left metatarsal IV, dorsal view. E, Left metatarsal IV, lateral view.

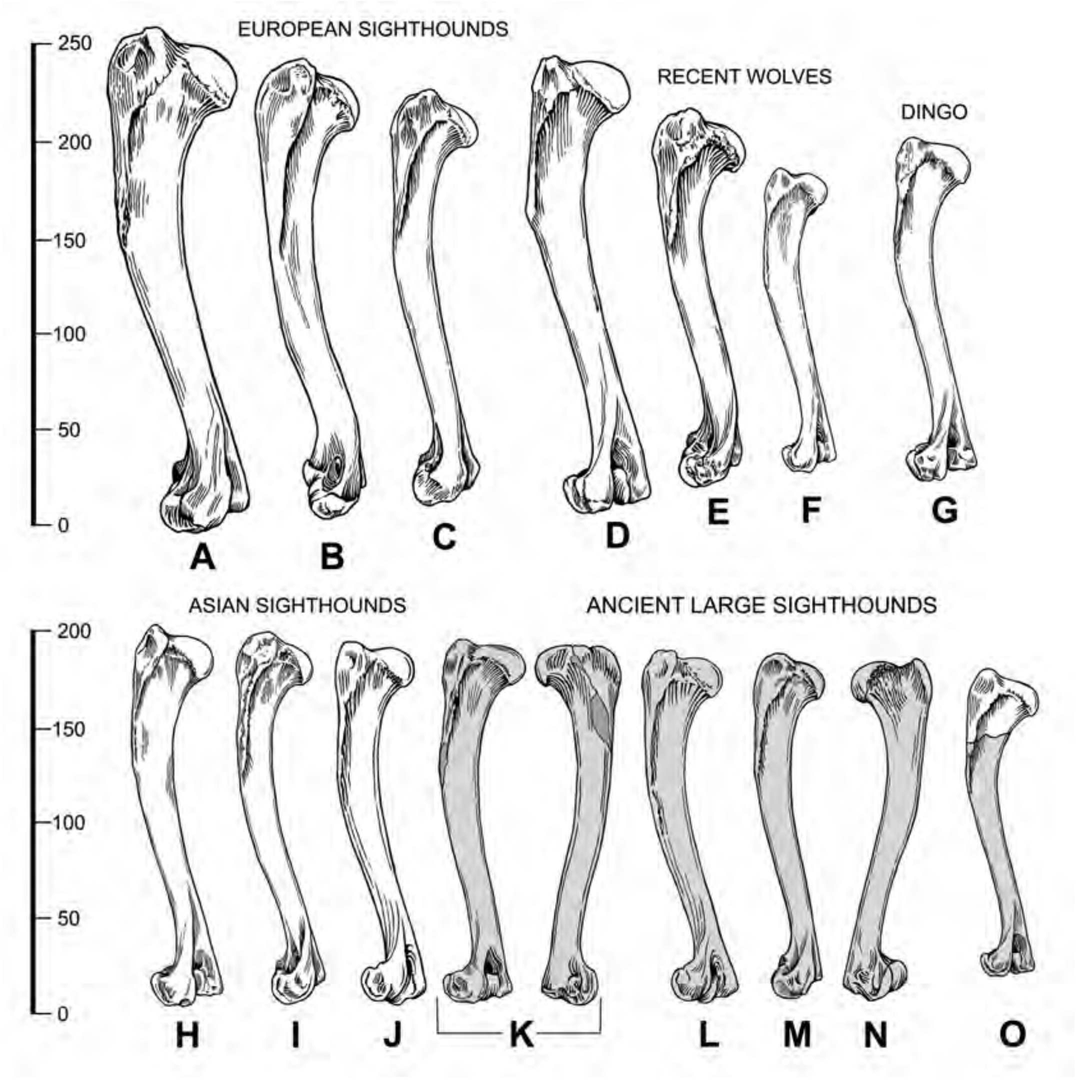

FIGURE S18

Humeri of ancient and recent sighthounds. All are lateral views unless otherwise noted. Some specimens reversed for ease of comparison. Abbreviations in this and Figs. 26–30: SH = Estimated height at shoulder in cm; GL = Greatest length in mm. Index calculated as (SD × 100)/GL. For more information concerning limb indexes, see Table 1.

A, Irish Wolfhound WSU-VA-C930-X. GL = 256.17; SH = 82.2; Index = 8.53. B, Scottish Deerhound YPM 7987. GL = 233.5; SH = 77.4; Index = 7.31. C, Russian Borzoi, LACM 30539. GL = 212.04; SH = 70.1; Index = 7.86. D, Alaska wolf KU 157331; oblique antero-lateral view. GL= 235.03; SH = 78.0; Index = 7.43. E, Mexican wolf MSB 83337. GL = 189.77; SH = 62.4; Index 8.23. F, Indian wolf FMNH 46079. GL = 154.20; SH 50.2; Index 7.59. G, Dingo MVZ 152804. GL = 177.73; SH = 58.3; Index 7.55. H, Greyhound MVZ 118988. GL = 194.8; SH = 64.2; Index = 6.40. I, Saluki LACM 22825. GL = 193.95; SH = 63.9; Index = 6.12. J, Afghan Hound (after Schoenebeck et al., 2019). GL = 189.71; SH = 62.4; Index appx. 6.5. K, Vindolanda Praetorium sighthound. GL = 189.89; SH = 62.5; Index = 6.92. L, Warmington sighthound (after Schoenebeck *et al*., 2019). GL = 180; SH = 59.1; Index = 7.78. M, “Tunnel dog” from Tepe Sarab, n. Iraq FMNH Paleo/37/S-I-2A. GL = 175.64; SH = 57.6; Index = 7.45. N, Vindolanda V06-34A 5550. GL = 165 (estimated); SH = 54 (estimated); Index = 6.8 (estimated). O, Vindolanda V06-34A 5550 (proximal end restored). GL = 165 (est), SH = 54 (est), Index 6.8 (est).

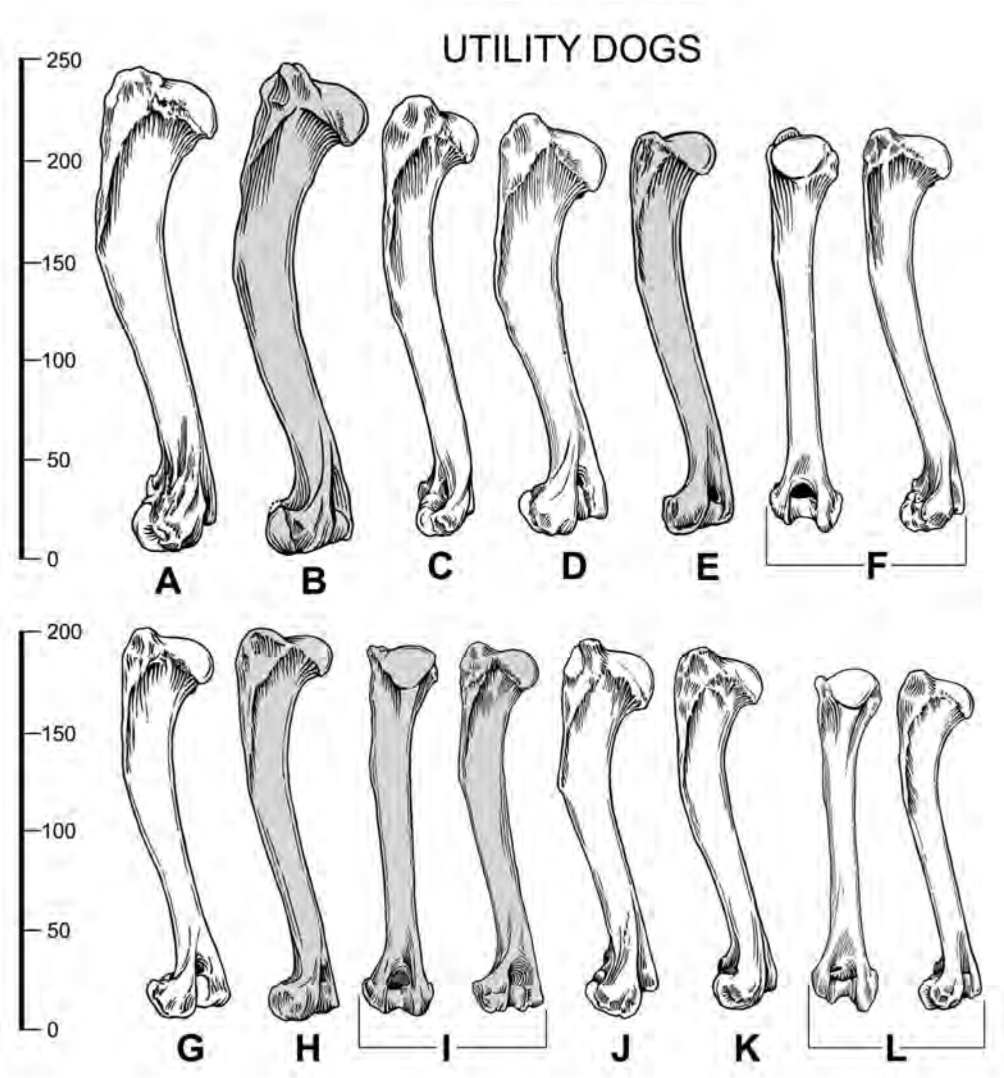

FIGURE S19

Humeri of ancient and recent utility and guard dogs. All are lateral views unless otherwise noted. Some specimens reversed for ease of comparison. A, St. Bernard FMNH 57430. GL = 238.72; SH = 79.2; Index = 8.48. B, “Varg” from the Saqqara dog tombs (Ikram, pers. comm. 2020). GL = 237; SH = 79; Index = appx. 9. C, Hungarian Komondor CAS 26776. GL = 212.92; SH = 70.4; Index = 8.50. D, Presa Canario CAS 28769. GL = 209.22; SH = 69.1; Index = 9.19. E, the Heidelberg–Neuenheim “grosshunde” (after Luttschwager, 1965). GL = 203; SH = 66.9; Index = appx. 8.1. F, Mastiff KU 147390. GL = 199.62; SH = 65.8; Index = 8.31. G, German Shepherd FMNH 168865. GL = 192.60; SH = 63.4; Index =7.97. H, Vindolanda V04A 994. GL = 191.18; SH = 62.9; Index 8.81. I, Vindolanda V04A 996, anterior and lateral views (reversed). GL = 187.71; SH = 61.7; Index = 8.16. J, Rottweiler CAS 30704. GL = 186.48; SH = 61.3; Index = 9.48. K, Old English Sheepdog LACM 31099. GL = 180.66; SH = 59.3; Index = 9.78. L, Canaan Dog imported from Israel LACM 52198. GL = 174.9; SH = 57.3; Index = 7.96.

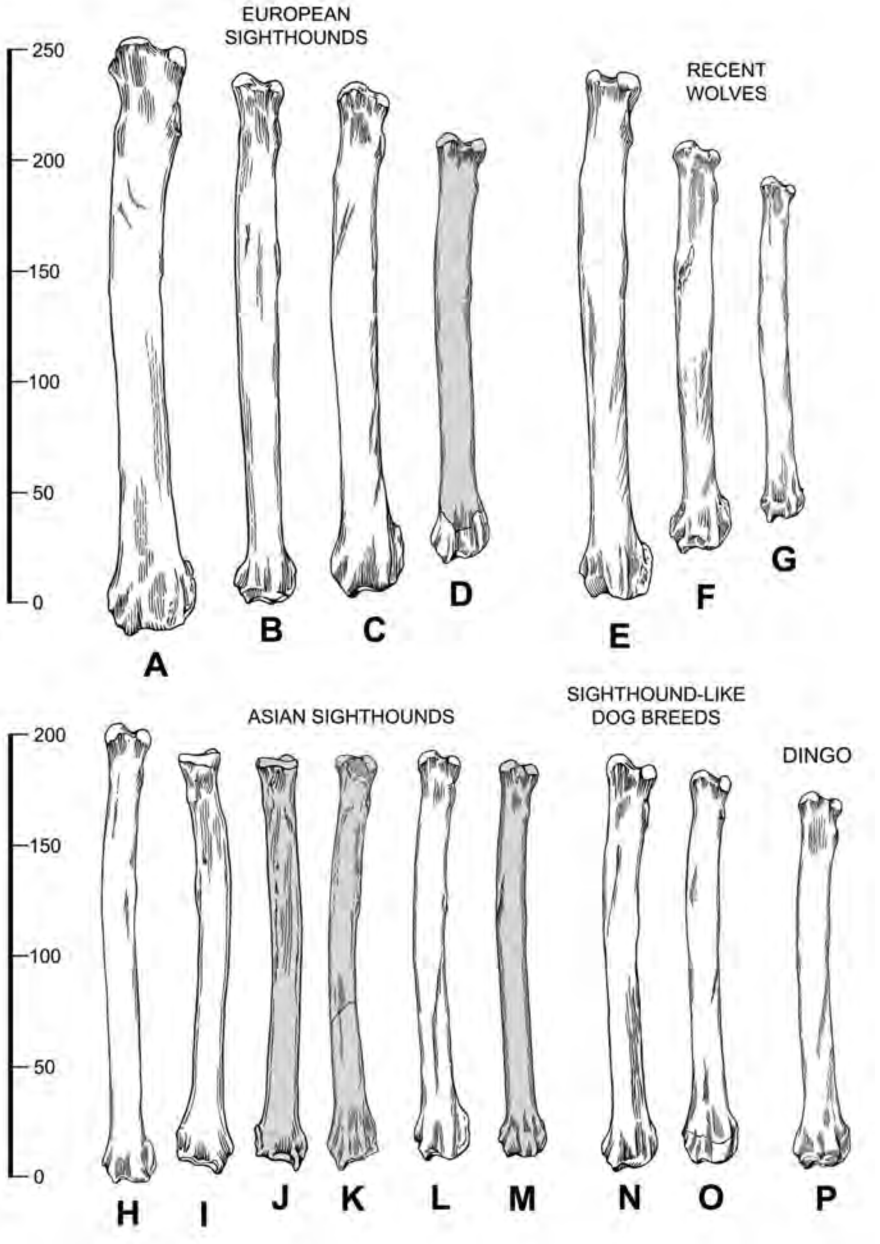

FIGURE S20

Radii of ancient and recent sighthounds. All are anterior views unless otherwise noted. Some specimens reversed for ease of comparison. A, Irish Wolfhound WSU-A-C390-X. GL = 270.54; SH = 84.1; Index = 7.99. B, Borzoi LACM 30539. GL 240.21; SH = 74.4; Index = 6.67. C, Scottish Deerhound YPM 7987. GL = 234.21; SH = 72.5; Index = 7.79. D, Vindolanda V04A 1010 (distal end restored). GL = 195 (est); SH = 60.1; Index = appx. 7.5. E, Alaska wolf KU 157331. GL = 239.92; SH = 74.3; Index = 7.82. F, Mexican wolf MSB 83337. GL = 187.22; SH = 57.6; Index = 7.58. G, Indian wolf FMNH 46079. GL = 157.5; SH = 48.1; Index = 7.31. H, Saluki LACM 22825. GL = 208.1; SH = 64.0; Index = 6.45. I, Afghan Hound (after Schoenebeck *et al*., 2019) (reversed; posterior view). GL = appx. 193; SH = appx. 60; Index = appx. 7.2. J, the Warmington sighthound (after Schoenebeck *et al*., 2019). GL = 189.0; SH = 58.1; Index = appx. 7.2. K, Vindolanda Praetorium sighthound (reversed). GL = 188.52; SH = 58.0; Index appx. 7.2. L, Greyhound MVZ 118988. GL = 186.3; SH = 57.3; Index = 7.2. M, “Tunnel dog” from Tepe Sarab, n. Iran FMNH Paleo/37/S-I-2A. GL = 180.42; SH = 55.4; Index = 6.66. N, Doberman Pinscher LACM 30730. GL = 189.56; SH = 58.3; Index = 8.08. O, Irish Setter LACM 31092. GL = 178.9; SH = 54.9; Index = 7.70. P, Australian Dingo MVZ 152804. GL = 171.44; SH = 52.6; Index = 7.96.

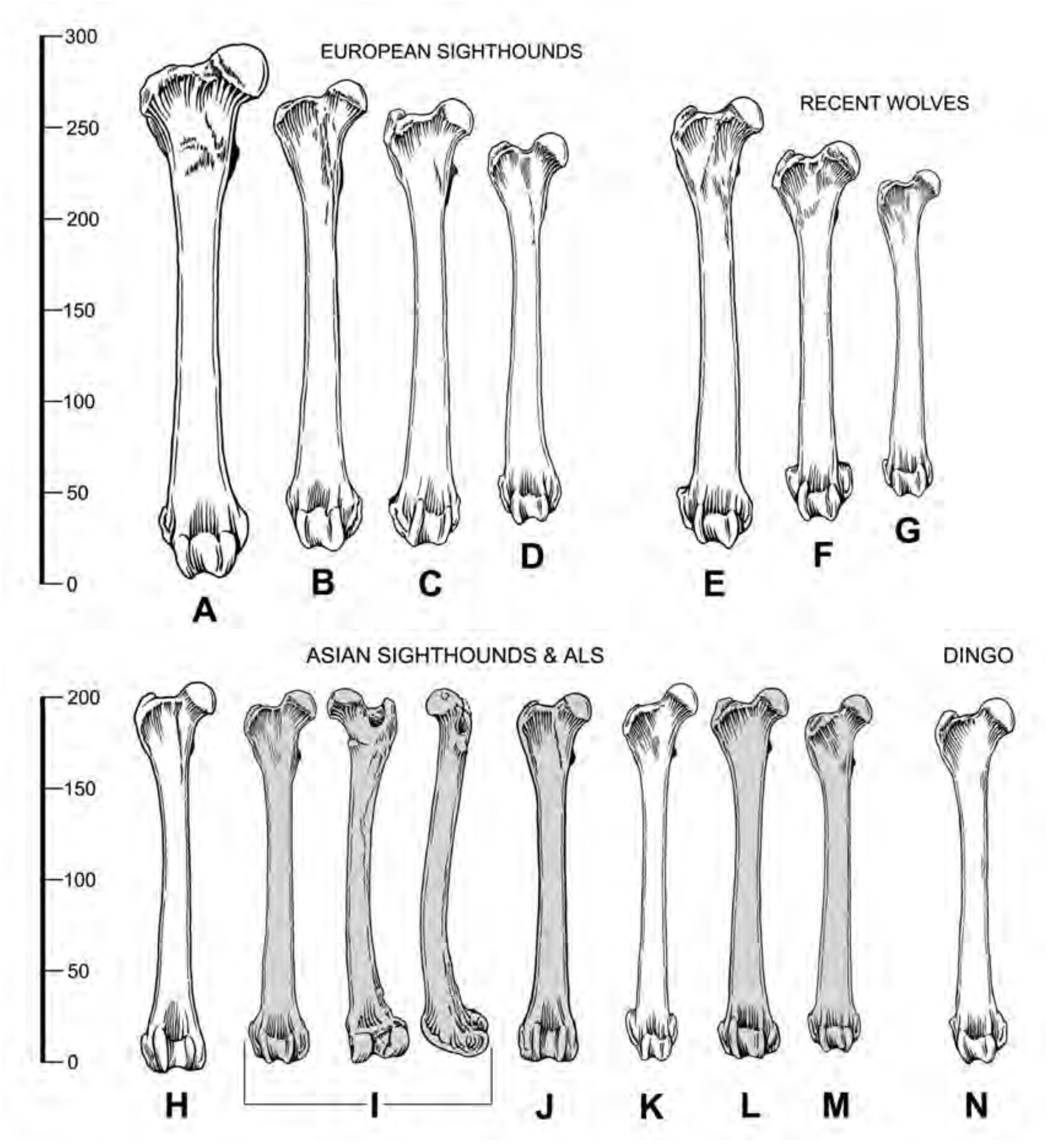

FIGURE S21

Femurs of ancient and recent sighthounds. All are anterior views unless otherwise noted. Some specimens reversed for ease of comparison. A, Irish Wolfhound WSU-VA C930-X. GL = 287.08; SH = 88.8; Index = 7.06. B, Scottish Deerhound YPM 7987. GL = 259.01; SH = 80.0; Index = 6.53. C, Borzoi LACM 30539. GL = 247.4; SH = 76.4; Index = 6.78. D, Greyhound MVZ 118988. GL = 210.14; SH = 64.7; Index = 6.57. E, Alaska wolf KU 157331. GL = 240.92; SH = 74.3; Index = 7.37. F, Mexican wolf MSB 83337. GL = 203.04; SH = 62.5; Index 7.75. G, Indian wolf FMNH 46079. GL = 174.81; SH = 53.6; Index = 6.94. H, Afghan Hound (after Schoenebeck *et al*., 2019). GL = appx. 213; SH = appx. 66; Index appx. 6.8. I, Vindolanda Praetorium sighthound (anterior, posterior, and medial views). GL = 205.47; SH = 63.2; Index = 6.40. J, the Warmington sighthound (after Schoenebeck *et al*., 2019) (reversed). GL = 203; SH = 62.4; Index = 6.40. K, Saluki LACM 22825. GL = 201.8; SH = 64.05; Index = 5.79. L, Vindolanda VR-104 3158. GL = 198.3; SH = 61.0; Index = 6.40. M, "Tunnel dog" from Tepe Sarab, n. Iran FMNH Paleo/37/S-I-2A. GL = 195.97; SH = 60.2; Index = 6.89. N, Australian Dingo MVZ 152804. GL = 195.17; SH = 60.0; Index = 7.16.

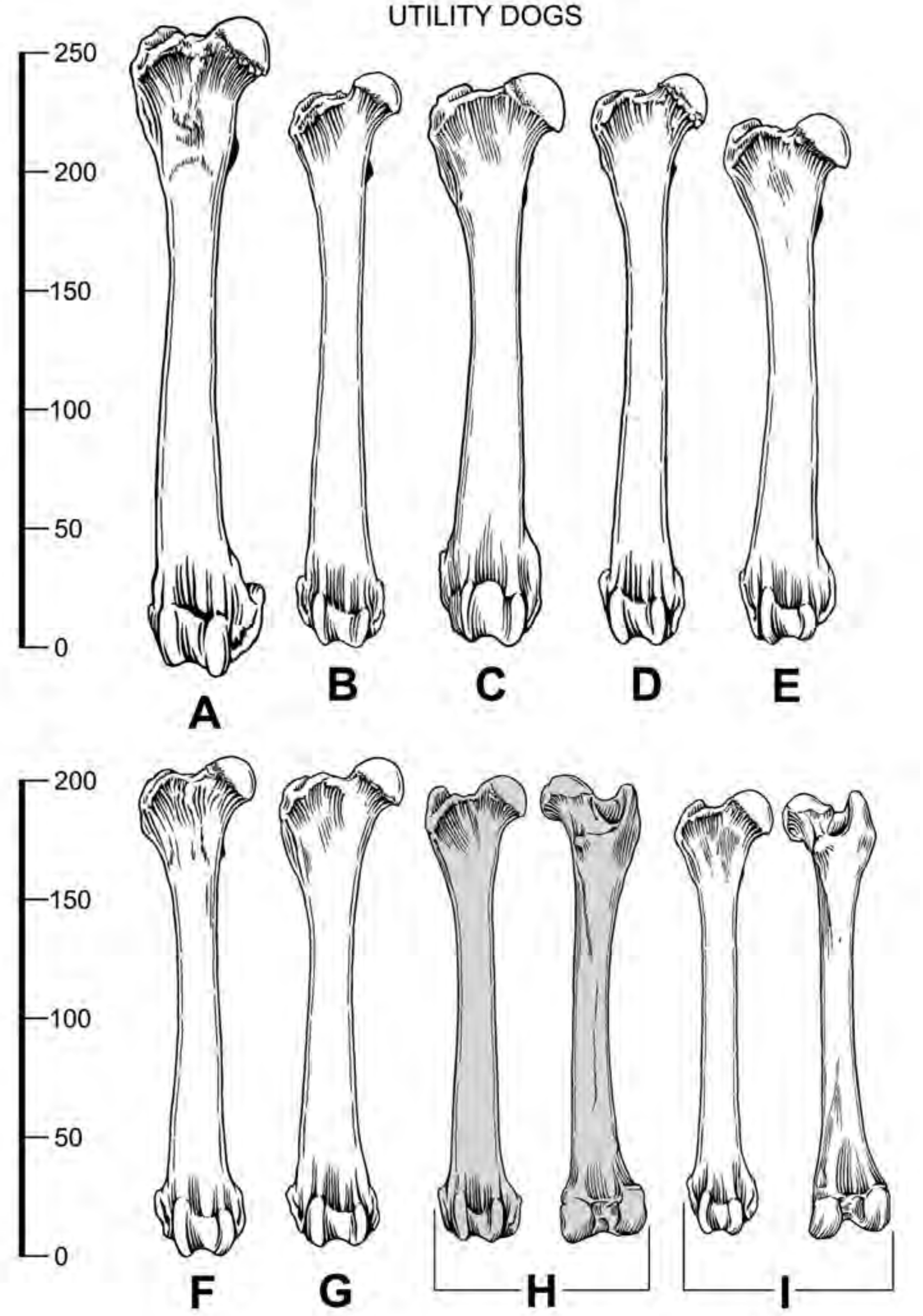

FIGURE S22

Femurs of ancient and recent utility and guard dogs. All are anterior views unless otherwise noted. Some specimens reversed for ease of comparison. A, St. Bernard FMNH 57430. GL = 270.58. SH = 83.7; Index = 6.82. B, Mastiff KU 147390. GL = 236.85; SH = 73.1; Index = 7.90. C, Presa Canario CAS 28769. GL = 235.55; SH = 72.7; Index 8.10. D, Hungarian Komondor CAS 26776. GL = 235.22; SH = 72.6; Index = 6.80. E, Old English Sheepdog LACM 31099. GL = 216.9; SH = 66.8; Index = 8.17. F, German Shepherd FMNH 168865. GL = 204.44; SH = 62.9; Index = 7.74. G, Rottweiler CAS 30704. GL = 201.68; SH = 62.0; Index = 8.57. H, Vindolanda II-85-E7A 2841 (reversed; anterior and posterior views). GL = 191.9; SH = 59.0; Index = 8.90. I, Canaan Dog from Israel LACM 52198 (anterior and posterior views). GL = 187.46; SH = 57.6; Index = 7.45.

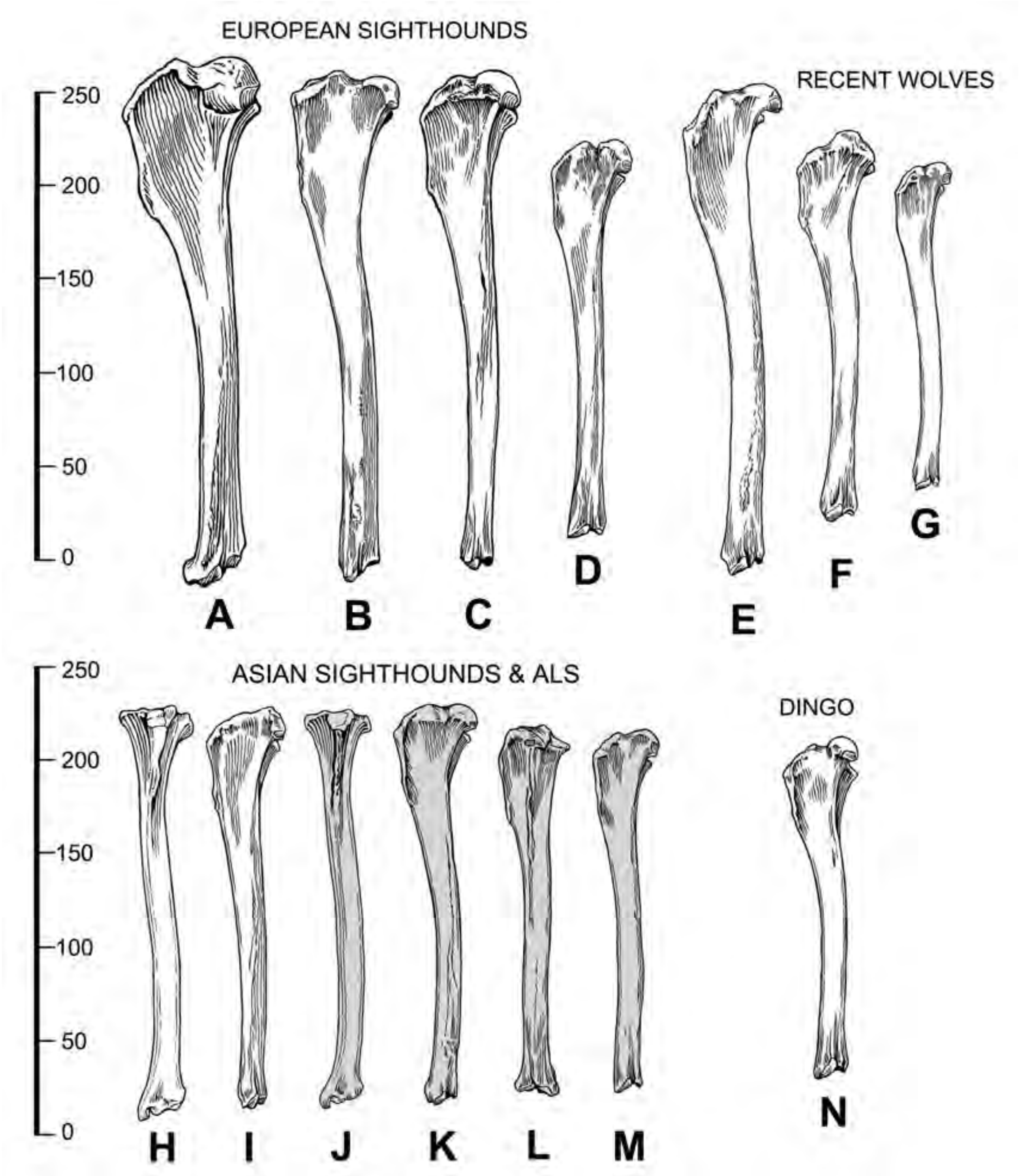

FIGURE S23

Tibias of ancient and recent sighthounds. All are lateral views unless otherwise noted. Some specimens reversed for ease of comparison. Index calculated using width of proximal end of bone, not minimum shaft diameter (Pb × 100/GL). A, Irish Wolfhound WSU-VA C930-X. GL = 284.83; SH = 84.1; Index = 20.24. B, Scottish Deerhound YPM 7987. GL = 270.91; SH = 80.0; Index 16.99. C, Borzoi LACM 30539. GL = 267.18; SH = 78.9; Index = 15.87. D, Greyhound MVZ 118988. GL = 212.66; SH = 63.0; Index = 18.09. E, Alaska wolf KU 157331. GL = 263.6; SH = 77.91; Index 17.79. F, Mexican wolf MSB 83337. GL = 209.01; SH = 60.09; Index 19.37. G, Indian wolf FMNH 46079. GL = 175.87; SH = 52.3; Index 16.88. H, Afghan Hound (after Schoenebeck *et al*., 2019) (anterior view). TL = appx. 217; SH = appx. 65; Index = appx. 17. I, Saluki LACM 22825. GL = 215.26; SH = 63.8; Index 16.30. J, the Warmington sighthound (after Schoenebeck *et al*., 2019) (anterior view). GL = appx. 214; SH = appx. 63; Index = appx. 17. K, Vindolanda Praetorium sighthound. GL = 214.51; SH = 63.1; Index = 17.45. L, Vindolanda VJ = 4 10116 (lateral view). GL = 198.55; SH = 59.0; Index = 17.90. M, "Tunnel dog" from Tepe Sarab, n. Iran Paleo/37/S-I-2A. GL = 198.03; SH = 58.8; Index = 16.98. N, Australian Dingo MVZ 152804. GL = 182.73; SH = 54.3; Index = 19.57.

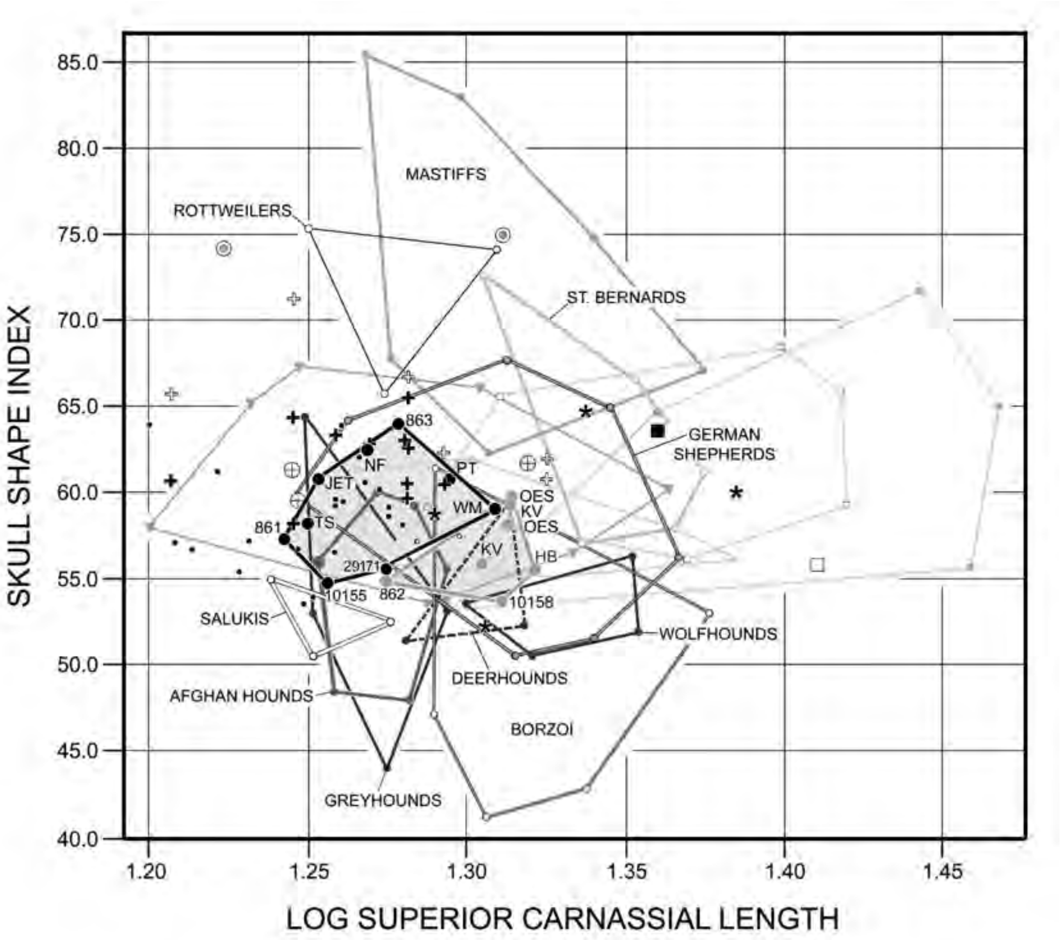

FIGURE S24

MTA analysis of skull shape (or cranial index) calculated as (ZW × 100)/BL.

In this and all MTA analyses, the groups containing Vindolanda dogs and other ancient specimens also contain modern representatives of ancient breeds which consistently plot with the archaeological dogs. Two groups are mapped on each MTA chart: large sighthounds (ALS, heavy black boundary) and guard dogs (AGD, heavy gray boundary); both are filled with gray tone for clarity.

Comparative populations of wolves and dingoes are drafted in the background. Wolves are represented by small squares: dark gray squares = North American wolves; white squares = Mexican wolves; light gray squares = Indian wolves. Dingoes are represented by gray triangles.

Symbols: asterisk = Great Dane; circle with cross = Canaan Dog; circle with gray dot = Presa Canario; black plus = Tac Gorsium specimens that are probably large sighthounds. White plus = Tac Gorsium specimens that are probably guard dogs (data from Bökönyi, 1984). Open circle = Classe (data from Farello, 1993). Note, not all symbols appear in every MTA chart.

Abbreviations: PT = Vindolanda Praetorium Hound, V1997-19 16742; FM = Forum dog no. 1 (measurements courtesy Ian Baxter, *pers. comm.*, 2015; jaw depth estimated from photo). HB = Heidelberg–Neuenheim “grosshunde” (after Luttschwager, 1965); JET = feral Sloughi from Jebel El Teir, Minya Province, Egypt; KV = Kuvasz; TS = Tepe Sarab; KOM = Hungarian Komondor; NF = Norfolk Street (data from Baxter, *pers. comm.*, 2015). OES = Old English Sheepdog; KV = Kuvasz; V = “Varg,” large dog from Saqqara dog tombs; WM = Warmington; large black square = Chinese Wolf; large open square = Tuscan wolf; numbers = Vindolanda specimens.

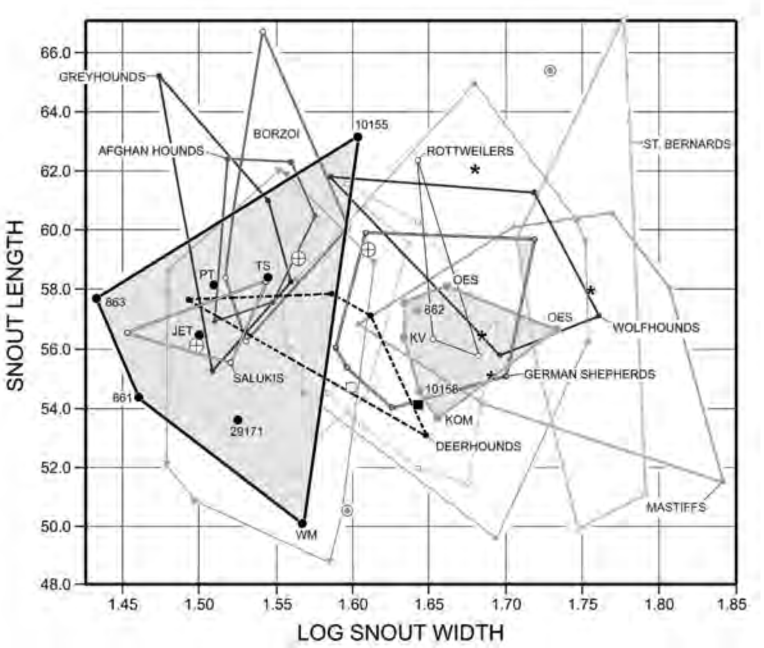

FIGURE S25
MTA analysis of snout length, calculated as (NA × 100)/BL.

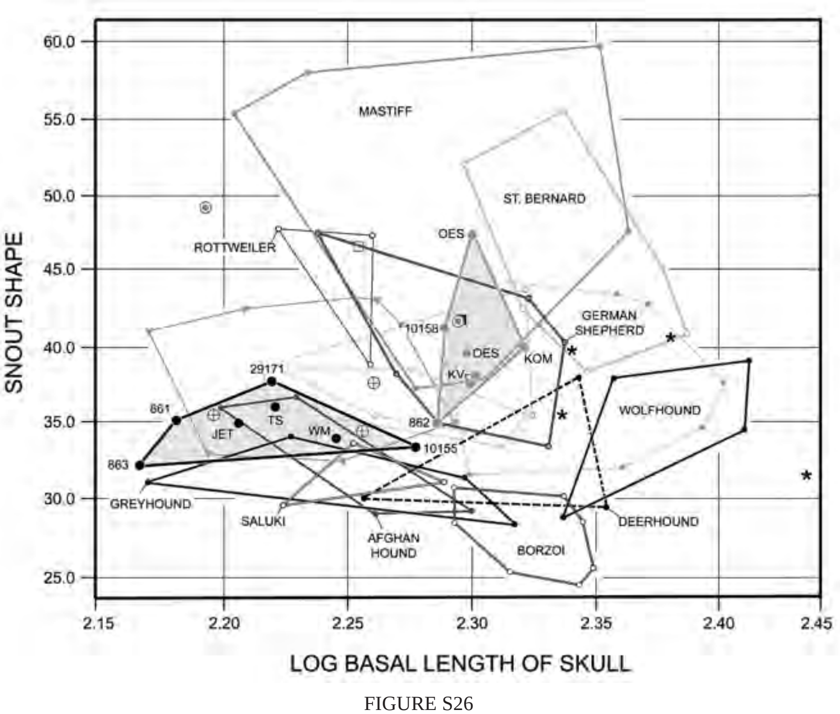

FIGURE S26
MTA analysis of snout shape, calculated as (SW × 100)/NA.

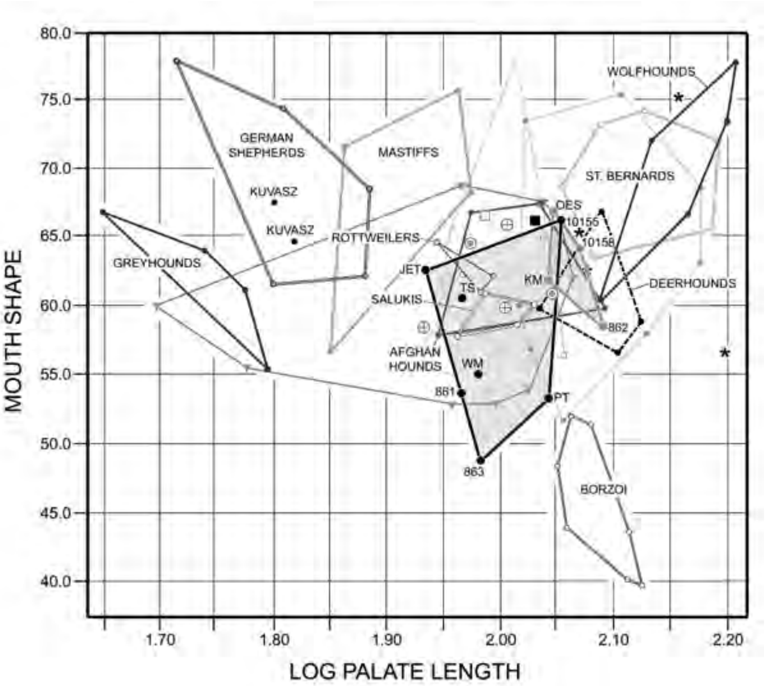

FIGURE S27

MTA analysis of mouth shape, calculated as (SW × 100)/PW.

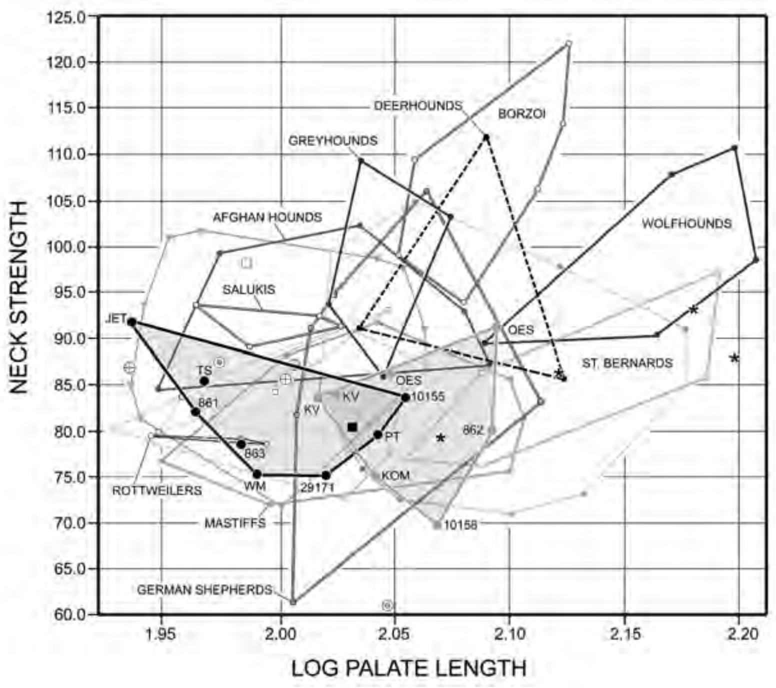

FIGURE S28

MTA analysis of neck strength, calculated as (RA × 100)/PW.

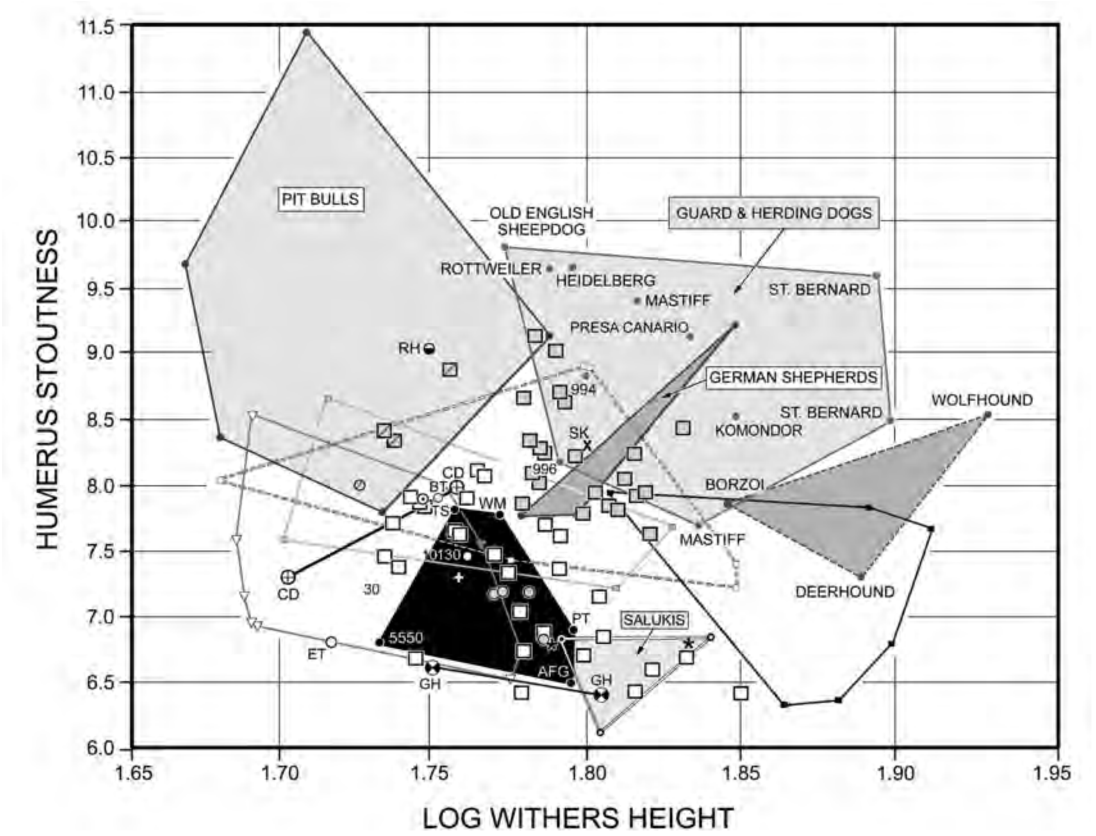

FIGURE S29

MTA analysis of humerus stoutness, calculated as SD × 100/GL. In this and subsequent limb bone MTA's, hull shading is to enhance clarity.

Abbreviations in this and following limb MTA's: AFG = Afghan Hound. BT = Balat, Egypt (data from Churcher, 1993). GH = Greyhound. TS = Tepe Sarab. PT = Vindolanda Praetorium sighthound. RW = Rottweiler. WM = Warmington.

Symbols: Large open squares, Tac Gorsium specimens likely to be sighthounds; large gray squares, Tac Gorsium specimens likely to be utility/guard dogs; slash gray squares, Tac Gorsium specimens likely to be bulldogs. Open circle = Balat, Egypt (data from Churcher, 1993). Gray circle = Elms Farm (data from Albarella, 2000). White circle/ET = Ein Tirghi (data from Churcher, 1993). Asterisk = Thistleton 1441 (data from Baxter, 2010a). White plus symbol = Norfolk Lane 186 (data from Baxter, 2010b). Slash gray circle = Love's Farm (data from Baxter, 2018). "X" symbol/SK = Stukeley's Farm 8284 (data from Baxter, 2018). Dotted white circle = Causeway Lane 3925 (data from Baxter, 2010b). Half black circle/RH = Rothwell Haigh humerus no. 1 (data from Ayton, 2014). Circle with plus/CD = Canaan Dog. Black and white pinwheel/GH = Greyhound.

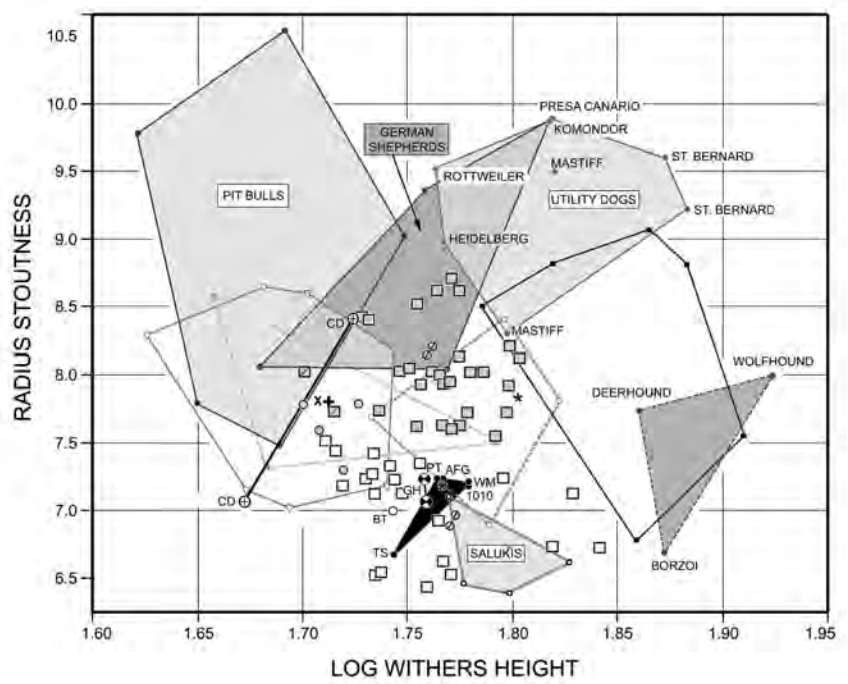

FIGURE S30

MTA analysis of radius stoutness, calculated as SD × 100/GL.

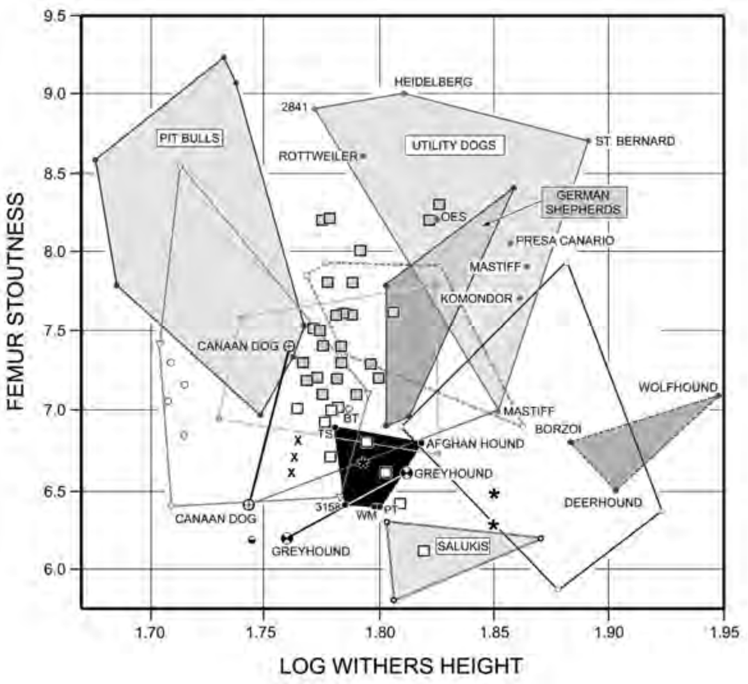

FIGURE S31

MTA analysis of femur stoutness, calculated as SD × 100/GL. “X” symbol on this plot = Classe (data after Farello, 1995).

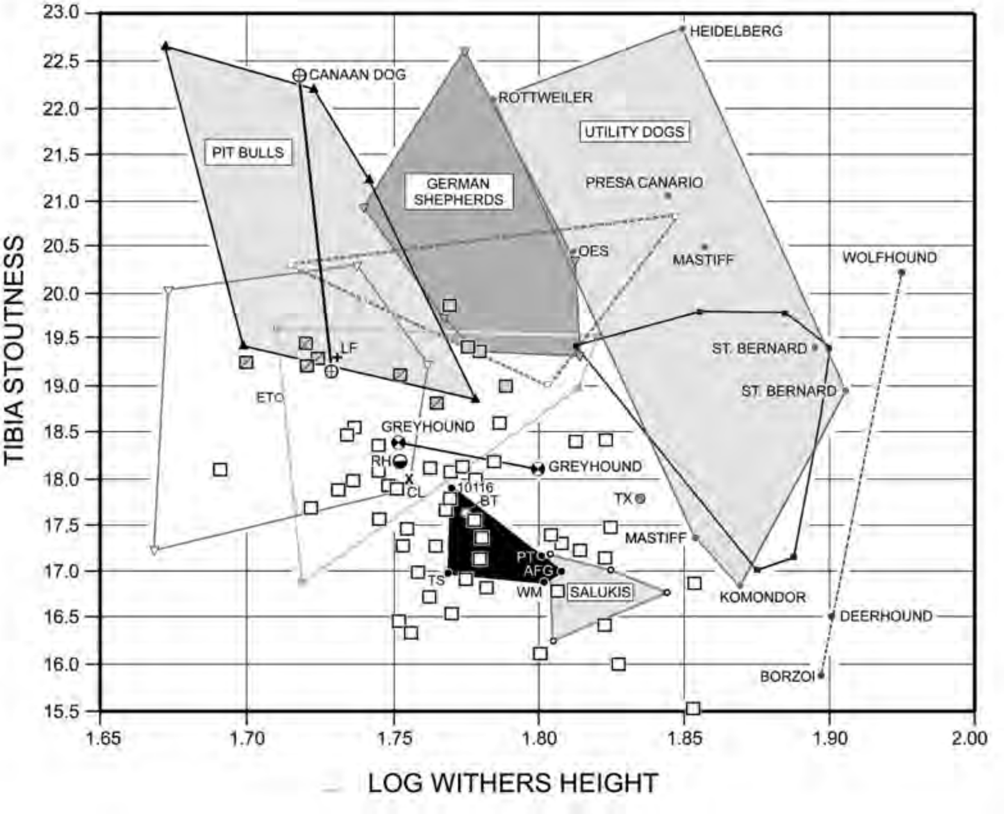

FIGURE S32

MTA analysis of tibia stoutness, calculated as BP × 100/GL. “X” symbol on this plot = Classe (data after Farello, 1995). Gray circle/ TX = Thistleton 4300-L (data from Baxter, 2010b).