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The dogs of Roman Vindolanda, Part I:
Morphometric techniques useful in differentiating domestic and wild canids

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ABSTRACT: The Roman-era fort-village complex at Vindolanda in northern England, occupied from about A.D. 50 to A.D. 415, has yielded extensive well-preserved remains of the domestic dog, *Canis familiaris*. Herein, utilizing a novel combination of biostatistical techniques to identify parameters that best differentiate canids, we test the hypothesis that the inhabitants of Vindolanda selectively bred dogs. We also differentiate dog remains from wolves and foxes, similarly-sized canids that occur throughout Eurasia. The Vindolanda dogs are less morphologically diverse than modern dogs but much more diverse than dogs of the British Neolithic and Iron Age. They are as morphologically diverse as dogs excavated from other Romano–British sites, and only slightly less diverse than the whole known population of Roman-era dogs sampled from across Europe and North Africa. Vindolanda dogs thus underwent greater directional selection than expected from natural environmental forces, suggesting that selective breeding rather than random panmixis maintained diversity. The Vindolanda dog sample will make an ideal subject for DNA analysis, since it contains dogs undergoing incipient diversification from dingo-like ancestors.

KEYWORDS: *CANIS FAMILIARIS*, CRANIOMETRICS, DE GROSSI MAZZORIN-TAGLIACOZZO ANALYSIS, DOMESTIC DOG, MULTIVARIATE ANALYSIS, PRINCIPAL COMPONENT ANALYSIS, ROMANO–BRITISH, VINDOLANDA

RESUMEN: El fuerte-poblado romano de Vindolanda en el norte de Inglaterra fue ocupado desde el 50 al 415 A.D. y ha proporcionado una importante colección de restos bien conservados de perro, *Canis familiaris*. En este trabajo, utilizando una combinación inédita de técnicas bioestadísticas para determinar los parámetros que mejor diferencian cánidos, verificamos la hipótesis referida a una cría selectiva de perros por parte de los habitantes de Vindolanda. Al tiempo, discriminamos los restos de perros de los de lobo y zorro común, dos especies de cánidos de talla semejante al perro distribuidos por toda Eurasia. Los perros de Vindolanda se encuentran morfológicamente menos diferenciados que sus parientes actuales pero mucho más que sus parientes británicos del Neolítico y Edad del Hierro. Su diferenciación morfológica es igual de amplia que la de los perros procedentes de otros yacimientos romano-británicos y solo ligeramente inferior a la documentada para todos los perros de época romana procedentes de Europa y el Norte de Africa. Por ello, parece que los perros de Vindolanda sufrieron una selección direccional superior a la esperada cuando se asume sólo la existencia de presiones ambientales lo cual sugiere que fue una cría selectiva, y no tanto una panmixis aleatoria de individuos, lo que mantuvo tal grado de diversificación. Los perros de Vindolanda constituyen un grupo ideal para realizar análisis de

ADN toda vez que parece incorporan individuos que manifiestan una diversificación incipiente a partir de antecesores con aspecto de dingo.

INTRODUCTION

The oldest undisputed dog remains go back about 15,000 years (Nobis, 1979; Crockford, 2000b; Morey, 2010), although the origin of dogs remains a contested topic. It now seems probable that there is no single source population for domestication but rather people from various areas independently brought wolf pups into captivity and began the domestication process.

Canid remains are frequently found at archaeological sites. Often these are attributed to dogs, but few researchers have rigorously tested how to tell dog remains from wolves or foxes, similarly-sized canids that occur throughout Eurasia (see Davis & Valla, 1978). Herein, we present criteria for differentiating dog, wolf, and fox remains and document the range of morphological variation in the dogs of Vindolanda, a nearly 2,000 year old site near Hadrian's Wall in north–central England which lay at the northwestern fringe of the Roman Empire. The canid remains constitute the largest and best-preserved sample of dog bones from any single site of Roman date in Britain.

With the current recognition of nearly 350 breeds of dogs by the World Canine Organization (Fédération Cynologique Internationale, FCI), it is clear that intense selection by humans has had a great effect on the morphology of this animal. Another major goal of this study is thus to characterize the initial differentiation of distinctive dog phenotypes from a generalized "primitive" morphology. We develop a comparative database of more than 500 recent specimens including red fox (*Vulpes vulpes*) and two samples of wolf (recent North American *Canis lupus* and late Pleistocene *Canis* from Natural Trap Cave, Wyoming; Martin & Gilbert, 1978). Feral *Canis familiaris* (Australian dingoes, Carolina dogs from the southeastern

U.S., and New Guinea singing dogs) are included in some comparisons. Our sample of modern domestic dogs comprises 179 individuals belonging to 83 breeds.

We extend the groundbreaking work of Harcourt (1974) and Baxter and colleagues (Baxter, 2002, 2010a, 2010b; Baxter & Nussbaumer, 2009; Phillips *et al.*, 2009) and introduce a novel procedure for morphometric analysis which combines principal components analysis (PCA) with the ratio comparison technique of De Grossi Mazzorin & Tagliacozzo (2000).

SITE LOCATION AND EXCAVATION HISTORY

Vindolanda is a fort–village complex situated 3 km south of Hadrian's Wall in northern England (Figure 1). It was occupied almost continuously from about A.D. 50 to the fall of the Roman Empire
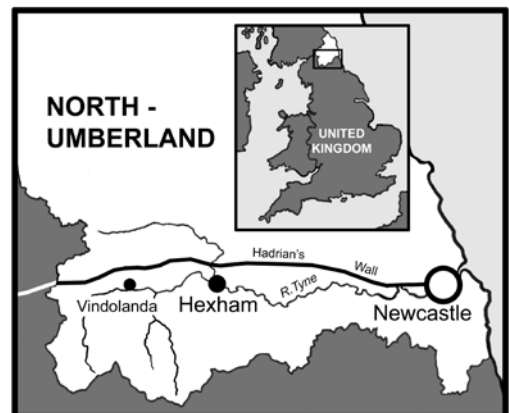

FIGURE 1

Vindolanda's location, 3 km (2 mi) south of Hadrian's Wall, within the United Kingdom and the county of Northumberland.

in A.D. 415 and beyond (Birley, 2003). Systematic excavation begun in the 1960s has yielded a collection of over 20,000 bones of birds and mammals. Fifty years of excavation at Vindolanda has demonstrated a complex succession of nine forts built one on top of the other over the whole period of its occupation (see Birley, 2003 and Blake, 2014 for summary). Bones, including those of dogs, have been recovered from every Vindolanda context and time period (Hodgson, 1977; Hambleton, 2003; Bennett, 2005, 2014; Bennett & Timm, 2013). Of these, some 520 or about 2.6% pertain to the domestic dog, *Canis familiaris*. We review and interpret the time-stratigraphic and specific context associations of Vindolanda dog bones in Part II of this series on the dogs of Roman Vindolanda (Bennett & Timm, 2016).

MATERIALS AND METHODS

Recovery, Comparison, Measurement and Analytical Techniques

Most Vindolanda bones were recovered by standard hand troweling methods, except those from below the East Granary (Bennett & Timm, 2013) which were recovered by 0.5-mm wet and dry sieving. Measurements were taken with electronic calipers and recorded to the hundredth mm. Parameters are a combination of those recommended by Lüps (1974), Driesch (1976), Nussbaumer (1978, 1982), and Baxter & Nussbaumer (2009) (Figures 3, 4). The relative downbending (klinorhynchy) or upbending (airorhynchy) of the snout was assessed using a six-inch fine-toothed contour gauge.

We employ a total of 26 variables in order to maximize sample size while ensuring a robust set of measurements for each skeletal element. Numerous literature reports on dogs of the Roman era reference collections unearthed and reported after Harcourt (1974); these are summarized in our dataset as "post-1974". In analyses utilizing previously published data, we ignore the small error
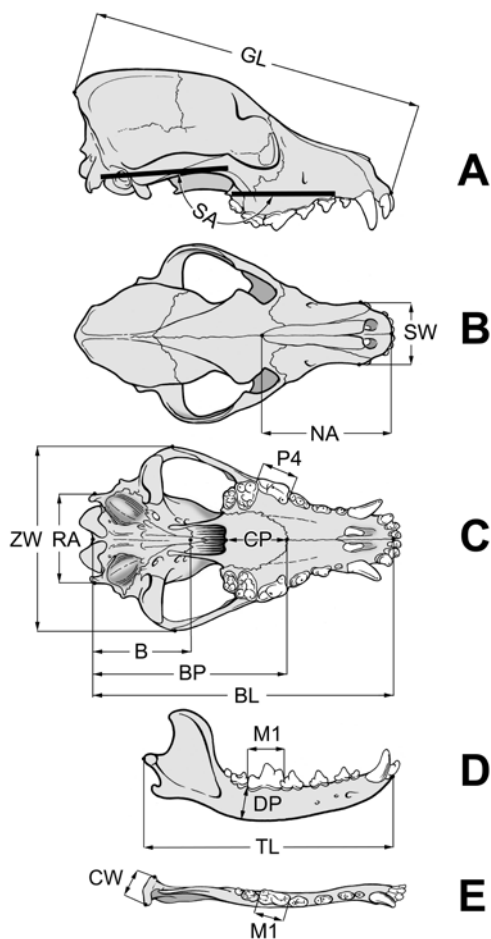

FIGURE 2

Measurements on skull and jaws. Heavy bars in (A) delineate the orientation of the basicranium and palate; the parameter SA (skull angle, called "β" by Nussbaumer, 1982; Baxter & Nussbaumer, 2009) represents the angular difference between them. (D, E) Measurements on jaw rami.
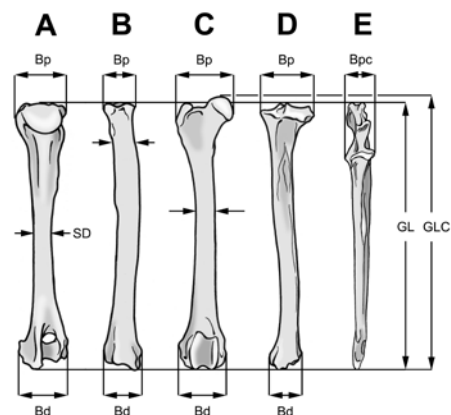

FIGURE 3

Measurements on limb bones. Letter abbreviations after Driesch (1976). (A), humerus; (B), radius; (C) femur; (D) tibia; (E) ulna.
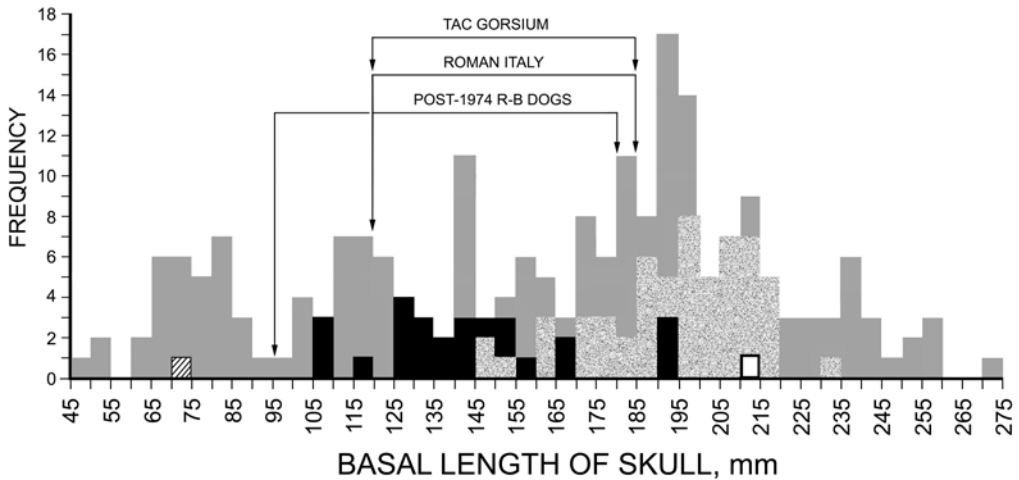
FIGURE 4

Raw size of skulls. Tac Gorsium data from Bökönyi (1984); Roman Italy from DeGrossi-Mazzorin & Tagliacozzo (2000); Classe from Farello (1995); Heidelberg–Neuenheim from Luttschwager (1965); Yasmina from MacKinnon & Belanger (2002).

that arises from different researchers performing the measurements (99% of measurements utilized in this study were taken by the senior author). We also ignore the small difference between minimum shaft diameter and mid-shaft diameter (we label this "composite" factor MSD). Statistical analysis was performed with Version 1.91 of the PAST freeware (Hammer *et al*., 2001).

Measurements and abbreviations for skulls and jaws are given in Figure 2 (A–E) and for limb bones in Figure 3 (A–E).

Procedure for Multivariate Analysis

The simplest analytical technique we employed consists of selected ratios, called indexes (Harcourt, 1974) (Figure 9). We utilized Principal Component Analyses (PCA's; Figures 10, 11) primarily to predict parameters that best differentiate canid skulls and jaws, and then constructed De Grossi Mazzorin–Tagliacozzo Analyses (MTA's, see discussion below; Figures 12–20) which effectively display them.

MTA (De Grossi Mazzorin & Tagliacozzo Analysis): Building upon Harcourt's (1974) work, De Grossi Mazzorin & Tagliacozzo (2000) hit upon the very useful idea of plotting limb stoutness index against projected withers height. MTA graphically compares a linear measurement with a ratio. Ideally the linear measurement is representative of

other measures of size, and the ratio represents a readily-interpretable aspect of body shape or conformation. The MTA technique can thus be generalized, for example to produce easily-interpreted graphical representations of selected skull parameters (Figures 12–15).

Limb-bone MTAs (Figures 16–20) efficiently separate dogs of different conformation and are especially useful because archaeological dog limb bones often survive in large numbers (for example Ayton, 2011). We use Harcourt's (1974) stoutness index (with MSD as numerator) for humerus, radius, and femur, but not for tibias or ulnas because the point selected for measurement of MSD on a bone with a continuously tapering shaft seems rather arbitrary. Therefore, for tibias we use a "stoutness index" (calculated as width across the proximal articular surface, Bp × 100) / bone length) (Figure 17), while for ulnas we use the breadth across the base of the humeral articulation (Bpc × 100/ bone length) (Figure 20). Utilizing a different numerator in calculating the tibia and ulna ratios yields different vertical scales, but the overall picture as shown by the MTA's is consistent with results for humerus, radius, and femur (Figures 16–20).

Because the number of parameters measured on postcranial bones was small and were known beforehand to be diagnostic, MTA's were constructed without the use of PCA in the analyses of limb bones (Figures 16–20 and see visual key, Figure 21). The very large dataset of modern domestic

dogs not included in PCA's has, however, been included in our MTA's whenever it was useful in providing an overall sense of morphometric range.

PCA (Principal Component Analysis): All measurements were converted to their base-10 logarithms prior to analysis, to make the allometric relationships between dimensions linear (Gould, 1966), to make all dimensions of approximately equal statistical weight (their means and ranges are of the same order of magnitude), and to reduce some biases common in biological data (positive skew, and small dimensions being inherently less variable than large) (Jolicoeur, 1963; Jolliffe, 2002: 24). Modern domestic dogs were omitted from PCA to give the remaining wild-type canid samples comparable statistical weight.

Herein, we significantly extend the multivariate analysis of canid bone measurements pioneered by Morey (1992, 2010) and Baxter and colleagues. For reasons outlined below, we prefer PCA to the DFA (discriminant function) or CVA (canonical variate) techniques used by some previous authors. PCA is not a technique for discriminating groups, but for visualising trends and clusters in multivariate data (Jolliffe, 2002: 1). A series of mutually orthogonal axes (the principal components, or PCs), with their origins at the data's multivariate mean, are fitted sequentially to account for as much as possible of the variability left unexplained by all previously-defined PCs (Jolliffe, 2002). The contribution of each of the original variables (here, the log-transformed dimensions) to each PC is calculated using "loadings" (Table 1) determined by the axis-fitting calculations (see Jolliffe, 2002 for an explanation of the mathematics employed). Geometrically, PCA can be thought of as re-cen-

tering the origin of the original variable axes (x, y, z, ...) to the center of the "cloud" of data-points (at its multivariate mean), and then rotating the Cartesian axes to the axes of the ellipsoid which best approximates the "data-cloud" (PC1, PC2, PC3, ...) (Hammer & Harper, 2006: 83). When the first two or three PC's account for most of the variation, the data-cloud can be usefully displayed in one or two two-dimensional plots using PC's as axes (see figure 4.5 of Hammer & Harper, 2006).

The 95% confidence ellipses included on our plots help to visualize any contrast in overall trend between the samples; their long axes are the line of best correlation between the two PC-scores for a sample, and their widths are a measure of the poorness of fit to that correlation (Jolliffe, 2002). The plots are biplots because they include "rays" for each variable defined by the PC loadings for that variable (Jolliffe, 2002: 90). The rays are useful for interpretation: their lengths show the relative amount of variation accounted for by each variable; they graphically show the contrast between variables for particular PC-scores (projections onto a PC-axis that are positive show they increase that PC-score, while negative projections show they reduce it); and variables that correlate closely have rays that lie close together (Jolliffe, 2002: 92).

We chose PCA over DFA or CVA for this study primarily because problems of functional interpretation are fewer and inferring causes for variation is simpler. PCA differs from DFA (a method for defining a formula that distinguishes two pre-defined groups), and canonical variate analysis (the extension of DFA used to distinguish more than two groups). Confusingly, CVA is sometimes also called DFA (as for example in Phillips *et al*., 2009).

0	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8	Axis 9	Axis 10	PC	Eigenvalue	% variance
BL	0.2908	0.2782	0.1213	0.023	-0.06584	-0.01941	-0.06443	-0.2068	0.4532	0.7522	1	0.101366	93.889
BP	0.303	0.2723	0.1325	-0.0518	-0.01066	0.1877	-0.0833	-0.06591	0.6113	-0.6273	2	0.00317995	2.9454
B	0.2605	0.3604	0.4818	-0.04089	0.1314	0.4821	0.1383	0.3516	-0.4135	0.07113	3	0.000930978	0.86231
P4	0.2952	-0.1861	-0.3345	0.6492	0.5379	0.2157	-0.04257	0.06789	0.04118	0.03159	4	0.000666405	0.61725
SW	0.3569	-0.2668	-0.00189	-0.5317	0.4535	-0.02885	0.3444	-0.4287	-0.0984	-0.01287	5	0.000608249	0.56338
ZW	0.3063	-0.03318	0.2254	-0.1187	0.2557	-0.5542	-0.6197	0.2603	-0.1193	-0.04047	6	0.000433925	0.40192
RA	0.302	0.275	-0.04772	0.269	-0.1489	-0.5806	0.6023	0.134	-0.08007	-0.1103	7	0.000320207	0.29659
CP	0.3733	0.191	-0.7154	-0.3346	-0.2741	0.1605	-0.1582	0.2179	-0.1607	0.03392	8	0.000258853	0.23976
PW	0.3334	-0.705	0.2018	-0.00363	-0.3919	0.104	0.1325	0.3596	0.1888	0.06425	9	0.000150888	0.13976
PL	0.3251	-0.0499	0.1343	0.3044	-0.4088	0.06252	-0.2448	-0.6151	-0.3956	-0.1241	10	4.85E-05	0.044908

TABLE 1

Parameter loadings for PC analyses. The Lüps basicranial measurements for skulls (BL, BP, B) account for the most variable and the greatest discriminatory power, as does condyle with (CW) for jaw rami.
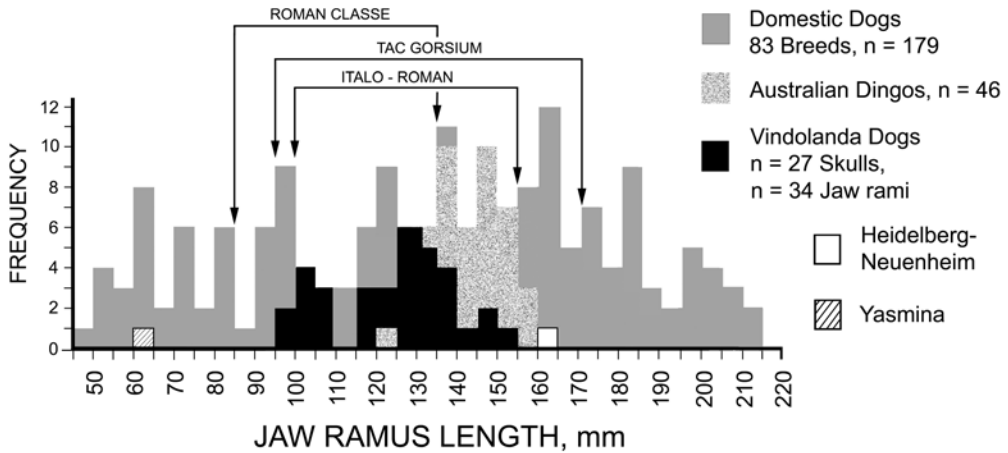
FIGURE 5

Raw size of skulls. Tac Gorsium data from Bökönyi (1984); Roman Italy from DeGrossi-Mazzorin & Tagliacozzo (2000); Classe from Farello (1995); Heidelberg–Neuenheim from Luttschwager (1965); Yasmina from MacKinnon & Belanger (2002).

In PCA the data for all the groups are pooled, the loadings for the variables are calculated to account for as much variability as possible regardless of group membership, and the analyst is left to assess the nature of the variability which might distinguish groups. In CVA the pre-defined groups are kept separate, the loadings for each variable on each canonical variate function (the functions are used as the axes in CVA plots) are calculated to maximize the differences in variability between the pre-defined groups compared to the variability within those groups (Reyment & Savazzi, 1999: 174), and the analyst uses the CV functions to assign individuals to the most appropriate group. This re-scaling to maximize group differences can mean that novel groups go unrecognised, the values of the loadings can be quite different even if the samples used to define the groups are similar, and the interpretation of the functions are obscure (Reyment & Savazzi, 1999: 173, 204).

Because dog morphotypology does not have the same basis as the assignment of breed identity, it is not appropriate on the basis of morphometric analysis to suggest that any ancient dog "belongs to" any modern breed. The present study focuses on differentiating the Vindolanda dog population *as a whole* from other canid groups. A range of dog morphotypes is certainly present in the Vindolanda dog collection; their particular characteristics and methods for distinguishing them are the subject of forthcoming papers (Bennett & Timm, in prep.).

RESULTS

Frequency of Skeletal Elements

A total of 520 bones of domestic dogs have been recovered from excavations carried out between 1960 and 2014 at Vindolanda (2.6% of all bones recovered). The collection includes 39 partial to nearly complete skulls (due to breakage, not every measurement could be taken on every skull). Six of the skulls have at least one associated jaw ramus; five have associated postcranial elements. There are 59 jaw rami, of which 9 (15%) are juvenile with evidence of erupting teeth. The total Vindolanda collection comprises a maximum number of 317 individuals distributed over a stratigraphic range of approximately 350 years [detailed stratigraphic analysis appears in Part II (Bennett & Timm, 2016)].

Raw Size Distribution

That more than one size-class of dog existed at Vindolanda has previously been demonstrated through study of pawprints impressed in ceramic building materials (Higgs, 2001; Bennett, 2012). In Figure 4, Vindolanda skulls complete enough to obtain a measurement of basal length are compared to a sample of 83 domestic dog breeds and to three

FIGURE 6

Series of humeri (to scale) demonstrating size range of Vindolanda dogs, with comparisons to wolf, Australian dingo, and seven modern domestic breeds. A, Dachshund LACM 30598, 74 mm; B, Pomeranian KU 51-Z, 78 mm; C, Vindolanda VH-102 29712, 92 mm (reversed); D Vindolanda E93-112 3190, 94 mm (estimated); E, Vindolanda V06-54A 5832, 96 mm (reversed); F, Scotch Terrier LACM 30541, 99 mm; G, Vindolanda V02-17016 (SF 8659), 120 mm; H, Cocker Spaniel UNSM ZM-15573, 136 mm; I, Vindolanda V14-33B 29151, 150 mm; J, Chow-chow LACM 30423, 151 mm; K, Vindolanda VI-82 10132, 153 mm; L, Dingo ANM M-7386, 164 mm; M, Greyhound UNSM ZM-14252, 172 mm; N, Vindolanda VI-24 10129, 179 mm; O, Vindolanda V04A 996, 188 mm (reversed); P, Vindolanda V1997-19 16742, 190 mm; Q, Great Pyrenees, KU 165573, 207 mm; R, Wolf UNSM-ZM 28814, 242 mm. Institutional abbreviations: ANM = Australian National Museum; KU = The University of Kansas; LACM = Los Angeles County Museum of Natural History; UNSM ZM = University of Nebraska Zoological Museum.

types of feral dogs. Most of the Vindolanda skulls range from 125–160 mm in basal length. The median size of modern feral dog skulls equals the size of the largest Vindolanda skulls, while the smallest modern feral dog skulls lie near the median size for Vindolanda skulls.

Dog jaw rami are far more frequently found on archaeological sites than skulls. As with the skulls, the Vindolanda jaws fall near the center of the very wide range represented by modern domestic dogs (Figure 5), and the median size of the Vindolanda dogs is smaller than the median size for Australian dingoes. The size range of Vindolanda dogs is less than that for Tac Gorsium site in Hungary (Bökönyi, 1984) and much less than Heidelberg–Neuenheim site in Germany (Luttschwager, 1965). The late-Roman site at Classe in Italy (Farello, 1995) contains some jaws significantly smaller than any so far found at Vindolanda. Baxter (2010 a, b) has reported small Romano–British dogs but the Yasmina skull (MacKinnon & Belanger, 2002) is smaller than any so far known from Roman Britain.

Baxter (2002, 2010a, 2010b) was the first to clearly distinguish between dwarfs (chondrodystrophic dogs; see Koch *et al*., 2003; Parker *et al*., 2009), which have limb bones that are short, thick, broadened at both ends, and often twisted, vs. miniatures (whose smallness is due to pituitary or thyroid dysfunction; Crockford, 2000a; Sutter *et al*., 2007; Boyko *et al*., 2010). The limb bones of miniatures, though small, are normally or almost normally proportioned and straight. Dwarf dogs are very common on Romano–British sites, with numerous finds of their distinctive limb bones. Baxter (2010b) points out that we know less about the miniatures; to date the only nearly-complete skeletons that have been published come from Yasmina (MacKinnon & Belanger, 2002) and Heidelberg–Neuenheim (Luttschwager, 1965). In Roman Britain, there appear to have been at least two different types of miniature dog, the smaller the size of a Chihuahua, Pomeranian, or Maltese (about 25–30 cm shoulder height), the larger about the size of a Miniature Poodle (around 30–35 cm shoulder height) (Baxter, 2010a, b).

The range in Vindolanda limb bone lengths (Figures 6–8) parallels the range in skull and jaw sizes. The tallest are shorter than small wolves, while the shortest are taller than some of the smallest modern dogs and also taller than Roman-era dogs from Neidelberg–Neuenheim (Luttschwager, 1965) or Yasmina (MacKinnon & Belanger, 2002). Neither pawprints in tile (Bennett, 2012) nor cranial material indicates the presence of the smallest form at Vindolanda, but a few small tibias and femurs (Figure 8A, B) are as small as the smallest Romano–British dogs reported by Harcourt (1974), Baxter (2002, 2010a, b) and Ayton (2011).
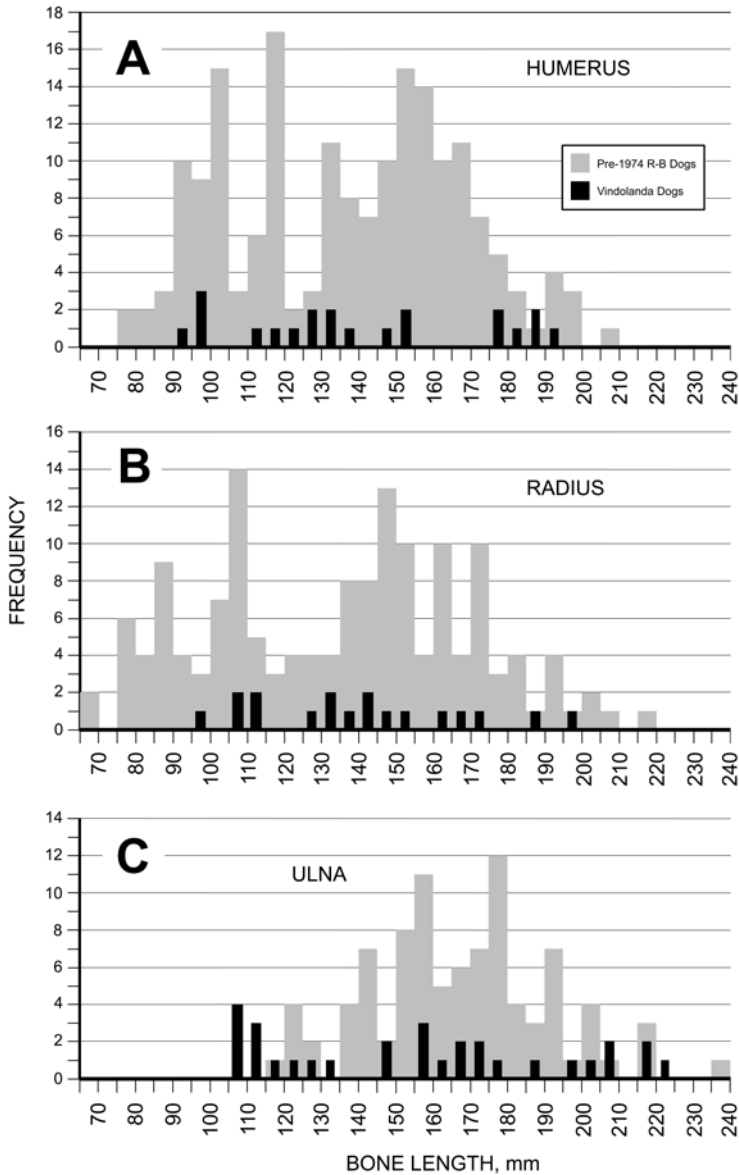
FIGURE 7

Raw size of long bones of the forelimb: humerus (A), radius (B), ulna (C).

Results of Morphometric Analysis

Cranial Index (Figure 9): The range represented by Vindolanda cranial and limb bone indexes is much less than those pertaining to domestic dogs (limb bone indexes are represented on the "y" axis in our MTA analyses, Figures 12–20). The range of skull indexes equals that of dingoes. Snout widths of Vindolanda dogs are greater, while snout length is less. Ratios describe conformation, so that overall it appears that the inhabitants of Vindolanda preferred dogs with broad heads, broad snouts, and muzzles proportionally somewhat shorter than those of dingoes.
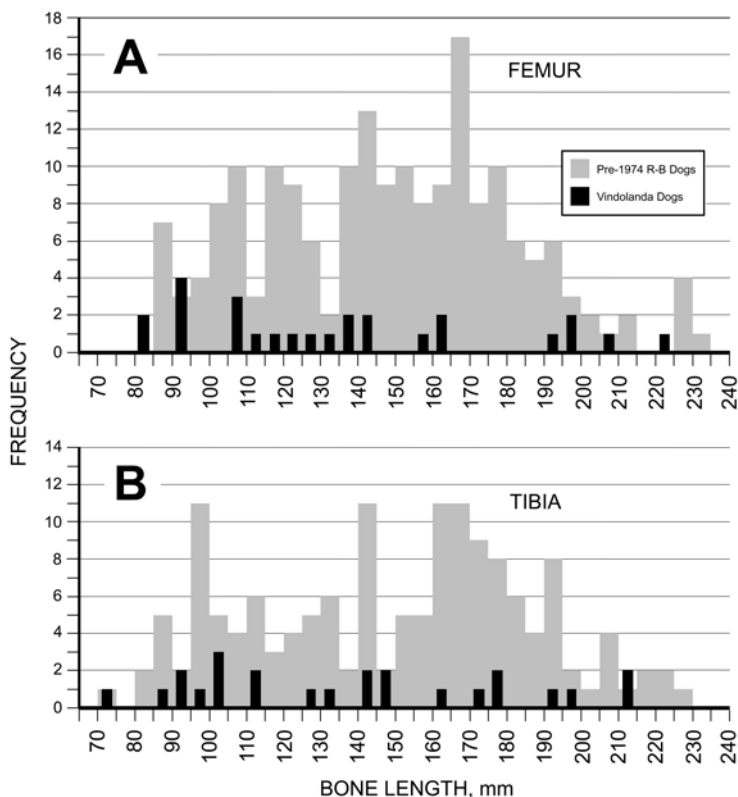
FIGURE 8

Raw size of long bones of the hind limb: femur (A), tibia (B).

Principal Components Analysis (PCA): The first principal component of the PCA on the four jaw parameters accounts for the great majority of the variation in the data (96.6%), and all the loadings are positive (all the biplot rays on Figure 10A are positive for PC1), making PC1 a rough allometric size measure for these canid types. Mandible depth (DP) is a good proxy for size, having a significant loading for PC1 but near-zero loading for PC2. The biplot shows foxes have the smallest jaws, dingoes are about average, wolves the largest, and Vindolanda dogs have a range of jaw sizes much greater than any other canid type, suggesting that Vindolanda dogs underwent greater directional selection than expected from natural environmental forces.

Components PC2 and PC3 accounted for comparable amounts of the remaining variation (1.6% and 1.1%, respectively). The biplot of PC2 and PC3 (Figure 10B) shows a considerable contrast between jaw length (TL) and condyle size (CW) (their biplot rays point in nearly opposite directions). The average positions for the canid types (the centers of their 95% confidence ellipses) were reasonably well-separated along this "axis of contrast", even the two types of wolf (which were not distinguished on Figure 10A). A jaw "shape" variation that contrasts between canid types is therefore likely to be expressed by a ratio of CW/TL. Since size is principally related to jaw depth, we use DP in an MTA plot with this ratio to discriminate canid types (Figure 12).

The first principal component of the PCA on 10 skull parameters accounts for the great majority of the variation (93.7%), and all the loadings are positive (all the biplot rays on Figure 11A are positive for PC1), making PC1 a rough allometric skull-size measure for these canid types generally. Zygomatic width (ZW) and palate length (PL) are the main measures of size, having significant loadings for PC1 but near-zero loadings for PC2; carnassial length (P4) might also be a workable
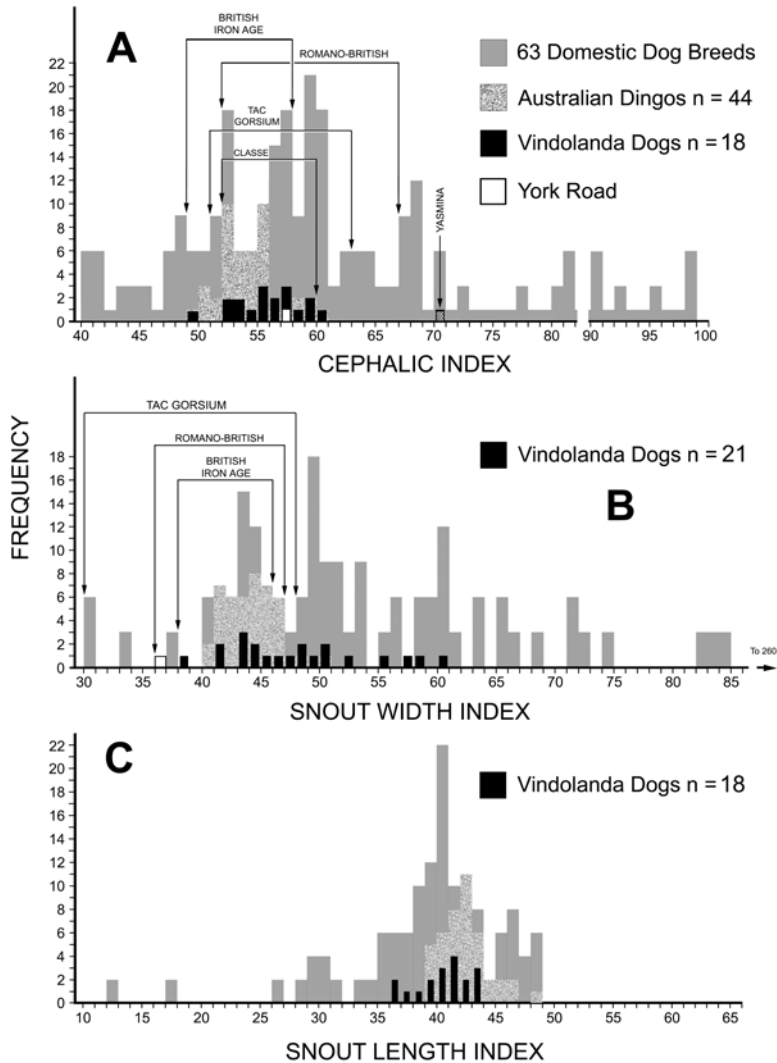
FIGURE 9

Harcourt's (1974) skull indexes applied to a sample of modern domestic dogs, Australian dingoes, the Vindolanda dogs, and several European dog-producing sites of Roman and Iron Age date. (A) Cephalic index, (B) Snout width index, (C) Snout length index. British Iron Age and Romano–British ranges from Harcourt (1974); Tac Gorsium (Bökönyi, 1984), Classe (Farello, 1995); York Road (Baxter, 2002).

general size measure, although its PC2 loading was somewhat larger. The biplot (Figure 11A) is similar to that for the jaws (Figure 10A): foxes are small-skulled, dingoes about average, wolves large, and Vindolanda dogs much more morphologically diverse than natural wild-type canids.

Component 2 accounted for considerably more of the remaining variation (2.9% of the total) than PC3 (0.9%); it is possible that PC3 principally represents natural variation (differences in skull size

and shape expected between twins, for example) or measurement error (Figure 11B). The loadings of PC2 tend to be positive for parameters of the back of the skull (B, BP, RA) and negative for mouth parameters (PW, SW, perhaps P4) suggesting that brain-case shape contrasts with mouth shape. The conclusion that the fore-part and hind-part of the skull are fairly free to grow in different ways within domestic dogs (Drake & Klingenberg, 2010) may thus also be true for other canids.
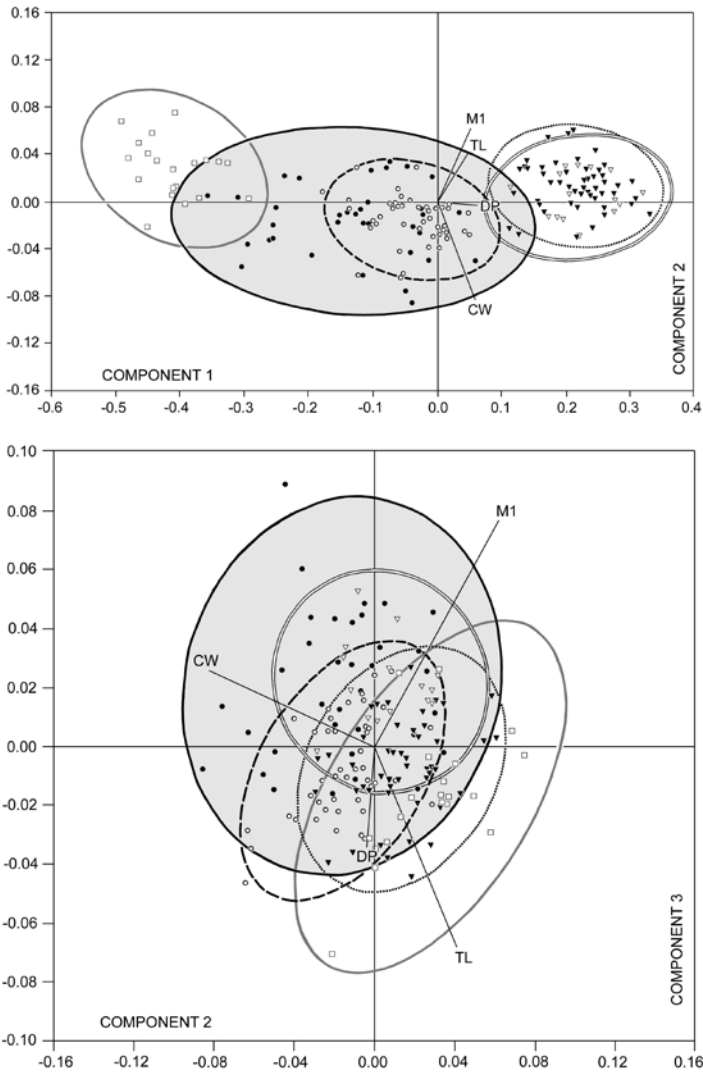
FIGURE 10

Principal component (PC) plots for jaw rami. Ellipses represent 95% confidence. See Figure 1 for measurement abbreviations.

The biplot of PC2 and PC3 (Figure 11B) shows a close relationship between palate width (PW) and snout width (SW); the greater loading of PW suggests that palate length tends to increase much faster than snout width. These two dimensions contrast with braincase dimensions, especially spine-articulation width (RA) (their biplot rays point in nearly opposite directions). The average positions for the canid types (the centers of their 95% confidence ellipses) are reasonably well-separated along this "axis of contrast". A skull "shape" variation that contrasts between canid types is therefore likely to be expressed by a ratio of RA/PW. Since palate length is the better preserved of the two comparable measures of "size", we used PL in an MTA plot with this ratio to discriminate canids with differing relative neck strength (Figure 13). The considerable contrast in allometry between SW and PW suggests that mouth shape may also alter significantly with mouth size; a ratio expressing the "pointedness" of the snout (SW/PW) was therefore plotted with mouth size (PL) as an MTA (Figure 14).
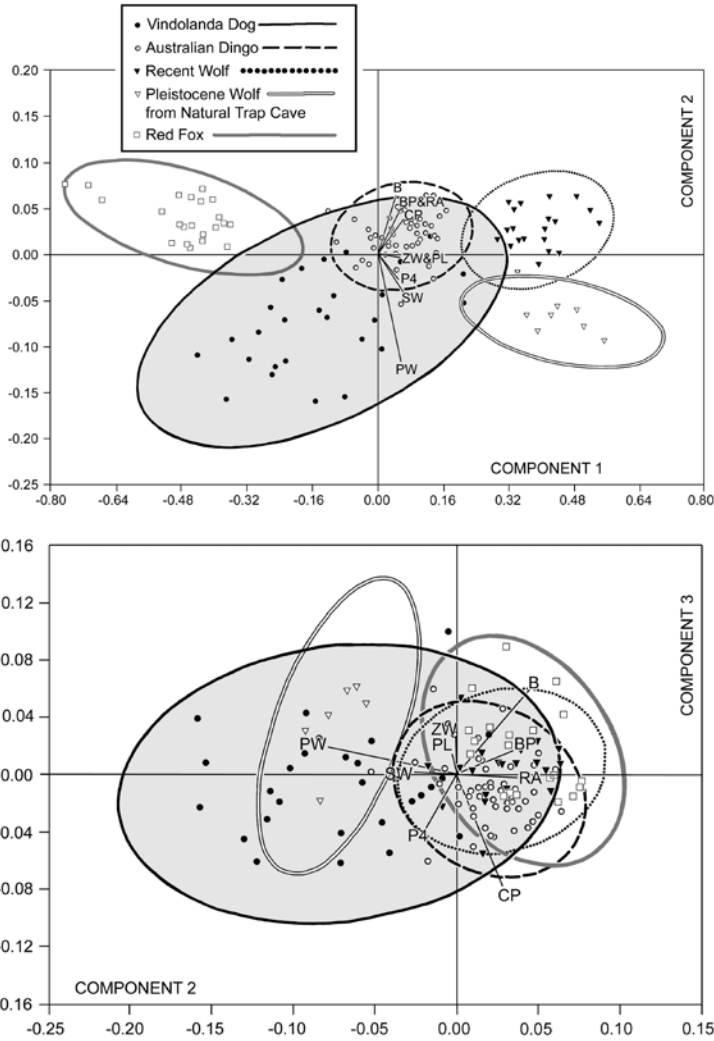
FIGURE 11

Principal component analysis (PCA) plots for skulls, based on 10 measured parameters. Ellipses represent 95% confidence. See Figure 1 for measurement abbreviations.

De Grossi Mazzorin–Tagliacozzo Analysis (MTA): The bones of wolves are clearly differentiated by MTA from those of dogs, and the analysis suggests that wolf bones are generally rare or absent from Roman-era archaeological sites across Europe. Limb elements of foxes, however, are more problematic. The postcranial elements of dogs most likely to be confused with red fox are the tibia and femur; indeed, there is no guarantee that some bones reported in the literature as dogs, and treated as such in our analyses, do not actually belong to foxes (particularly likely in the case of Romano–British tibias, Figure 17). Forelimb elements overlap much less (Figures 18–20). Limb bones of foxes can be differentiated on the basis of detailed morphology from those of small dogs, and in a forthcoming paper we contrast fox postcranials from Vindolanda with small dogs of modern times and the Roman era.

MTA plots make it clear that the Vindolanda dog population, like Roman-era collections from other localities, is much more morphologically
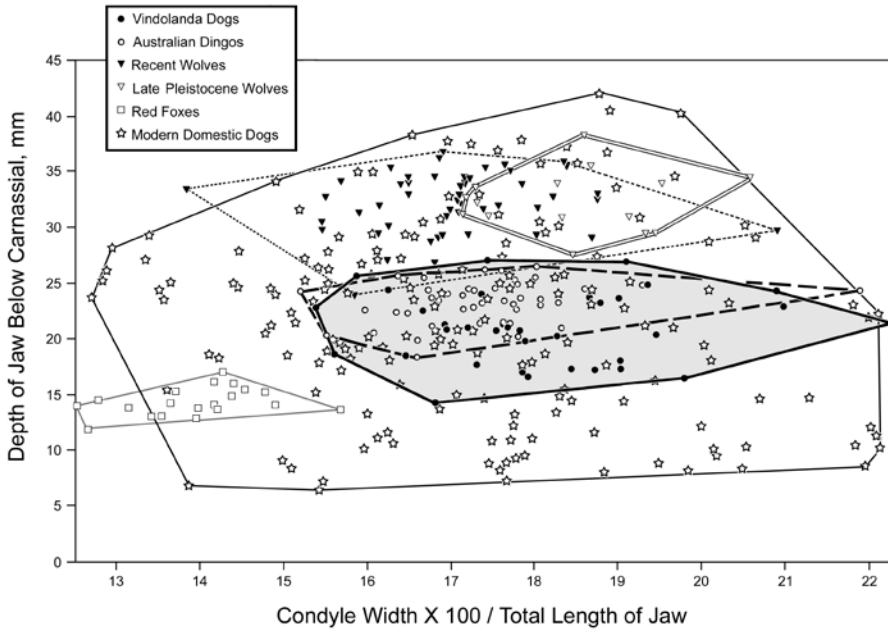
FIGURE 12

MTA plot for jaw grip strength. In this and subsequent figures, the Vindolanda hull is shaded gray for added clarity. Abbreviations as in Figure 2.
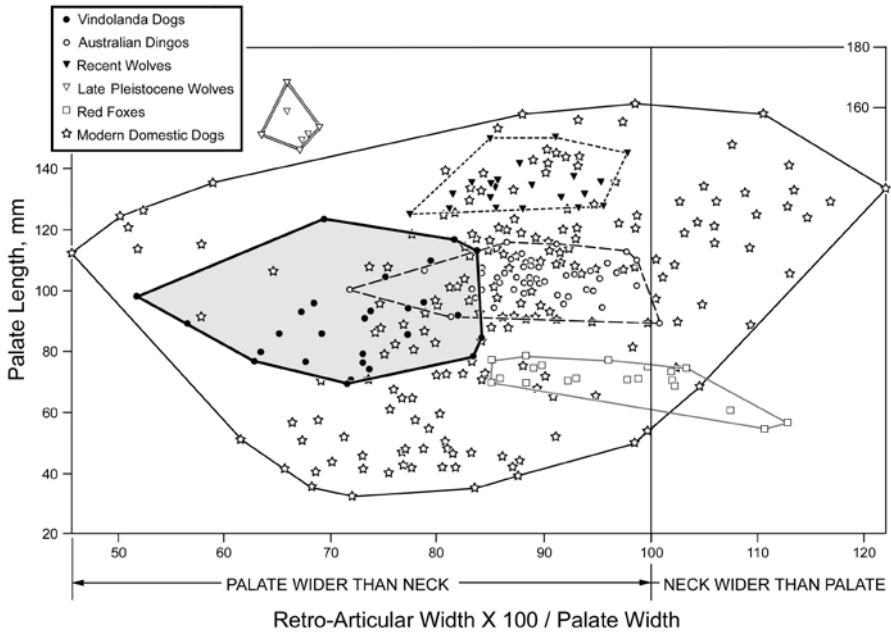

FIGURE 13

MTA plot for relative neck strength. Abbreviations as in Figure 2; symbol key as in Figure 12.
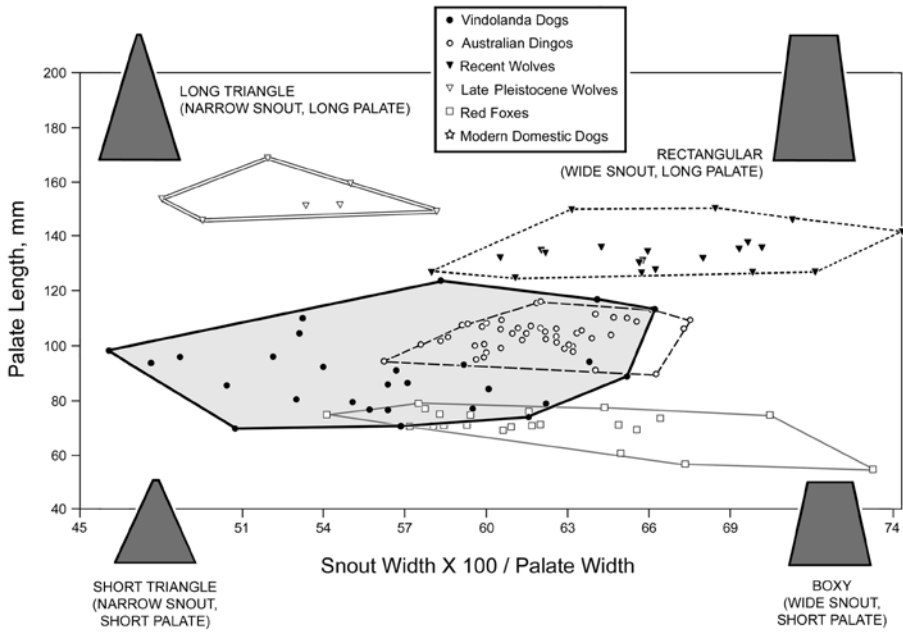
FIGURE 14

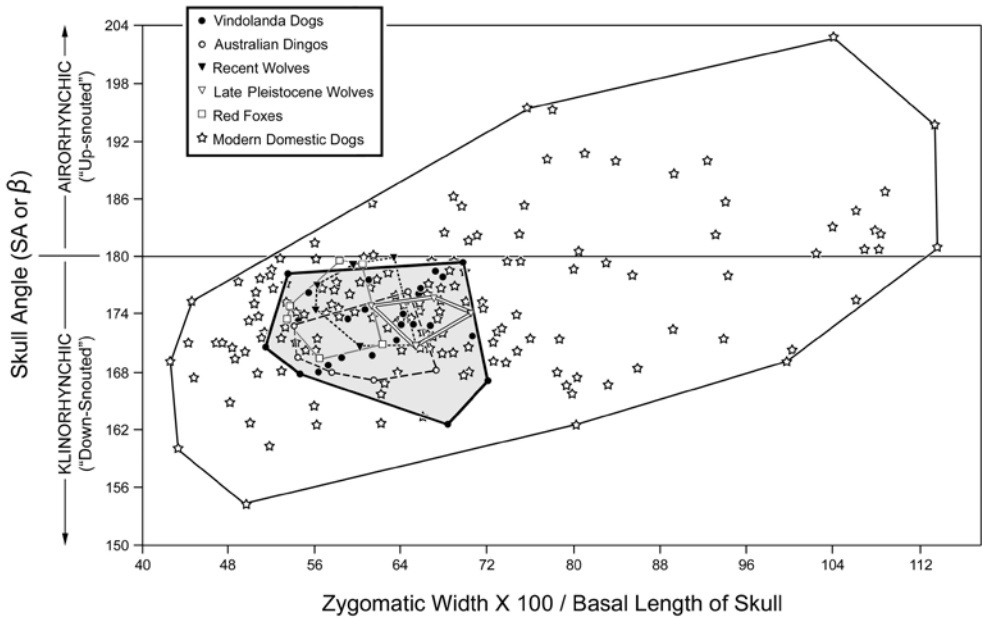MTA plot for mouth shape. Abbreviations as in Figure 1; symbol key as in Figure 12.

FIGURE 15

MTA plot for snout declination (SA or β), showing that all wild, feral, and ancient canids studied are klinorhynchic. The many airo-rhynchic modern dogs (stars above the 180° line) belong to such breeds as Pugs, Boston Terriers, English Bulldogs, Pekingese, Pomeranians, and Lhasa Apso.

diverse than the putative "primitive" dog mor-
photype represented by the Australian dingo. As
predicted by Harcourt's (1974) work, we find that
Romano–British dogs are also much more diverse
than those of the British Neolithic, but interestingly
there is no conformational overlap between "prim-
itive" Australian Dingoes and our small sample of
Neolithic dogs.

The Vindolanda population does not cover as
great a morphologic range as that of the sample of
modern domestic dogs included in this study, nor
does the area of the Vindolanda hull in Figures 16–
21 equal that of other Romano–British collections
compared. The very large sample from Tac Gorsi-
um equals or even (in presenting very stout radii,
humeri, and femurs for dogs of medium height)
exceeds the range for our sample of domestic dogs.

Snout Declination: Nussbaumer (1982) invent-
ed the measurement technique and gives valuable
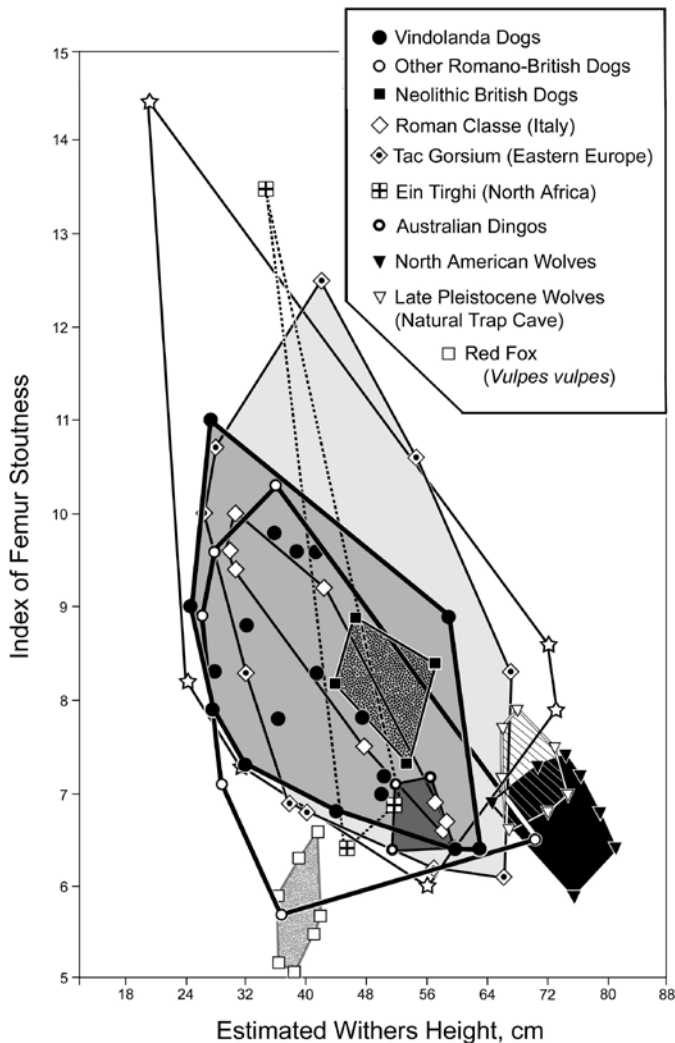comparative data. Snout declination is measured

FIGURE 16

MTA plot for femurs. Index of femur stoutness computed as GL × 100/msd (see Figure 2 for anatomical abbreviation). Tac Gorsium data from Bökönyi (1984); Ein Tirghi (Churcher, 1963); Roman Classe (Farello, 1995); British dogs of the Neolithic (Burleigh *et al*., 1977). Romano–British data are all post-1974, reported by Baxter (2002, 2010a, b, and pers. comm.), Baxter & Nussbaumer (2009), Grimm (2007), and Ayton (2011). In this and next several figures, only extreme data points that define the various hulls are shown, except Vindolanda data points which are plotted as black dots. Stars = recent domestic dogs.
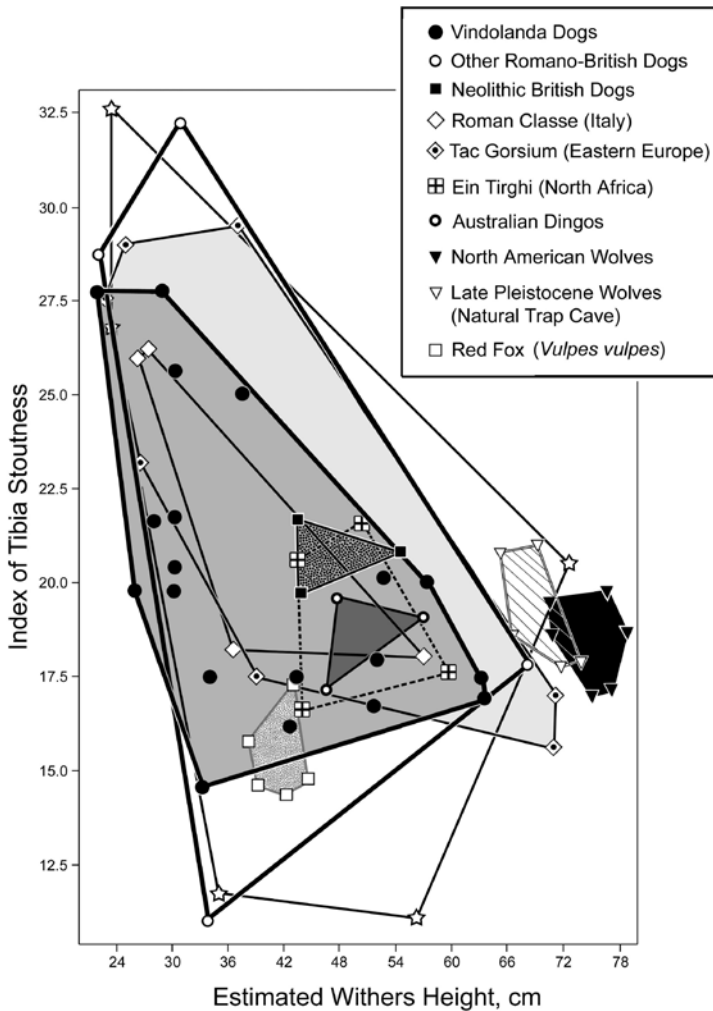
FIGURE 17

MTA plot for tibias. Vindolanda dogs are compared with several British and European continental dog-producing sites of Roman and Neolithic date. Index of tibia stoutness computed as GL × 100/Bp. Sources as in Figure 17; key to symbols as in Figure 16; anatomical abbreviations Figure 2.

by applying a carpenter's contour-gauge along the midline basicranium and caudal palate, transferring the resulting shape to paper, then using Photoshop tools to measure the angular difference between the basicranium and palate. Results are accurate to about +/- 1°. All Vindolanda dogs are klinorhynchic ("down-snouted"), with a few falling into the 0 to 10° range. The MTA plot (Figure 15) of cranial index vs. SA (called "β" by Nussbaumer, 1982 and Baxter & Nussbaumer, 2009) shows that the range in Vindolanda dog skulls is greater than in modern wolves, Pleistocene

wolves, red foxes, or Australian dingoes; and that the range in modern dogs is in turn much greater than in the Vindolanda collection of skulls. The most klinorhynchic modern dogs are certain types of terriers, i.e. Bull, Scotch, and Bedlington, which can be as much as 26° "down-snouted". The total range of klinorhynchy among Vindolanda dogs is 0.8 to 17.5° "down", whereas the total range in the sample of modern domestic dogs included in our study is from 23° airorhynchic ("up-snouted") to 26° "down-snouted".
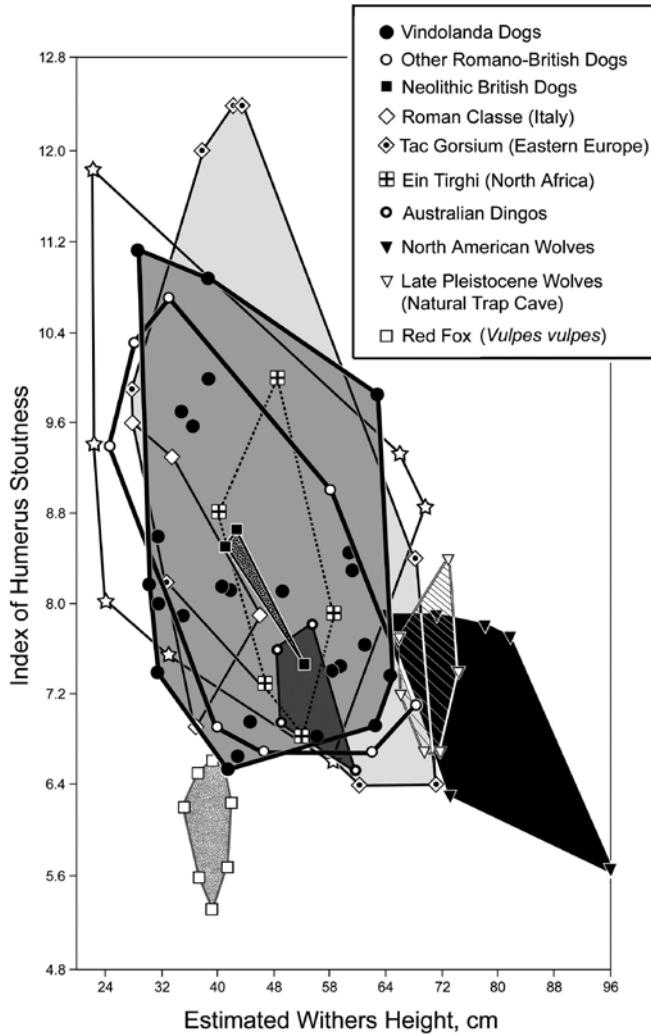
FIGURE 18

MTA plot for humeri. Vindolanda dogs are compared with several British and European continental dog-producing sites of Roman and Neolithic date. Index of humerus stoutness computed as GL × 100/msd. Sources as in Figure 17. Key to symbols as in Figure 16; anatomical abbreviations Figure 2.

DISCUSSION

The Study of Variability in Roman-Era Dogs

Several reports document dog diversity from Roman-era sites on the European continent and North Africa (Churcher, 1963; Luttschwager, 1965; Bökönyi, 1984; Farello, 1995; Bartosiewicz, 2000; De Grossi Mazzorin & Tagliacozzo, 2000; MacKinnon & Belanger, 2002). Using a sample of 1200 long bones, 154 skulls and 325 mandibles from 80 sites in Ireland and Britain ranging in age from Mesolithic to post-Roman, Harcourt (1974) demonstrated a dramatic increase in the range of British dog types—especially the advent of small dogs standing less than 35 cm high—coinciding approximately with the beginning of the Roman occupation of the British mainland. With more refined dating, Clark (1995) suggested that small dogs first appear in the British archaeological record somewhat earlier, in the late Iron Age. Our
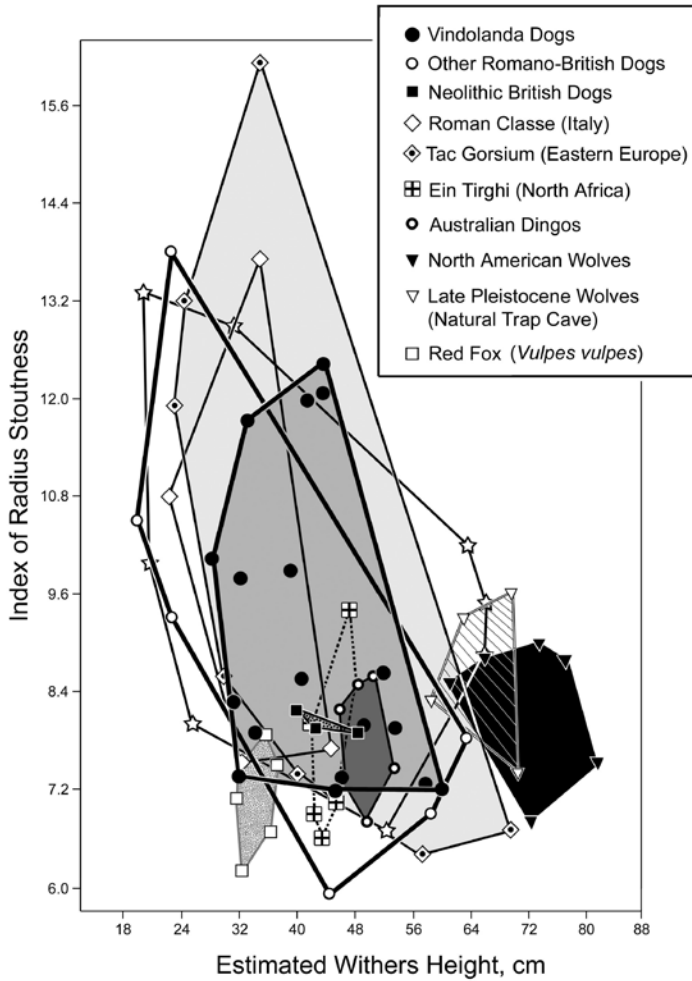
FIGURE 19

MTA plot for radii. Vindolanda dogs are compared with several British and European continental dog-producing sites of Roman and Neolithic date. Index of radius stoutness computed as GL × 100/msd. Sources and key to symbols as in Figure 16; anatomical abbreviations Figure 2.

results confirm that deliberate selection for phenotypes different from a putative dingo-like ancestor began no later than the Neolithic in Britain.

Harcourt's (1974) indexing technique proved useful in differentiating dog types, especially cranial length vs. zygomatic breadth (cephalic index), snout length vs. skull length (snout length index), and muzzle breadth vs. snout length (snout width index) (Figures 9A, B, C). His work primarily relies upon these factors plus raw size for differentiation. Harcourt (1974) also developed multiplication factors for the estimation of dog stature ("shoulder" or "withers" height) from length measurements

of isolated limb bones. Because they were created from a population of dogs of normal ("eumorphic") build, these factors are most accurate for dogs of medium height but tend to overestimate withers height in short-statured dogs, especially the bandy-legged "brachymel" dwarfs such as modern Dachshunds and Corgis (Baxter, 2002). Harcourt (1974) also introduced the very useful concept of relative limb stoutness, the ratio of minimum shaft diameter to length.

De Grossi Mazzorin & Tagliacozzo (2000) built upon Harcourt's work by creating bivariate plots of limb stoutness index against projected withers
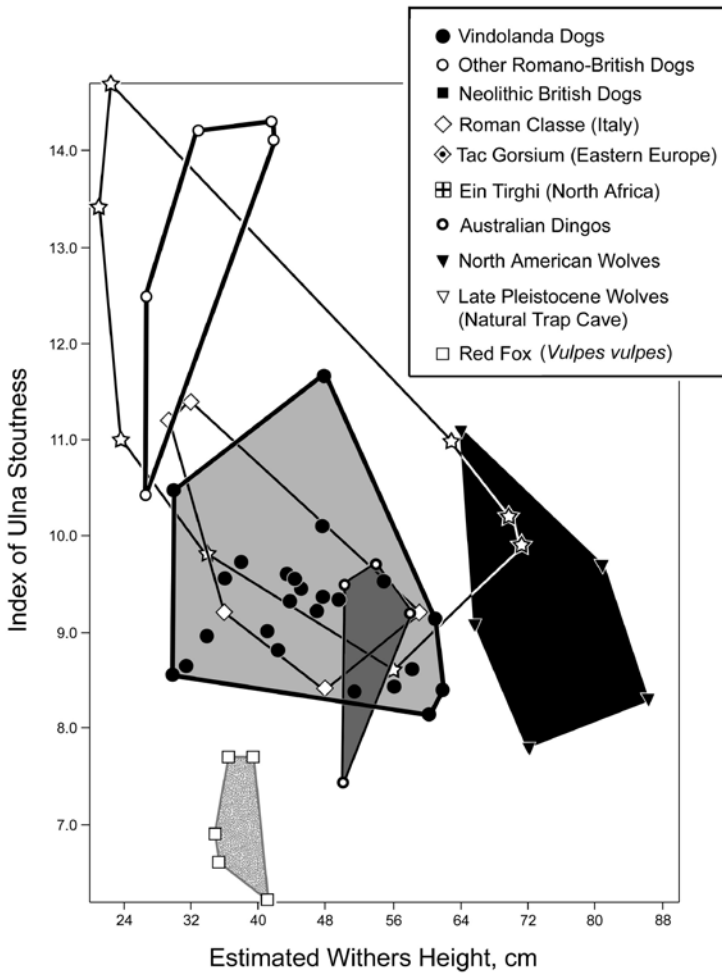
FIGURE 20

MTA plot for ulnas. Because Bpc is rarely reported, Vindolanda dogs are compared only with dwarf and miniature Romano–British specimens reported by Baxter (2002, 2010a, b, and pers. comm.); the hulls enclosing Baxter's specimens and those from Vindolanda are disjoint because very small dogs are rare at Vindolanda. Pleistocene wolves are omitted because no ulnas were available. Ulna stoutness computed as GL × 100/Bpc. Key to symbols as in Figure 16; anatomical abbreviations Figure 2.

height ("MT" analyses or MTA's). The resulting charts are easy to interpret and allow quick visual differentiation of long-bone material pertaining to dwarf, miniature, normal, gracile, and massive dogs (Figures 16–21). MTA shifts the emphasis away from heavy reliance upon skulls and jaws and is useful because archaeological cranial material is sometimes unavailable and often fragmentary, whereas limb bones often survive whole and in large numbers (Churcher, 1963; Bökönyi, 1984; Johnstone & Albarella, 2002; Grimm, 2007; Ayton, 2011).

Morphometric Techniques for Distinguishing Canids

This study responds to numerous pleas in recent literature (Clark, 1995; Baxter, 2000; Clutton-Brock, 2000; Cram, 2000; Crockford, 2000a, b) for new, practical approaches to the differentiation of canids. Multivariate analysis is not new –Clutton-Brock *et al*. (1976) applied it to the problem of differentiating dogs in the British archaeological record, and Morey (1992) used it for American ones– but it was otherwise essentially ignored in the study of archaeological dogs until studies by Baxter and
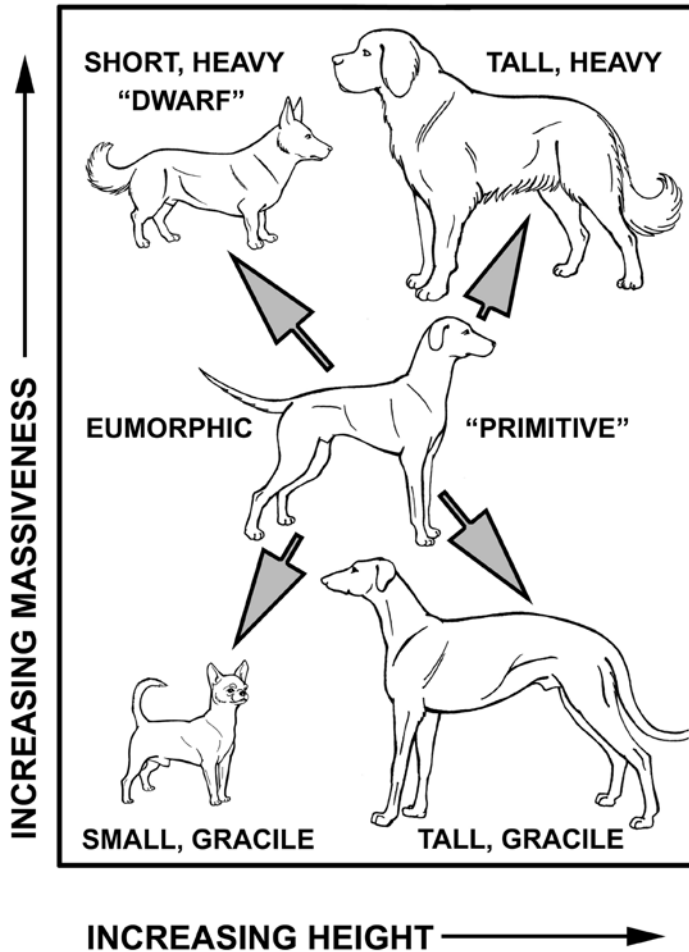
FIGURE 21

Visual key for the interpretation of Figures 15–19.

colleagues (Baxter & Nussbaumer, 2009; Phillips *et al.*, 2009). Possibly because the results it produces are easier to interpret, Harcourt's (1974) indexing technique by contrast became standard.

Although less sophisticated than multivariate analysis, indexes remain useful in differentiating canids. In some cases –especially where the parameters which make up the index are likely to reflect different selective pressures and thus different rates of growth– individual linear measurements work better than indexes. For example, Clutton-Brock (1969) suggested that the length of the superior carnassial in wolves is typically greater than the combined length of the superior M2 and M3, the reverse being characteristic of domestic dogs. Our measurements demonstrate this to be true 65% of

the time, with modern domestic dogs, Australian dingoes, modern wolves, and some of the Vindolanda dogs all presenting exceptions. However, PCA led us to realize that P4 length alone correctly identifies dog vs. wolf over 90% of the time (Figure 11; i.e., P4 length > 22 mm likely indicates a wolf).

A completely different approach has been taken by Nussbaumer (1982). His technique for measuring klinorhynchy–airorhynchy in dog skulls is both novel and useful, and Baxter & Nussbaumer (2009) applied it to a dog from Iron Age Britain. We find airorhynchy ("up-snoutedness") to be an excellent character which occurs only in certain types of modern dogs (Figure 15). No wild or feral dog we have so far examined is airorhynchic,

although some are essentially straight-headed with skull angle (SA or "β") = 180°. Low degrees of klinorhynchy (180 to 170°, i.e. from 0° to 10° of "down-snoutedness") are characteristic of both wolves and certain breeds of large dog, for example German Shepherd/Alsatian, Mastiff, Newfoundland, Greenland Dog, and Wolfhound. Some small modern breeds which are "incipiently" or occasionally airorhynchic, for example Pekingese, Pug, and Spitz, also record in the 0° to 10° range. Airorhynchy does not, however, correlate merely with smallness; there are many breeds of small dog that are moderately to strongly klinorhynchic, for example Dachshund, Mexican Hairless, and miniature and toy Poodles (and see Nussbaumer, 1982). All Vindolanda dogs are klinorhynchic.

Like Harcourt's (1974) technique, De Grossi-Mazzorin & Tagliacozzo's (2000) innovative (MTA) method relies upon ratios but contrasts the ratio with a linear measurement. In contrast to PCA or DFA, MTA presents few interpretive difficulties, but especially when many parameters are measured it offers no guidance as to which should be compared. The MTA technique becomes more useful after PCA identifies which parameters have the greatest discriminatory power.

The PCA's and MTA's employed in this study demonstrate that the population of dogs from Roman Vindolanda encompass a far greater range in size and morphology than dogs from earlier archaeological periods. The Vindolanda dogs also far exceed a comparison sample of Australian dingoes, which represent the putative "primitive" morphology achieved by feral, pariah, and village dogs worldwide when they are allowed panmictic access to mates (Morey, 1992; Corbett, 1995; Cruz *et al*., 2008). The sample of dog skulls from Tac Gorsium (Bökönyi, 1984) in turn exceeds the range presented by Vindolanda, especially in containing numerous large dogs, while the Rothwell Haigh collection (Ayton, 2011) contains limb bones of very small "toy" dogs, which likely came from animals with skulls like that of the small dogs from Thistleton (Baxter, 2010a, b), Heidelberg–Neuenheim (Luttschwager, 1965), or Yasmina (MacKinnon & Belanger, 2002). These were lap-dogs, probably unable to survive without specialized human care (MacKinnon & Belanger, 2002). Dogs smaller than 35 cm shoulder height were certainly present at Vindolanda, but the majority had the stout-limbed morphology characteristic of dwarfs rather than the fine, straight limbs of miniatures.

Functional Implications of Morphological Differences

Small dogs, as well as a wide range of dog morphotypes, first appear in Britain in the late Iron Age (Harcourt, 1974; Cark, 1995). This is important, because it implies that the husbandry techniques required for the production and maintenance of phenotypic distinctiveness were not invented by the Romans, but were already widely known. Clark (1995) observes that phenotypic change in domestic dog populations is primarily due to changes in peoples' attitudes and preferences; Ellis *et al*. (2009) agree and observe that "it is fair to expect that [selective breeding] has not followed the path that natural selection would have prescribed". Driven by breeder selection, dog skull shape can be quickly altered; Drake & Klingenberg (2008) demonstrate marked change in a sample of skulls of St. Bernards that occurred over a time span of only 120 years. Such changes usually have functional significance; thus, phenotypic differences in the Vindolanda population of dogs compared to other canids are not likely to be due to random "drift" but rather to directional selection.

Stepwise PCA–MTA assists in identifying trends in phenotypic change, and the significance of such studies becomes greater when PCA identifies parameters that not only have discriminatory power but biomechanical significance. Our study highlights several instances of directional selection:

(1) The index of width between the retro–articular processes (RA) vs. palate width (PW). We term this comparison "neck strength" (Figure 13).

(2) The index of snout width (SW) vs. palate length (PL), which we term "mouth shape" (Figure 14).

(3) The index of jaw condyle width (CW) vs. depth of jaw below the carnassial, which describes the robustness of the jaw and is an indicator of grip strength (Figure 12).

(4) Increase of relative stoutness in all limb bones compared to wild canids, Australian dingoes, and Iron Age British dogs (Figures 16–20).

(5) Increase in the range of shoulder (or "withers") height compared to wild canids, Australian dingoes, and Iron Age British dogs (Figures 6–8, 16–20).

The width between the retro–articular processes on the occiput is a measure of the strength of the attachment of the head to the neck and of the overall strength of the neck (Radinsky, 1981; Ellis *et al.*, 2009). In our MTA analysis (Figure 13), the small sample of Late Pleistocene wolves stands apart. They have long, wide palates –big "maws" (Figure 14)– but necks that are noticeably weaker than modern wolves or many Vindolanda dogs, which may imply that they were primarily scavengers (carcasses don't wriggle). At the opposite extreme, red foxes are the most likely of the groups studied to have neck attachments wider than their palates, not necessarily because their necks are strong but because their skulls are very narrow. Domestic dogs with RA greater than 100% of PW are of two types: either they have been bred to be narrow-headed (English Collie, Greyhound, Borzoi, Afghan Hound), or they have been bred to have strong necks (German Shepherd/Alsatian, Deerhound, Wolfhound). Narrow-headed domestic breeds can be thought of functionally as fox analogs, but exceptionally broad-necked domestic breeds are a novelty (see Radinsky, 1981). There are many domestic breeds (Shar-Pei, Chow-Chow, English Bulldog, Mastiff, Cane Corso) that have historically been associated with dog-fighting; they fall below the 100% line even though they have strong necks because they also have exceptionally wide palates. The Vindolanda dog population overlaps Australian dingoes and represents development from an ancestral dingo-like morphology, with a definite trend toward proportionally wide palates.

There is more overlap in mouth shape (Figure 14), with some Vindolanda dogs having rather fox-like mouths. The Vindolanda population and the Australian dingo overlap almost completely, so that in this character also the Vindolanda population appears to be a development out of a dingo-like ancestral morphology. Both Late Pleistocene and modern wolves have relatively long heads and plot separately from dogs, but the Natural Trap wolves have less pointed snouts.

The width of the jaw condyle has not often been reported for dogs of the Roman era, but this parameter should be measured along with depth below the carnassial because both have obvious biomechanical significance: robustness in either parameter relates directly to grip strength (Radinsky, 1981). The wider the jaw condyle, the stronger and more stable is the attachment of the jaw to the skull, and the more difficult for large or wrig-

gling prey to dislocate the articulation. At the same time, depth of jaw below the carnassial is a direct measure of the strength of the ramus, analogous to MSD for limb bones. MTA (Figure 12) separates wolves and foxes from dingoes and the Vindolanda dog population, which broadly overlap. Both of the latter trend toward broader condyles on jaws of only moderate stoutness. Overlap between dingoes and the Vindolanda dogs probably represents the primitive condition, but some directional selection is evident in the thinner-jawed Roman-era dogs.

The shoulder height of the dog, as well as the stoutness of its limb bones, strongly affects its locomotor capabilities and its potential utility as a courser, terrier, guard dog, war dog, or fighting dog. While the limb bones of most Vindolanda dogs are no stouter than those of Australian dingoes, 34% of Vindolanda forelimb elements and 43% of hindlimb elements are very stout indeed –stouter than dingoes or even the stoutest-limbed Pleistocene wolf. That this is a trend driven by directional selection, and not merely a characteristic of dogs bred on a dwarfing gene, is suggested by the fact that most humeri, femurs, and tibias of British dogs of the Iron Age are also stouter than those of either wolves or dingoes. Romano–British dogs from sites other than Vindolanda, as well as from sites in Continental Europe and North Africa, show the same trend.

The trend in withers height among Roman-era dogs is toward smallness; only the biggest dogs from Tac Gorsium equal the height of Pleistocene or modern wolves, while the great majority are smaller. 37% of Vindolanda dogs as predicted by forelimb elements, and 57% of hindlimb elements, come from animals that stood less than 40 cm high. Again, directional selection is suggested by the fact that British Iron Age dogs fall into the dingo size range, while many Roman-era dogs from Vindolanda and other sites are either smaller or larger than dingoes.

The Beginning of Dog Breed Differentiation

Dogs from the European Mesolithic and Neolithic appear to have originated from dingo-like ancestors (Morey, 2010; Sacks *et al.*, 2013). Dog morphotypes distinctively different from dingoes in height, limb stoutness, and skull shape become common in the Iron Age. Small dogs appear in the

late Iron Age and become common in the Roman period. Several of these ancient morphotypes are similar to, but not exactly like, modern dog breeds. In some cases, reasons for differences between ancient and modern dog breeds can be historically documented; for example, the Irish Wolfhound (Phillips *et al*., 2009), the Pug and the Dachshund (Dennis-Bryan & Clutton-Brock, 1988), and the St. Bernard (Drake & Klingenberg, 2008).

The advent of long-distance semen shipping since the 1970s has accelerated phenotypic change by permitting a limited number of popular sires to produce more than 1000 litters in their lifetime. The highly unequal contributions of a few males are not only the reason for unequal genetic contribution of the sexes in modern dogs (Sundqvist *et al*., 2006), but are the functional equivalent of a genetic bottleneck. Consumer preference for phenotypic extremes of height, shortening of the muzzle, and stance or way of going fuel debate in many modern breeds (Sampson & Binns, 2006). Narrowly-defined dog breed standards (Crowley & Adelman, 1998) and the high commercial value of purebred dogs that strictly fit the definition (Cunliffe, 1999) create strong directional selective pressure (Sundqvist *et al*., 2006). Phenotypic extremes achieved through inbreeding add to genetic load (Calboli *et al*., 2008); many veterinarians and geneticists today define dog breeds not by appearance or behavior but by the suite of genetic disorders to which they are prone (Lindblad-Toh *et al*., 2005; Cruz *et al*., 2008).

Modern breeds of dog differ widely in conformation, size, pelage, color, behavior, physiology, and susceptibility to disease (Coppinger & Coppinger, 2002; Freedman *et al*., 2013). Such is the range in domestic dog skull shape that it not only exceeds that of other domesticated species, but of the entire order Carnivora (Drake & Klingenberg, 2010). We demonstrate herein that neither the Vindolanda dogs, nor any other known population of Roman-era dogs, comes close to matching the huge morphological range of modern domestic dogs.

Distinctive forms of domestic dog are well attested by the Neolithic in the Middle East and by the Paleo-Indian period in the Americas (Turnbull & Reed, 1974; Lawrence & Reed, 1983; Olsen, 1985; Crockford & Pye, 1997; Schwartz, 2000; Barsh *et al.,* 2006). Because the gene complex for chondrodysplasia is inherited as an autosomal dominant, short, bandy-legged dogs may spontaneously appear in a population (Parker *et al*., 2009), but once they do appear they can be –and have often been– maintained by isolation, as for example in both Aztec Mexico (Valadez Azúa, 2000) and by the ancient Egyptians (Churcher, 1963; Brewer *et al*., 2001). By the late Iron Age, not only dwarf but miniature or "toy" dogs were being deliberately bred in Europe (Clark, 1995; Boyko *et al*., 2010); such dogs were also then bred on, along with bigger sorts of dog, throughout the Roman Empire. An abundance of Roman writing and artwork attests to this and corroborates zooarchaeological studies of dog bones of diverse shapes and sizes found on many Roman-era sites in Great Britain and on the European continent (Part II, Dogs of Roman Vindolanda; Bennett & Timm, 2016).

Numerous genetic studies of dog breeds using autosomal markers demonstrate that the physical traits that distinguish dog breeds are inherited (Koskinen, 2003; DeNise *et al*., 2004; Parker *et al*., 2009; Vaysse *et al*., 2011). Such studies led Parker *et al*. (2009) to conclude that most dog breeds have a very recent origin; this is supported by research utilizing mtDNA which also indicates that breeds have not been isolated for a very long time (Sundqvist *et al*., 2006; Quignon, 2007). Parker *et al*. (2009) suggested that modern breeds may have developed from "less codified phenotypic varieties after the introduction of the breed concept and the creation of breed clubs in Europe in the 1800s."

These results contrast with the widespread view that many dog breeds have ancient origins (Crowley & Adelman, 1998). Naturalistic artwork going back as much as 4,000 years represents dogs with conformation, pelage, color, and behavior characteristics strikingly similar to that of some modern dog breeds (Toynbee, 1973; Clutton-Brock, 2000). Sundqvist *et al*. (2006) and Parker *et al*. (2009) posit the existence of distinctive phenotypes bred in widely-separated communities, and Larson *et al*. (2012) suggest that the failure of DNA studies to clearly differentiate most modern breeds of dog is due to repeated human-mediated mixing of lineages that had previously been maintained in isolation.

Harcourt (1974) demonstrated that Romano–British dogs exceed the range of variability of dogs of the British Neolithic, yet our analysis demonstrates almost no overlap in limb bone morphology between the latter and Australian dingoes (Figures 16–20). This suggests that cultural preferences, expressed through a degree of directional selection in Europe, were already at work during the Neolithic to make domestic dogs look and function differently from Australasian dingoes (and certainly dif-

ferently than wolves). We demonstrate directional selection affecting the Vindolanda dog population in neck strength, mouth shape, jaw grip strength, and limb stoutness.

The Vindolanda collection of domestic dog remains is important not only because of its broad range of size and phenotype, but because it is approximately 1950–1600 years old, and thus lies near the beginning of dog breed diversification in Europe. Rather than representing the intermingling of formerly-separate dog bloodlines, the Vindolanda collection samples the initial diversification of modern domestic dog breeds, and thus has the potential to assist in identifying the point of origin in time and space of several modern dog lineages.

ACKNOWLEDGEMENTS

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